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FEATURE ARTICLE

Reconstructing trophic position over the past century for five Puget Sound fish species

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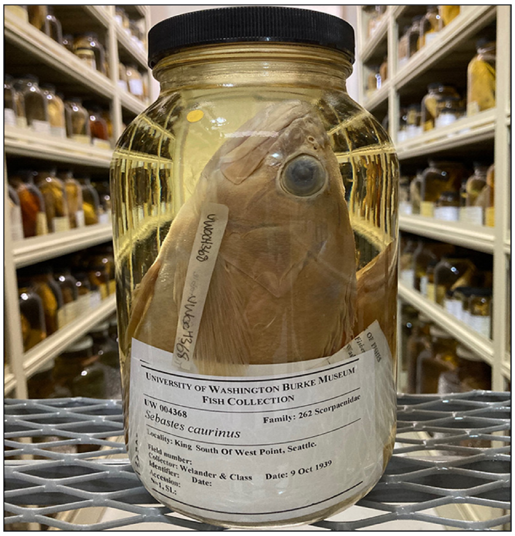
ABSTRACT: The comparison of historical and modern food web dynamics allows ecologists to test whether the trophic connectivity we observe today is 'normal' in its historical context. Fish densities and abundances have changed across time, making it likely that fish trophic interactions and their trophic positions have also changed. Historical trophic data of marine fishes can now be extracted from the tissues of fluid-preserved specimens held in natural history collections via compound-specific stable isotope analysis of amino acids (CSIA-AA) of nitrogen. We conducted CSIA-AA to quantify trophic position change over the past century in 5 ecologically important fishes of Puget Sound, Washington, USA: Pacific hake *Merluccius productus*, walleye pollock *Gadus chalcogrammus*, copper rockfish *Sebastes caurinus*, English sole *Parophrys vetulus*, and Pacific herring *Clupea pallasii*, and examined the canonical trophic (glutamic acid) and source (phenylalanine) amino acids. For all fishes except copper rockfish, trophic position, glutamic acid, and phenylalanine values remained similar across time. For copper rockfish, glutamic acid but not phenylalanine values increased over time, indicating an increase in this species' trophic position. The observed increase in copper rockfish trophic position may be a function of diet switching and declining prey quality rather than a consequence of rockfish consuming higher trophic level prey. This study leverages more than 100 yr of trophic data of fishes representing various feeding guilds and demonstrates that some fish species may be more trophically resilient to major environmental change than expected. Efforts should be made to identify and conserve the trophic interactions of species experiencing change.



Fluid-preserved copper rockfish *Sebastes caurinus* of the University of Washington Burke Museum Fish Collection.
Photo by: K. P. Maslenikov

KEY WORDS: Trophic ecology · Natural history collections · Compound-specific stable isotope analysis · Glutamic acid · Nitrogen · Phenylalanine

1. INTRODUCTION

Quantifying the trophic connectivity or food web linkages of fishes can shed light on food web stability (McCormack et al. 2019), the nutritional quality of fish stocks for people (Thilsted et al. 2016), and how

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global change affects ecosystems (van der Putten et al. 2004, Phillips et al. 2020). By studying the trophic change of freshwater organisms in response to introduced, exotic, and invasive species, restoration efforts have vastly improved in their efficacy (e.g. Vander Zanden et al. 2003). Relative to freshwater systems, data to indicate how marine food web linkages have shifted through time and in response to mounting anthropogenic pressures for most ecosystems are sparse (e.g. Hu et al. 2022).

Thus far, change in historical marine fish diet has been observed mainly by examining the gut contents of fishes (e.g. Hanson & Chouinard 2002, Townhill et al. 2021) and compiling and comparing various historical data sets to assess change. For example, Pinnegar et al. (2015) amassed data from 2 databases and ascertained stomach data of 255 727 North Atlantic pelagic fish from 1837–2012 to elucidate predatory–prey interactions across time. Whereas some studies are planned to address historical trophic change, other studies have emerged when ‘forgotten’ data were found. For example, insights into forage fish diet of the late 1960s from the Strait of Georgia were described nearly 60 yr later after archival gut contents data were found during the disbandment of a research council (Osgood et al. 2016). When these historical data were compared with contemporary data, researchers found that the frequency of energy-dense prey items consumed by Pacific salmon had declined (Duffy et al. 2010, Beamish et al. 2012). This type of finding could support the management of Pacific salmon, a group of fishes that is declining from fishing pressure and climate change stressors (e.g. Walters et al. 2019, Welch et al. 2021, Wilson et al. 2022). Accordingly, accruing historical ecological data provide valuable information on past ecosystem dynamics and sustainability.

With the advent of stable isotope ecology, marine biologists have been able to describe trophic interactions more precisely since the late 1970s (DeNiro & Epstein 1981, Minagawa & Wada 1984, Peterson & Fry 1987). Bulk stable isotope analysis (SIA) of carbon and nitrogen provides information on the diet and trophic relationships of fishes by using fish tissue and environmental samples (e.g. Jenkins et al. 2018). Using SIA of fish bone collagen, Ólafsdóttir et al. (2021) demonstrated that the trophic position of Atlantic cod has decreased during the past ~1200 yr. The authors reduced environmental uncertainty by limiting the geographical range of the samples examined, and admirably, did not attempt to describe specific dietary changes given the limitation of extracting historic data. As in the case of Ólafsdóttir et al. (2021) and other historical studies, providing environmental context via representative primary producer samples is often not possible, as such samples were never collected in conjunction with the fish. A newer isotope method, compound-specific stable isotope analysis of amino acids (CSIA-AA), reduces the necessity to have representative primary producer samples (e.g. McMahon & McCarthy 2016; see Section 2.3 for more detail) and therefore can greatly improve the certainty of a study.

The trophic position of some freshwater fishes has recently been ascertained with CSIA-AA (e.g. Blanke et al. 2017, Bowes et al. 2020), and applying this method to marine fishes would allow us to explore historical trophic change that is intertwined with marine environmental change. Marine trophic dynamics could change in response to anthropogenic change in either the physical/chemical or biological properties of an ecosystem. Whereas trophic change due to fluctuating numbers of predators and prey is readily apparent because the organisms are physically present or absent, it can be more cryptic when it is influenced by bottom-up processes (e.g. Eger & Baum 2020). Activities such as logging and farming increase surface runoff of nutrients into marine systems, which can subsequently increase primary production (e.g. Silva et al. 2022). Changing primary production levels can reverberate through higher trophic levels (TLs) by changing the abundance of and competition for primary consumers and, in turn, influencing predators’ trophic positions (van der Lee et al. 2021).

