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Chu, Alexandra

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Archival Tissues Identify Trophic Narrowing of Marine Foodwebs Preceding Nutrient
Deficiencies in California Chinook Salmon

By

ALEXANDRA NICOLE CHU
THESIS

Submitted in partial satisfaction of the requirements for the degree of

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DAVIS

Approved:

Carson Jeffres, Chair

Rachel Johnson

Sean Godwin

Committee in Charge

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ABSTRACT

In 2020, California Central Valley Chinook salmon were found to be affected by thiamine deficiency complex (TDC), a nutritional disorder associated with insufficient vitamin B₁. The emergence of TDC coincided with marine food-web restructuring following the 2014–2016 northeast Pacific marine heatwave. Although marine diet shifts have been proposed as a cause of TDC, it is unknown whether measurable changes in marine feeding ecology preceded its detection in 2020. To reconstruct historical marine feeding patterns, we used carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope analysis of 996 archived scales from fall, winter, and spring run Chinook salmon from 2013–2023. Because scales retain a chemical record of marine feeding history, they provide a retrospective view of dietary diversity through time. Dietary diversity was quantified using Bayesian standard ellipse area (SEA_B) and within-cohort $\delta^{15}\text{N}$ standard deviation.

Dietary niches contracted prior to and during the documented TDC period across all three runs, indicating a narrowing of the marine prey base. Winter run, the run most affected by thiamine deficiency, showed the earliest and most severe contraction, with isotopic niche size declining by 87% between 2016 and 2021. Comparisons between pre-TDC and TDC years showed average niche reductions of 49% in winter run, 37% in fall run, and 26% in spring run. Trophic variability (SD of $\delta^{15}\text{N}$), a measure of how broadly fish fed across different levels of the food web, was more strongly associated with egg thiamine concentration than overall niche size (SEA_B) and explained approximately twice as much variation in egg thiamine. Importantly, isotopic niche contraction preceded the first documented occurrence of TDC, indicating that archived scales could have provided advance warning of population-level vulnerability. The simultaneous contraction of dietary niches across three genetically and ecologically distinct Chinook salmon runs suggests ecosystem-scale restructuring of the California Current prey community.

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1 INTRODUCTION

1.1 HISTORICAL AND GEOGRAPHICAL CONTEXT

The Sacramento–San Joaquin River Basin, California’s largest watershed at roughly 27,000 square miles, supports all four runs of Chinook salmon (*Oncorhynchus tshawytscha*): fall, late fall, winter, and spring. These runs co-occur only in the Sacramento River, making it the only system in California where adult Chinook salmon are present year-round (Healey, 1991; Rutter, 1904; Stone, 1883; Vogel & Marine, 1991). These Evolutionarily Significant Units (ESUs) are defined by the season in which adults return to freshwater to spawn (Lindley et al., 2007; Williams et al., 2007; Yoshiyama et al., 2000). Among them, the winter run ESU is listed as endangered under both state and federal Endangered Species Acts (NMFS, 1994, 1999; Office of the Federal Register, 1999).

Few species shape an ecosystem as directly as Chinook salmon in California’s Central Valley (CCV). Their carcasses deliver marine-derived nutrients that support at least 137 different species, from bears to riparian plants (Cederholm et al., 2000). When commercial fisheries are open, these runs generate roughly \$900 million in annual economic activity for the state (Julienne & Morse, 2021). For indigenous communities, salmon are not simply a resource, but a pillar of cultural identity and spiritual practice shared across many west coast nations. Chinook salmon were once abundant in the California Central Valley; tribal histories describe extraordinary spawning runs, and early commercial catch records suggest up to 1–2 million spawners per year (Gerstung, 1971; Yoshiyama et al., 1998). That era is gone. Today, Chinook salmon persist at a fraction of their historical abundance.

Chinook salmon face numerous challenges in today’s environment. Large dams block access to most historical spawning and holding habitats in the upper Sacramento, Feather,

American, and San Joaquin tributaries, extirpating entire populations (NMFS, 2014; Yoshiyama et al., 1998). Below the dams, water diversions and pollution have degraded what remains (NMFS, 2014). Drought worsens the damage. Low flows dewater redds and strand juveniles, while river temperatures climb past thermal thresholds for incubation and rearing (Moyle et al., 2017; NMFS, 2014). In 2021, an estimated 75% of endangered winter run Chinook salmon died from elevated water temperatures (NOAA Fisheries, 2023). Today, winter run are federally listed as endangered, spring run as threatened, and even the relatively robust fall run are heavily supported by hatchery production (Mantua et al., 2025; Yoshiyama et al., 1998).