One of the largest, most commercially and ecologically important marine systems in the USA is the Puget Sound estuary in Washington state (Puget Sound National Estuary Program 2020). Since the 1850s Fraser Goldrush (Fraga 2020), Puget Sound coastal watersheds have been altered by logging, with lowlands experiencing extensive urbanization and industrialization over the past decades (Brandenberger et al. 2008, 2011, Simenstad et al. 2011, Kennedy et al. 2015). Generally, land-use change of coastal watersheds has increased the nutrient levels of estuarine environments (e.g. Kemp et al. 2005, Rabalais et al. 2007). In Puget Sound, deforestation and subsequent agricultural practices have resulted in periods (after 1970) of hypoxia, but because parts of Puget Sound are extremely deep or have ample mixing with coastal seawater, cultural eutrophication has not occurred (Brandenberger et al. 2011, Ahmed et al. 2019). Natural nutrient enrichment does occur in Puget Sound, but its influence on primary production is localized (~3 km^2) and short-lived (2 mo). Therefore, capturing potential bottom-up changes in food web dynamics will be particularly challenging.

Since the Fraser Goldrush, Puget Sound's fishes have been targeted for artisanal and commercial harvest and have been differentially exploited across time (Greene et al. 2015, Essington et al. 2021). Bottom trawling for groundfish was regularly used during the 20th century until the 1980s, when stocks were so depleted that management closed the groundfish fishery (reviewed in Essington et al. 2021). The diets of piscivores could have shifted towards lower-TL prey during this time due to a fishing-driven dearth of prey resources, or they might have remained stable because of a decline in competition for forage fish. During this same time period, changing regulations regarding the harvest and protection of marine mammal top predators occurred (reviewed in Roman et al. 2013). Because cetaceans and pinnipeds prey on forage fish, their presence, absence, and then return could also influence competition for forage fish prey among piscivorous fishes. With declining forage fish availability and oscillating competition for forage fish prey, there is potential that piscivores may have shifted from consuming energy-dense forage fish to less lipid-rich fishes and invertebrates, such that it is probable that their trophic position may be generally declining across time.

Our objective was to examine 5 commercially important fish species of Puget Sound of varying trophic positions and natural histories that have been affected at different intensities by anthropogenic activities. Overall, we hypothesized that we would observe trophic change over the past century, and using species-specific historical background information, we outline our predictions by functional feeding group. Each estimated current TL shown below is from Froese & Pauley (2022).

2. MATERIALS AND METHODS

2.1. Predictions and natural history of Puget Sound fishes

2.1.1. Pelagic, omnivorous forage fish: Pacific herring *Clupea pallasii* (TL = 3.2)

We predicted that the trophic position of Puget Sound Pacific herring would not change across time. In Puget Sound, Pacific herring are an important pelagic forage fish, and they feed on zooplankton, which are assumed to be abundant (Keister et al. 2018). Moreover, Pacific herring spawning biomass has declined, and natural mortality has increased for fish of all size classes from 1973–2008, contributing to a historical decline (e.g. Stick et al. 2014, Siple et al. 2016, 2018). Because general competition for zooplankton resources should be minimal and invertivore prey should be easily accessible, we expected little dietary and trophic shift in Pacific herring.

2.1.2. Benthic omnivore: English sole *Parophrys vetulus* (TL = 3.4)

We predicted that the trophic position of Puget Sound English sole would not change across time. English sole is a common species of flatfish (Family Pleuronectidae) that occurs in nearshore waters off the west coast of North America. English sole are tightly associated with bottom substrate, and they feed on polychaetes and bivalves year-round (Reum & Essington 2008). In Puget Sound, this species was heavily exploited until the 1950s, yet remained abundant through this period of exploitation and into the present day, even while other benthic fish species declined (Stewart 2005, Essington et al. 2021). Therefore, it was assumed that the invertebrate prey of English sole remained abundant through this period (e.g. Howe & Simenstad 2015), and we validated this in a gut contents study (see Supplement 1; both supplements available at www.int-res.com/articles/suppl/m706p001_supp.pdf). Given that polychaete and bivalve prey were always abundant, and periods of eutrophication in Puget Sound are localized and temporary (Ahmed et al. 2019), invertebrate abundance should remain consistently ample. At present, there are fewer competitors for this prey, and therefore we expected no historical changes in English sole trophic position.

2.1.3. Pelagic piscivores: walleye pollock *Gadus chalcogrammus* (TL = 3.6) and Pacific hake *Merluccius productus* (TL = 4.4)

We predicted that the trophic position of 2 high-TL species, walleye pollock and Pacific hake, would decline across time. Both fishes are pelagic, and their diet consists mainly of small pelagic invertebrates like euphausiids and shrimp as well as fishes like Pacific herring *C. pallasi* and surf smelt *Hypomesus pretiosus* (e.g. Reum & Essington 2008, Bizzarro et al. 2017). Because Pacific herring populations have been declining (see Section 2.1.1), we expected the trophic positions of Pacific hake and walleye pollock to decrease across time as their diets shifted from fish to invertebrates. The frequency of occurrence for Pacific hake was greater in the latter half of the 20th century than in the first half, and walleye pollock frequencies have remained stable across the 20th century (Essington et al. 2021), competition among these species for forage fish prey may be significant. Because walleye pollock populations appear to be more resilient to change, we expected both species to decrease in trophic position but anticipated that the change would be smaller for walleye pollock than for Pacific hake.

2.1.4. Benthic demersal piscivore: copper rockfish *Sebastes caurinus* (TL = 4.1)

We predicted that the trophic position of copper rockfish would decrease across time. Copper rockfish are benthic–demersal fish that feed predominantly on other fishes (e.g. Pacific herring *C. pallasi*) and invertebrates (e.g. clams and shrimp) throughout their ontogeny; even as juveniles, nearly half their diet (by species) is fish (Bizzarro et al. 2017). In Puget Sound, the conservation status of copper rockfish varies by basin and ranges from precautionary to vulnerable (Palsson et al. 2009). These status classifications are related to a period of intensive harvest from the 1970s to 1990s (Williams et al. 2010) and large declines in biomass (of 40%) in some Puget Sound basins from the late 1970s to 2005 (Palsson et al. 2009). Though there has been management to limit copper rockfish exploitation for the past 3 decades, the population has not yet demonstrated signs of recovery, which may in part be related to their long lifespan and late reproductive maturity (Palsson et al. 2009). With forage fish availability declining and copper rockfish populations protected, we would expect competition among con- and heterospecifics to be increasing. This might drive copper rockfish to eat more lower-TL prey, particularly as they are benthic fish, closely linked to the substrate. Therefore, we expected that copper rockfish trophic position would decrease across time.