1.2 THE MARINE ENVIRONMENT: OCEAN VARIABILITY AND FOOD WEB CHANGE

The California Current Ecosystem (CCE) is one of the most productive eastern boundary upwelling ecosystems in the world (Checkley & Barth, 2009). Seasonal upwelling drives nutrient delivery to the surface ocean, supporting a highly diverse prey community that includes krill, juvenile rockfish, market squid, sardine, anchovy, and herring. For Chinook salmon, this prey diversity is essential. Forage species composition and availability directly shape juvenile growth, body condition, and survival during early ocean residence (Wells et al., 2016). This marine diet is the nutritional foundation that sustains their growth, survival, and reproductive success when they come back to spawn (Lerner & Hunt, 2025; Litz et al., 2017; Mantua et al., 2025).

The CCE is not static. Interannual variability driven by El Niño and the Southern Oscillation (ENSO) and decadal shifts associated with the Pacific Decadal Oscillation (PDO) shape the prey community available to foraging salmon (Ralston et al., 2015; Santora et al., 2017; Thayer et al., 2014). However, the restructuring that preceded Thiamine Deficiency Complex (TDC) was not a product of routine climate cycling. The 2014–2016 northeast Pacific marine heatwave was among the most anomalous ocean warming events on record, driving conditions that exceeded the

bounds of normal interannual variability (Di Lorenzo & Mantua, 2016; Free et al., 2023; Jacox et al., 2018). Warm, stratified conditions suppressed upwelling, reducing krill abundance while anchovy recruitment surged to record levels (Santora et al., 2020; Thompson et al., 2019). These conditions persisted, narrowing the prey base, and resulted in a simplification of the forage community available to Chinook salmon during their marine residence.

The marine diet of California Chinook salmon became significantly less diverse following the 2014-2016 marine heatwave. Historically, gut content analysis shows that California Central Valley Chinook salmon consumed a diverse diet of anchovies, krill, juvenile rockfish, market squid, sardine, and herring (Thayer et al., 2014). By 2020–2022, that diversity had collapsed: northern anchovy (*Engraulis mordax*) composed 89–100% of Chinook salmon diet by biomass, the lowest prey diversity ever recorded (Mantua et al., 2025; Thayer et al., 2014). This shift reflects not just increased anchovy abundance, but the reduced availability of the alternative prey that historically buffered salmon diets. Beginning in 2014, anchovy biomass in the California Current expanded markedly, altering the composition of the forage community (Stierhoff et al., 2023).

1.3 THIAMINE DEFICIENCY

The dietary shift toward anchovy dominance had a measurable physiological consequence. Beginning in 2020, Chinook salmon fry at multiple Central Valley hatcheries began exhibiting disoriented, corkscrew-like swimming followed by mass mortality (Foott, 2020). Initial suspicion focused on infectious disease, but investigation ultimately traced the cause to a maternal deficiency in vitamin B1, also known as thiamine, passed from mothers to their eggs (Mantua et al., 2021).

Thiamine deficiency had been documented in Great Lakes salmonids in 1968, when high offspring mortality struck coho salmon, Chinook salmon, steelhead trout, brown trout, and lake trout. Salmonids in the Laurentian Great Lakes, Lake Champlain, the New York Finger Lakes, and the Baltic Sea had all experienced similar symptoms tied to low thiamine (Amcoff et al., 1999; Fitzsimons et al., 1999; Honeyfield et al., 2005; Ketola et al., 2005; Ladago et al., 2020). But it had never been documented in California salmon before 2020 (Mantua et al., 2025).

Thiamine (vitamin B₁) is an essential vitamin that cannot be naturally produced in the body. It is mainly derived through diet and it plays a key role in brain function (Harder et al., 2018; Whitfield et al., 2018). Some symptoms of Thiamine Deficiency Complex are reduced growth, reproductive failure, neurological disorders, damage to the blood-brain barrier, immunosuppression, and increased parasitic infestation (Futia et al., 2017; Harder et al., 2018; Riley & Evans, 2008).

In Chinook salmon, diet composition appears to be the primary pathway through which thiamine deficiency develops. Diets dominated by anchovies can be particularly problematic. Anchovies have the highest thiaminase activity of any major Chinook salmon prey species, an enzyme that degrades thiamine in the gut of consumers (Honeyfield et al., 2005; Mantua et al., 2025). Anchovy are also low in thiamine and high in lipids, a combination that can compound the problem through oxidative stress (Keinänen et al., 2012).