2.2. Prediction testing

To test our predictions, we used CSIA-AA of nitrogen analysis on fluid-preserved fishes collected from 1906–2018 and held in the University of Washington Fish Collection (UWFC) at the Burke Museum of Natural History and Culture. We specifically examined the canonical trophic and source amino acids of nitrogen — glutamic acid and phenylalanine — as these amino acids provide information on the foraging habits of an organism and its environment, respectively (Chikaraishi et al. 2007, 2009, McMahon & McCarthy 2016) and have been validated for use on fluid-preserved fishes (Welicky et al. 2021). For each fish species described above, we asked (1) Has trophic position changed over time? (2) Was trophic change driven by changes in glutamic acid value (prey resources) and/or phenylalanine (primary production and environmental dynamics)? and (3) Were there discrete time points when rapid trophic change occurred? By addressing these questions, this study provides insight into the past and present trophic status of Puget Sound fishes, which has not been ascertained via other approaches.

2.3. Selection of amino acids of nitrogen

We selected glutamic acid and phenylalanine amino acids of nitrogen for analysis based on their capacity to quantify trophic position. Glutamic acid is considered a canonical trophic amino acid that reveals information about an organism's diet and metabolic processes because it undergoes extensive transamination from the cleaving of carbon–nitrogen bonds during the metabolism of nitrogenous materials (Chikaraishi et al. 2014). Therefore, glutamic acid values change in response to changing diet and nutrient assimilation (O'Connell 2017). In contrast, phenylalanine undergoes negligible transamination because it contains less nitrogenous material to be cleaved during metabolism (e.g. McMahon & McCarthy 2016). Therefore, phenylalanine values in consumers change minimally in response to changing diet and physiological processes (e.g. McMahon & McCarthy 2016). For this reason, phenylalanine is considered a canonical source amino acid that varies in response to both inorganic nitrogen sources as utilized by primary producers and the producer community composition (e.g. Chikaraishi et al. 2009, 2010, O'Connell 2017). As such, the stable isotope signature of phenylalanine should change in response to isotopically distinct nitrogen sources entering the food web. For example, increases in nitrogen from denitrification (Sigman et al. 2005), wastewater treatment facilities (Heaton 1986), and agricultural runoff from manure fertilization (Bateman & Kelly 2007) would result in an enrichment of ^{15}N relative to ^{14}N in the available nitrogen pool. If utilized by primary producers, the relative ^{15}N enrichment would be transferred to consumers and recorded in their phenylalanine stable isotope signature (Feddern et al. 2021, Ramirez et al. 2021).

Glutamic acid and phenylalanine values from CSIA-AA are robust to the preservation process used by natural history collections (Chua et al. 2020, Durante et al. 2020). A preserved organism's relative trophic position can be precisely estimated using glutamic acid and phenylalanine values (Welicky et al. 2021), and CSIA-AA has been readily applied to fluid-preserved freshwater fishes (Bowes et al. 2020).

2.4. Specimen selection and tissue extraction

Our goal was to sample 50 specimens for each of our 5 target fish species of similar length, with even distribution among the available decades from the UWFC at the Burke Museum of Natural History and Culture (Fig. 1A–E). The original preservation method for UWFC fishes was to place fresh or previously frozen fish specimens in 10% formalin for 24 h to 2 wk depending on fish size, then two 24 h water baths, followed by 70% ethanol for eternity. Welicky et al. (2021) validated that significant changes occur within the preservation process and stop after 24 h in ethanol. For some fish species, there were specimen-deficient decades; for those species, we increased the number of specimens used for other decades as evenly as possible (Fig. 1). We note that small sample sizes (n < 7) are robust for detecting historical change in trophic position using CSIA-AA (Thorp & Bowes 2017, McMahon & Newsome 2019). Whereas in bulk SIA, environmental variation must be accounted for by increasing sample size and sampling primary producer materials, in CSIA-AA, diet and environmental information can be obtained by examining different amino acids of the same individual sample (e.g. McMahon & McCarthy 2016). To account for the potential that there will be increased variance in CSIA-AA values with increasing TL, we built sampling

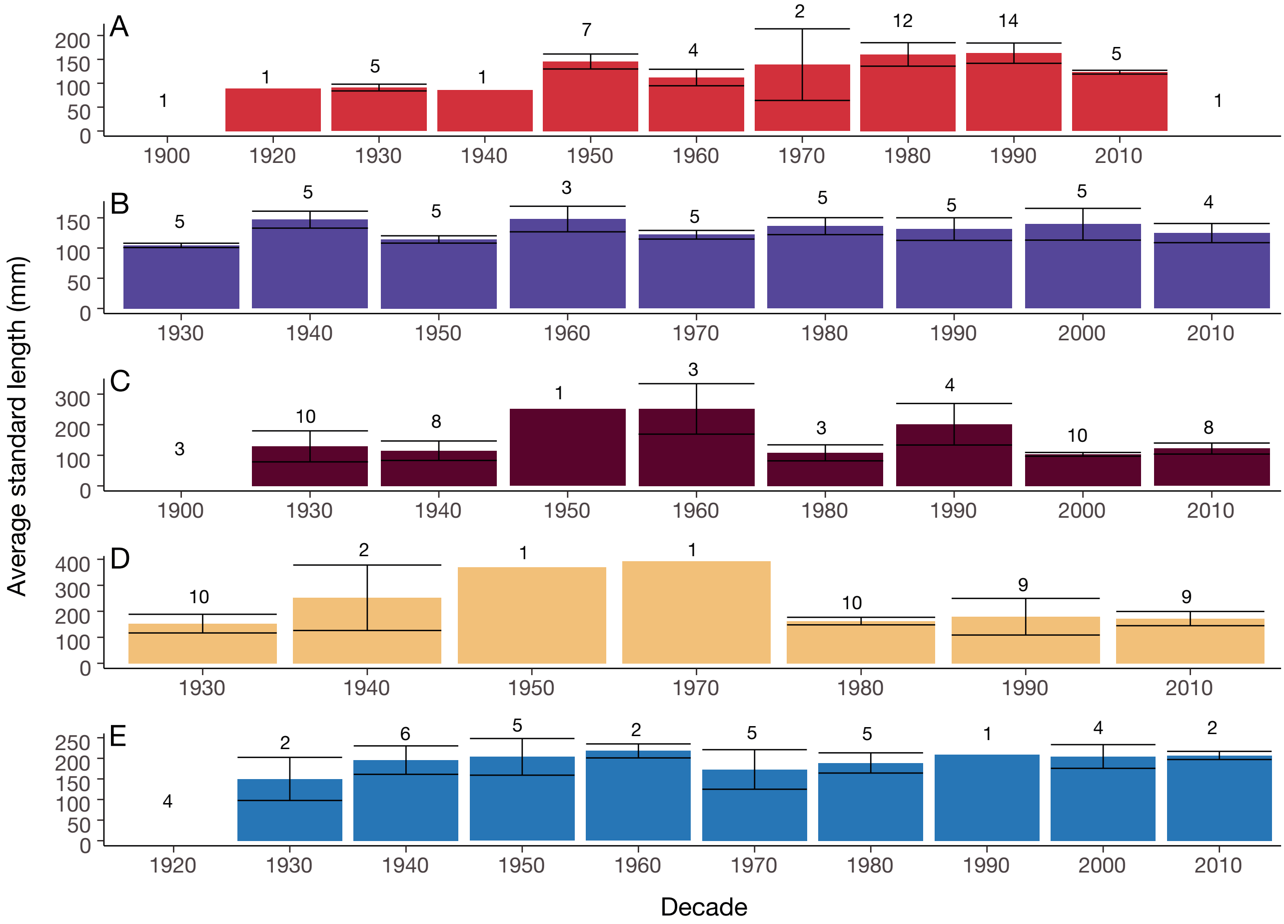

Fig. 1. Average (±1 SD) standard length and sample size (numbers above bars) for each fish species by decade. (A) Pacific herring; (B) English sole; (C) walleye pollock; (D) Pacific hake; (E) copper rockfish

power (at least 5-fold greater than commonly used) across time. For information regarding fish collection sites (used as a random effect in models; see Sections 2.7.1 and 2.7.2 for details), see Supplement 2. For each fish, we extracted muscle tissue while adhering to protocols from the UWFC, which aim to minimize damage to specimens in order to maximize the long-term utility of specimens for a variety of research purposes. For UWFC accession information of each specimen see Table S2 in Supplement 1. Tissues were stored in amber vials at −20°C until analysis.

2.5. CSIA-AA

We extracted and derivatized amino acids from each fish tissue sample using a modified acetyl chloride-pivaloyl chloride derivatization process. Stepwise derivatization, and drift correction procedures are fully detailed in Welicky et al. (2021); abridged details are in Supplement 2.

2.6. Trophic position calculation

We implemented Chikaraishi et al.'s (2009, 2014) formula (Eq. 1) and note that values reported should not be considered absolute. Preservation can enrich and deplete amino acid values, but preservation does act similarly within a species when individuals have been preserved with similar protocols (Welicky et al. 2021). Chikaraishi et al.'s (2009, 2014) formula takes the form below and has been modified with the beta and trophic discrimination factors reported in Bradley et al. (2015):

$$\text{Trophic position} = \{[(\delta^{15}\text{N}_{\text{GLU}} - \delta^{15}\text{N}_{\text{PHE}}) - (3.6‰)] / 5.7‰\} + 1 \qquad (1)$$

where 3.6‰ represents β (beta), the difference between $\delta^{15}N_{GLU} - \delta^{15}N_{PHE}$ in nonvascular primary producers. The value 5.7‰ is the trophic discrimination factor which represents the ^{15}N enrichment of glutamic acid relative to phenylalanine at each trophic step (Bradley et al. 2015). We selected the β value of non-vascular autotrophs (phytoplankton), the dominant primary producers in most marine systems, and this value is consistent across a diversity of studies (Ramirez et al. 2021). It is important to note that the Puget Sound food web does include vascular plants (i.e. eelgrass), and if vascular plant-derived nitrogen contributes to the food web, it would result in an underestimation of trophic position. Because our study can only assess relative trophic values due to its focus on fluid-preserved specimens, we caution that the trophic position estimates presented herein might be biased downward, though they are fully comparable within species. Importantly, trophic position estimates presented here are not comparable to those of differently preserved fish (Welicky et al. 2021).

2.7. Statistical analysis

All statistical analyses were completed in R version 1.2.1335 (R Core Team 2019).

2.7.1. Change of trophic position over time

To determine how the trophic position of each species has changed over the past century, we used generalized linear mixed models in which the response variable was trophic position. Trophic position was normally distributed, and therefore the model was fitted with a Gaussian distribution. We verified that trophic position, glutamic acid, and phenylalanine values were not temporally or spatially autocorrelated (see Supplement 2 for details). We also verified that fish size and year were not correlated (see Supplement 2 for details). For Pacific herring, size and year were significantly correlated. Therefore, after running the models below, we verified that the variance inflation factor (VIF) for each herring model was below the standard VIF threshold of 5 (Dormann et al. 2013; for further details see Supplement 1). In our models, we included fish standard length as a fixed effect because fish size, particularly a fish's gape size, can influence diet and prey selection (e.g. Luiz et al. 2019, Ríos et al. 2019). We also included the fixed effect of year (the year in which the sample was collected). To account for any potential variation among sites, we included a random effect of site in our models. We implemented the model below using the function 'glmmTMB()' in the R package 'glmmTMB' (Brooks et al. 2017):

$$\text{Trophic position}_{ijk} \sim \text{Year collected}_j + \text{fish standard length}_{ijk} + (1 \mid \text{site}_k) \qquad (2)$$

where the response variable *ijk* represents the trophic position value of the i^{th} fish collected from the k^{th} site in the j^{th} year. Year collected and fish standard length were centered and scaled. We report all values as average ± SD.

2.7.2. Determination of which amino acids drove trophic change over time

Because values for glutamic acid and phenylalanine are used to calculate trophic position, an observed change in either glutamic acid (e.g. due to change in diet composition) or phenylalanine (e.g. due to change in the $^{15}N/^{14}N$ composition of prey and/or primary producers) might drive any given change in trophic position. To narrow in on drivers of changing trophic position, we tested for change in glutamic acid and phenylalanine for each fish species. We modified Eq. (2) so that the response variable was glutamic acid or phenylalanine $\delta^{15}N$ ‰. Glutamic acid and phenylalanine each had a normal distribution, and thus these models were fitted with Gaussian distributions. Because phenylalanine values may fluctuate across time in response to environmental change, we recognized that linear models might not fit the data. Therefore, for any fish with a significant change in trophic position but no significant change in phenylalanine (‰), we conducted a generalized additive model for the response variable phenylalanine (Eq. 3). The model was implemented using the 'gam()' function in the R package 'mgcv' (Wood 2019). We used a global spline smoothing function 's' with up to 4 inflection points (or knots) for the variable year collected. Fish standard length was a fixed effect, and site was included as a random effect. Restricted maximum likelihood estimation was used for estimation of the smoothing parameter:

$$\begin{gathered}\text{Phenylalanine}_{ikj} \sim \text{s}(\text{Year collected}_j) + \\ \text{fish standard length}_{ijk} + \text{s}(1 \mid \text{site}_k)\end{gathered} \tag{3}$$

where the response variable *ijk* represents the phenylalanine value of the i^{th} fish collected from the k^{th} site in the j^{th} year.

2.7.3. Quantification of discrete time points of rapid trophic change

Generalized linear models allowed us to detect whether temporal change occurred, but they did not necessarily identify inflection points, or 'tipping points', in our time series. To assess whether there were any time points at which a significant shift in trophic position took place, we employed a breakpoint analysis for any mixed models in which year was a significant predictor. Using the package 'strucchange' (Zeileis & Hortorn 2002), we conducted an empirical fluctuation process on the model described as Eq. (2) and used the recursive residuals and cumulative sum model options. Justifications for model choices are detailed in Supplement 2.

3. RESULTS

The average glutamic acid $\delta^{15}N$, phenylalanine $\delta^{15}N$, and trophic position values of Pacific herring collected from 1909–2015 were 25.20 ± 1.73‰, 6.49 ± 1.15‰, and 3.65 ± 0.27, respectively. These values did not change significantly over time (Table 1, Fig. 2A, Figs. S2A & S3A in Supplement 2). For example, trophic positions in the 1930s, 1960s, and 2010s were 3.46 ± 0.10, 3.50 ± 0.38, and 3.52 ± 0.16. Finally, size was positively correlated with glutamic acid $\delta^{15}N$ and trophic position but not phenylalanine $\delta^{15}N$ (Table 1).

The average glutamic acid $\delta^{15}N$, phenylalanine $\delta^{15}N$, and trophic position values for English sole during 1930–2018 were 22.63 ± 1.66‰, 5.77 ± 1.59‰, and 3.33 ± 0.27, respectively. None of these response variables changed significantly over time (Table 1, Fig. 2B, Figs. S2B & S3B in Supplement 2). The trophic positions of English sole in the 1930s, 1960s, and 2010s were 3.33 ± 0.11, 3.28 ± 0.17, and 3.23 ± 0.32, respectively (Fig. 2B). Size was positively correlated with trophic position (Table 1).

For walleye pollock, data spanned 11 decades (1906–2017), and the average glutamic acid $\delta^{15}N$, phenylalanine $\delta^{15}N$, and trophic position values were 24.63 ± 2.01‰, 5.99 ± 1.28‰, and 3.64 ± 0.37, respectively. The average trophic positions in the 1930s, 1940s, and 2000s were nearly the same (3.56 ± 0.37, 3.49 ± 0.24, and 3.54 ± 0.15, respectively). Hence, none of these parameters changed across time (Table 1, Fig. 2C, Figs. S2C & S3C in Supplement 2). Size was positively correlated with glutamic acid $\delta^{15}N$ and trophic position but not phenylalanine $\delta^{15}N$ (Table 1).

For Pacific hake, from 1932–2016, glutamic acid $\delta^{15}N$, phenylalanine $\delta^{15}N$, and trophic position were on average 22.26 ± 1.71‰, 6.64 ± 2.53‰, and 3.11 ± 0.51, respectively. Neither glutamic acid $\delta^{15}N$ of Pacific hake nor their inferred trophic position changed over time (Table 1, Fig. 2D, Figs. S2D & S3D in Supplement 2). For example, the average trophic position in the 1930s was 3.13 ± 0.45, and in the 1980s, 1990s, and 2010s, it was 3.05 ± 0.38, 3.20 ± 0.46, and 2.89 ± 0.56, respectively. Size was positively correlated with glutamic acid $\delta^{15}N$ and trophic position, but not phenylalanine $\delta^{15}N$ (Table 1).

The average glutamic acid $\delta^{15}N$, phenylalanine $\delta^{15}N$, and trophic position values for copper rockfish from 1928–2012 were 26.12 ± 1.64‰, 5.34 ± 1.19‰,

Table 1. Results of 3 generalized linear mixed effect models for (a) Pacific herring *Clupea pallasii*, (b) English sole *Parophrys vetulus*, (c) walleye pollock *Gadus chalcogrammus*, (d) Pacific hake *Merluccius productus*, and (e) copper rockfish *Sebastes caurinus*. Results are indicated for 2 predictors: year of collection and standard length (SL). The variance and standard deviation are reported for the random effect, site. Predictor variables were scaled and centered before analysis. Significant p-values ($p \leq 0.05$) in **bold**

	Year				SL				Site	
	Est	SE	*z*	p	Est	SE	*z*	p	var	SD
(a) Pacific herring										
Glutamic acid	0.321	0.300	1.070	0.285	1.082	0.248	4.360	**<0.0001**	0.652	0.807
Phenylalanine	0.315	0.207	1.520	0.127	0.115	0.192	0.600	0.551	0.125	0.354
Trophic position	0.009	0.045	0.200	0.842	0.164	0.042	3.910	**<0.0001**	0.014	0.116
(b) English sole										
Glutamic acid	0.004	0.278	0.016	0.988	0.302	0.260	1.164	0.245	0.606	0.778
Phenylalanine	−0.367	0.239	−1.534	0.125	−0.259	0.239	−1.083	0.279	<0.000	<0.000
Trophic position	0.031	0.040	0.768	0.443	.0100	0.036	2.802	0.005	0.014	0.120
(c) Walleye pollock										
Glutamic acid	0.214	0.274	0.781	0.435	1.193	0.256	4.668	**<0.0001**	0.432	0.657
Phenylalanine	0.238	0.240	0.995	0.320	−0.108	0.199	−0.543	0.587	0.523	0.723
Trophic position	0.002	0.052	0.032	0.975	0.227	0.053	4.312	**<0.0001**	0.193	0.139
(d) Pacific hake										
Glutamic acid	0.002	0.23	0.008	0.993	0.844	0.23	3.667	**<0.001**	<0.000	<0.000
Phenylalanine	0.353	0.386	0.914	0.361	−0.026	0.387	−0.068	0.946	<0.000	<0.000
Trophic position	−0.061	0.075	−0.814	0.416	0.152	0.075	2.020	**0.043**	<0.000	<0.000
(e) Copper rockfish										
Glutamic acid	1.248	0.127	9.861	**<0.0001**	0.450	0.131	3.440	**<0.0001**	0.384	0.620
Phenylalanine	0.201	0.242	0.833	0.405	−0.100	0.206	−0.487	0.626	0.587	0.766
Trophic position	0.172	0.048	3.595	**<0.001**	0.104	0.043	2.400	**0.016**	0.002	0.042

and 4.03 ± 0.33, respectively. The trophic position of copper rockfish increased over time, and this was driven by a significant increase in glutamic acid δ^{15}N with no corresponding change in phenylalanine δ^{15}N values in either the generalized linear mixed model (Table 1, Fig. 3A–C) or the generalized additive model (year collected: $F = 0.663$, edf = 1, ref.df = 1, p = 0.427; sites: $F = 0.970$, edf = 11.95, ref.df = 26, p = 0.58; 69% deviance explained). In our linear mixed model, size was a positive, significant predictor of glutamic acid δ^{15}N and trophic position, but not phenylalanine δ^{15}N (Table 1, Fig. 3A–C). Body size and year were not correlated based on our preliminary data analyses (see Supplement 2). The average trophic position value increased from 3.57 ± 0.08 in the 1920s to 4.51 ± 0.5 in the 2010s. The 1930s had the smallest trophic position value (3.55 ± 0.17), and the 2010s had the largest trophic position value. After the 1930s, all trophic position values were above 3.6. Over the course of ~8.5 decades, glutamic acid δ^{15}N increased on average by 4.23‰ (Fig. 3A–C). From the breakpoint analysis, we determined no significant tipping points in glutamic acid δ^{15}N values, such that the increase in glutamic acid δ^{15}N was consistent across time ($S = 0.463$, p = 0.709).

4. DISCUSSION

Over the past century, the trophic positions of Pacific hake, walleye pollock, English sole, and Pacific herring have remained stable, with neither glutamic acid nor phenylalanine changing across time. In contrast, the glutamic acid but not phenylalanine values of copper rockfish increased over time, suggesting an increase in this species' trophic position. This increase over time is not an artefact of body size because we sampled fishes of similar size across decades and verified that year and fish size were not correlated. Rather, we posit that the observed increase in copper rockfish trophic position is a function of changing prey quality due to prey switching from higher- to lower-TL prey (e.g. Murie 1995). The growing difference between glutamic acid δ^{15}N and phenylalanine δ^{15}N suggests that a decline in prey quality may be associated with an amino acid imbalance for copper rockfish, resulting in increased trophic fractionation of ^{15}N relative to ^{14}N (Chikaraishi et al. 2015, McMahon et al. 2015).

Trophic position changes indicated by stable isotope data can be the result of multiple kinds of dietary shifts, including prey switching between

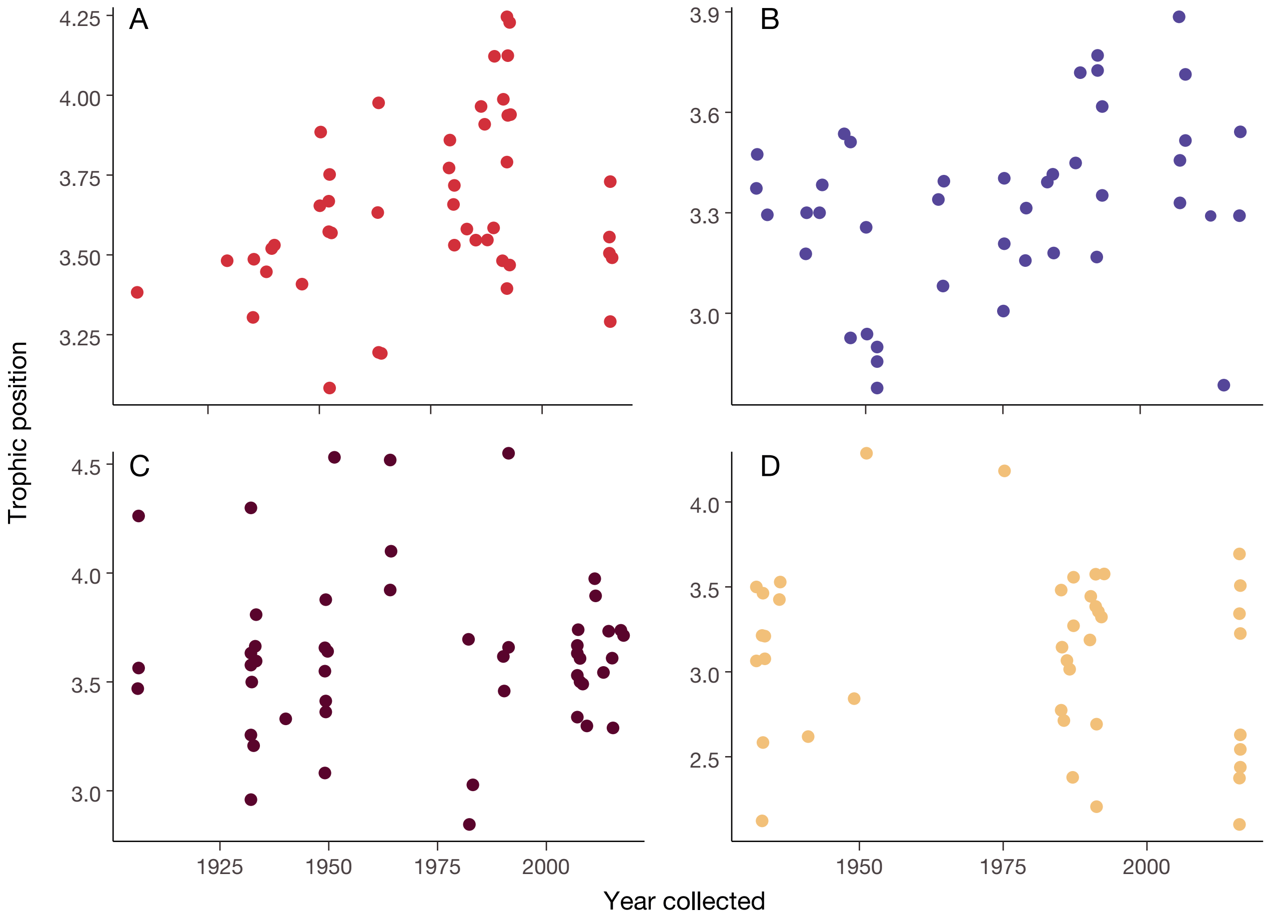

Fig. 2. Fish trophic position values across time and by species. (A) Pacific herring; (B) English sole; (C) walleye pollock; (D) Pacific hake

taxa of different TLs and consuming different sizes of the same prey that feed at different TLs (i.e. prey that experience ontogenetic shifts in diet). Such dietary shifts can alter the amount of energy and/or quality of nutrients obtained from prey. Prey quality can influence the nitrogen stable isotope values of consumers because of an overall protein content imbalance between consumer and prey and/or the imbalance of individual amino acids. Consuming lower-quality prey results in a greater enrichment of ^{15}N relative to ^{14}N in trophic amino acids with each trophic transfer (i.e. trophic enrichment factor; Chikaraishi et al. 2015, McMahon et al. 2015). Consumption of lower-quality prey (greater protein imbalance between consumer and prey) will therefore enrich the stable isotope signature of trophic amino acids, but not source amino acids, which is functionally an increase in the trophic enrichment factor between consumer and prey. If trophic enrichment (i.e. host metabolism and assimilation of energy) is assumed to be constant but is actually increasing due to a decline in prey quality, trophic position will appear to increase.

Prey switching to prey of lower quality or prey with a higher trophic position explains the increase in trophic position and glutamic acid $\delta^{15}N$ values and the stable $\delta^{15}N$ values of phenylalanine through time in copper rockfish. Based on changes in prey availability and stomach content analysis, a decline in prey quality offers the most plausible explanation. Pacific herring is an important prey source for rockfish (Murie 1995, Bizzarro et al. 2017), and their abundance has been declining over the past 4 decades in Puget Sound due to increased adult mortality in fish 3 yr and older (Siple et al. 2018). With a decrease in availability of Pacific herring, copper rockfish's close association with the substrate and 'sit-and-wait' foraging style might have necessitated prey switching to an alternative, benthic prey resource (Matthews 1990a,b). Recent studies examining Puget Sound copper rockfish stomach contents

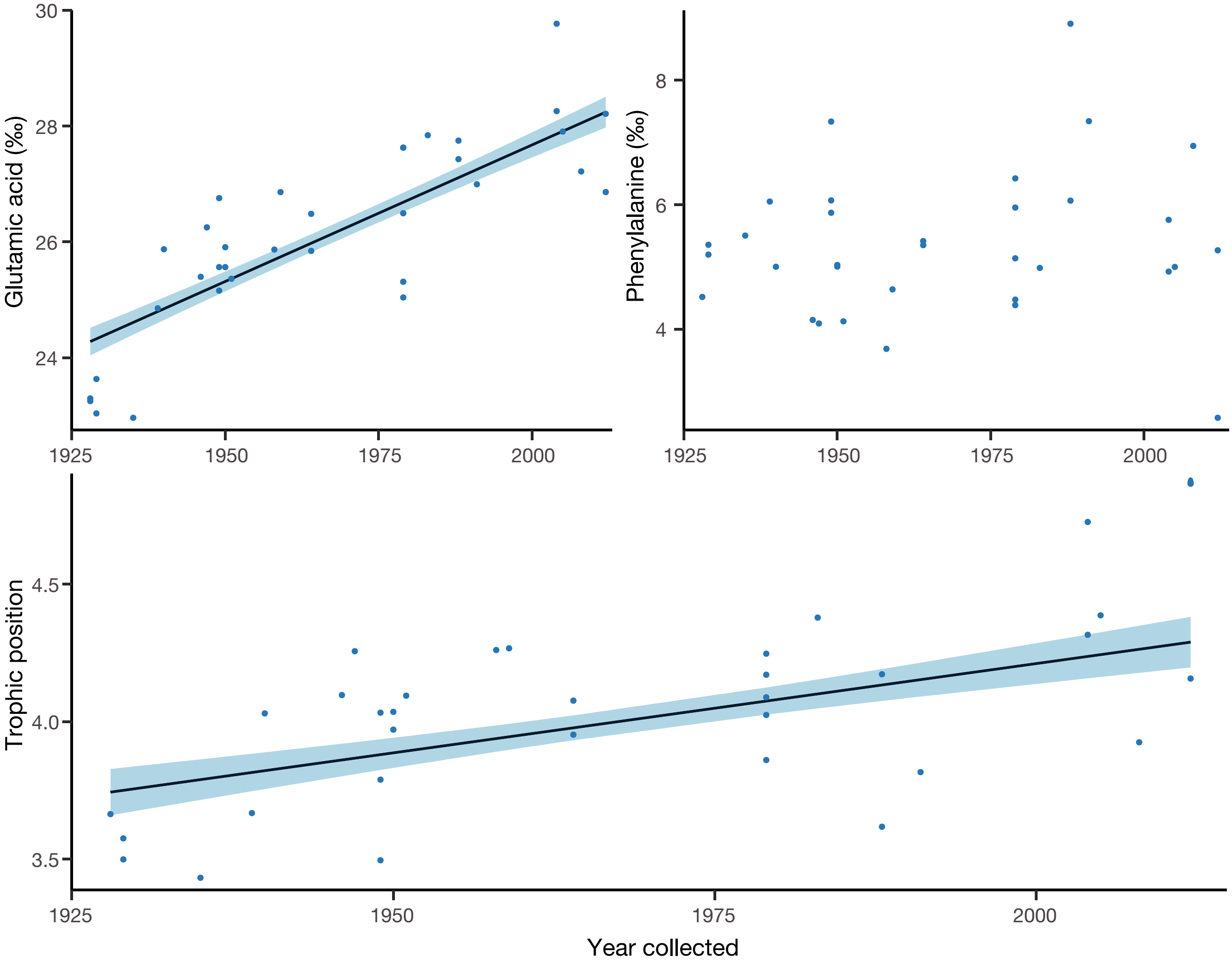

Fig. 3. Fish glutamic acid and phenylalanine values and trophic position for copper rockfish. For significant models, the predicted fit (black line) and 95% confidence band of the generalized linear mixed model (blue shading) are shown. For model predictions, standard length is fixed at the median of the data set

reported that there is greater consumption of crustaceans, particularly caridean shrimp, than teleost fish by copper rockfish compared to previous gut content studies conducted in the mid-1980s (Murie 1995, Turner et al. 2017). Although we might generally expect that the trophic position of crustaceans to be lower than that of herring because it is assumed crustaceans feed lower on the food web (e.g. Hannides et al. 2009, Downs et al. 2014), some crustaceans are omnivorous, scavenger feeders, which could inflate their trophic position (e.g. Pakhomov et al. 1999). Moreover, the trophic position of caridean shrimp might even resemble herring or other teleost fish if they feed on fragments of the same organism (e.g. Möllmann et al. 2004). Despite that shrimp and herring may have similar trophic positions if they are foraging on similar prey, the protein and lipid content of caridean shrimp is vastly different and of lower quality than that of teleost fish for rockfish consumers due to a greater amino acid imbalance in tissues (e.g. Chikaraishi et al. 2015). Accordingly, switching from a diet of herring or other teleost fish to shrimp is potentially driving the increasing glutamic acid values and associated trophic position of copper rockfish through time. Altogether, the stomach content data and prey abundance changes in Puget Sound indicate copper rockfish have experienced a diet shift through time, and a decline in prey quality offers the most likely explanation for the observed stable isotope and trophic position data as opposed to consumption of higher trophic position prey.

If copper rockfish are indeed foraging on lower-quality food, the amino acid imbalance in their diet may create energetic deficits which reduce their fecundity and thus have lasting effects on their population status. Numerous studies have documented that rockfish populations are threatened and that they have not recovered despite stringent groundfish management and trawling bans intended to offer protection (e.g. Palsson et al. 2009). It is to be expected that copper rockfish population recovery would be slow because they reach sexual maturity after 5–6 yr (Hannah 2014). The contemporary reproductive output of copper rockfish off the west coast of Oregon and California is less than it was in the 1980s (O'Farrell & Botsford 2006). A dietary shift of Puget Sound copper rockfish from herring to shrimp might cause nutritional deficits, thereby causing energetic deficits that limit reproductive potential. Although a low-quality diet can negatively influence the fecundity of any fish, this issue might be amplified in copper rockfish because of their extremely slow growth, smaller size relative to other rockfishes, and the production of large viviparous clutches (e.g. Love et al. 2002).

Because Pacific hake and walleye pollock are relatively large piscivores, we initially expected that their trophic positions might decline with time, mirroring the decline in Pacific herring and other forage fishes (Greene et al. 2015, Essington et al. 2021). Our data suggest that the trophic position of Pacific hake and walleye pollock did not change across time. We surmise that, unlike copper rockfish, these fishes are highly mobile and thus able to acquire sufficient prey through movement. Whereas copper rockfish are demersal fish with high site fidelity, Pacific hake and walleye pollock are pelagic, have low site fidelity, and are continuous swimmers (Matthews et al. 1986). The mobility of Pacific hake and walleye pollock enables these fish to travel further to capture more of the same prey type when it becomes less abundant, and increases prey diversity, which may occupy the same trophic position. We can infer higher levels of diet plasticity in Pacific hake than copper rockfish, as the range in trophic positions of Pacific hake was greater than the range of trophic positions that we observed for copper rockfish. Therefore, Pacific hake and walleye pollock might be more successful at tracking and consuming various forage fish regardless of their declining abundance. Accordingly, their trophic position might show greater range but not significantly change across time, as prey switching even within the same TL might be more common and/or changes in prey quality might be less apparent.

For English sole and Pacific herring, we were not surprised by the consistent trophic position values across time, because their invertebrate prey have long been assumed to be consistently abundant, and any prey switching that may have occurred would likely be to a similarly low-TL species. In 2018, a first report examining Puget Sound zooplankton biomass and diversity from 2014–2017 was published; zooplankton biomass and diversity were reported to be highly variable but abundant (Keister et al. 2018). The diet of English sole is composed mainly of bivalves and polychaetes, and Pacific herring feed mainly on zooplankton. These prey are all generally abundant and not targeted by commercial fishers. Though little is known about how competition could influence Pacific herring diet, we do know that English sole diet is distinct from similar fishes. Flatfishes like Pacific sanddab *Citharichthys sordidus*, rex sole *Glyptocephalus zachirus*, and rock sole *Lepidopsetta bilineata* have been reported to have seasonal guild shifts, shifting their diet from small fishes and invertebrates in summer to polychaetes and bivalves in fall and winter, whereas English sole are in the same guild year-round (Reum & Essington 2008). English sole overlap in diet with other demersal fishes such as spotted ratfish *Hydrolagus colliei* (Reum & Essington 2008), although competition among these species might be fairly minimal because ratfishes and flatfishes vary in their gape, teeth, and morphology, which can influence their foraging behavior and capacity to exploit different types of prey (Schafer et al. 2002, Ríos et al. 2019).

Changes in phenylalanine $\delta^{15}N$ can be associated with environmental variability (Feddern et al. 2021), but we did not observe any change in phenylalanine values across time. It could be that phenylalanine values did not change over time, change was not detectable in the consumers we examined, or using linear models limited our capacity to detect nonlinear processes. We evaluated the latter possibility by implementing generalized additive models and found again that phenylalanine did not significantly change across time. Our results support the recent work of Feddern et al. (2021), which sought to understand how marine ecosystems responded to environmental change from 1928–2014 by employing bulk carbon and CSIA-AA on the archival bones of Puget Sound harbor seals *Phoca vitulina* and conducting a dynamic factor analysis. The authors did not detect significant trends in phenylalanine over time, even though the Salish Sea has seen an increase in sewage treatment discharge (Mohamedali et al. 2011). Our results are also consistent with Brandenberger et al. (2011), who documented that over the past century, only small changes in nitrogen levels have occurred, and these changes are not large enough for ecosystem-level change.

Our use of fluid-preserved specimens from natural history collections imposes some constraints. For example, these specimens were collected over many years by many different collectors, often with various, divergent purposes in mind. This might cause individuals in the collection to be a non-representative subset of the actual population, with size, site, and collection-method biases, among others. Body size is directly associated with trophic position in marine fishes (e.g. Arim et al. 2010), and the majority of our results support this finding. However, our finding of increasing trophic position through time for rockfish is not an artefact of specimen selection, as we carefully selected fishes of similar size across decades, ensuring that year and fish size were not correlated. We also verified in a post hoc analysis that there was no significant interaction effect between size and year on rockfish trophic position (see Supplement 2). We understand that among-site variability in stable isotope values can be large, as the isotopic signatures of organisms and their environment are dynamic (e.g. Layman et al. 2012). We controlled for site variation in our models by making it a random effect and checked that each of our response variables was not spatially or temporally autocorrelated. Additionally, we recognize that this study — like all CSIA-AA studies on fluid-preserved specimens — was necessarily limited in replication due to the high costs of the laboratory procedures. We used one of the largest sample sizes to date among CSIA-AA studies. Regardless of the constraints of this research, this work emphasizes the critical importance of maintaining and valuing natural history collections. Because of the meticulous cataloging and preservation performed by natural history museums, we and other researchers can continue to uncover our ecological past and make more informed ecological predictions.

Over a period in which Puget Sound experienced substantial ecological change from fishing and urbanization, some species have remained trophically unchanged, suggesting some fish species may be more trophically resilient. This resilience might originate from the capacity of some fish to (1) forage on a diversity of prey within a TL, (2) move great distances to capture such prey, and/or (3) be adaptative to small environmental fluctuations. A combination of these factors could be what stabilizes fish trophic position and fortifies food web structure over time. We postulate if forage fish populations decline further or if predators cannot reach this prey, trophic connectivity may be significantly weakened and, in turn, trophic change could occur. This postulate can be supported by our copper rockfish case study, which provides indirect evidence that there are important food web feedback loops between fish population dynamics and trophic linkages. Accordingly, we argue that efforts should be made to identify and conserve the trophic interactions of species that are experiencing trophic change. Importantly, further studies examining what factors stabilize fish trophic position are critical for marine conservation.

Data availability. Data and analyses are available at https://github.com/rlwelicky/CSIA_Allfish.

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