Chinook salmon have long consumed anchovy as part of a mixed forage base. Historically, however, anchovy intake was buffered by other common prey like krill, juvenile rockfish, and market squid, that are low in thiaminase, higher in thiamine and lower in lipids (Mantua et al., 2025). The decline or reduced availability of these alternative prey may therefore be as consequential for nutritional status as increased anchovy consumption itself.

Thiamine deficiency can be treated – in hatcheries. Hatchery staff have found success giving thiamine injections to adult females (Fitzsimons et al., 2005; Futia et al., 2017; Koski et al., 1999). Egg immersion baths applied at fertilization are also effective at preventing TDC related mortality (Fisher et al., 1996; Kwak, 2021; Reed et al., 2023). These solutions have proven to be successful, but they only apply to hatchery fish. Wild Chinook salmon may still be suffering the full effects of thiamine deficiency, but may also receive thiamine supplementation from naturally occurring aqueous thiamine (Suffridge et al., 2023). Even in hatcheries, thiamine supplementation may mask the severity of the problem and potentially interfere with natural selection for thiamine resilience (Harder et al., 2025).

Whether TDC is driven mainly by a single dietary shift toward anchovy dominance, by food web simplification and loss of alternative prey, or by oceanographic forcing remains unresolved. These mechanisms are likely to interact and compound rather than act independently. Separating them requires an approach that can track population-level diet structure through time, before and after ocean conditions shifted.

Stable isotope analysis provides a powerful tool for reconstructing diet histories, movement patterns, and natal origins of animals (Hobson & Wassenaar, 2008; R. C. Johnson et al., 2016; Trueman & St John Glew, 2019). Carbon and nitrogen isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) are commonly used to quantify dietary diversity and trophic structure because they reflect different information about what an animal has eaten and assimilated. Carbon values change relatively little with each trophic transfer, so $\delta^{13}\text{C}$ is often used to identify primary carbon sources and foraging habitats (DeNiro & Epstein, 1978; Post, 2002). Nitrogen values show stronger trophic fractionation, meaning $\delta^{15}\text{N}$ becomes enriched as nitrogen moves from prey to consumer. This makes nitrogen isotopes

useful for estimating trophic position (DeNiro & Epstein, 1981; Minagawa & Wada, 1984; Post, 2002).

Together, carbon and nitrogen isotopes can be used to describe population-level dietary diversity. Cohorts that fed across a wider range of prey types, carbon sources, or trophic levels are expected to occupy a larger area in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ isotope space than cohorts relying on a narrow subset of prey (Bearhop et al., 2004; Layman et al., 2007). We used two complementary isotope metrics to evaluate changes in dietary diversity. Bayesian standard ellipse area (SEA_B) quantifies the size of the isotopic niche in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space (Jackson et al., 2011). Within-cohort $\delta^{15}\text{N}$ standard deviation provides a more focused measure of trophic variability by isolating just the variation along the trophic axis. Higher $\delta^{15}\text{N}$ variability indicates that individuals within a cohort fed across a wider range of trophic positions. Lower $\delta^{15}\text{N}$ variability suggests greater convergence on prey from similar trophic levels. If Chinook salmon diets became increasingly dominated by anchovy, that narrowing should be detectable isotopically. A cohort feeding on diverse prey across multiple trophic levels should show greater $\delta^{15}\text{N}$ variability and larger isotopic ellipses in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space. A cohort relying more heavily on one dominant prey type should show the opposite pattern: smaller ellipses and lower trophic variability.

If food web simplification contributed to the development of TDC, we expect isotopic niche area (SEA_B) to contract during the years leading up to its detection in 2020. Such a contraction would suggest that Chinook salmon were drawing from a narrower range of prey items than in previous decades. We further predict a reduction in within-cohort $\delta^{15}\text{N}$ variability, indicating that individuals occupied a more restricted trophic space and relied on a less diverse prey community. Together, these patterns would support the idea that loss of alternative forage species, rather than

increased anchovy abundance alone, altered the nutritional landscape experienced by Central Valley Chinook salmon.

Testing these predictions requires a dietary record that extends beyond the period when TDC was first observed. Conventional diet data provide only snapshots in time and are unavailable for much of the period preceding the 2020 outbreak. Stable isotope analysis of archived fish scales offers a means of reconstructing long-term changes in marine diet and trophic structure.

Scale collagen integrates dietary inputs across the fish's lifetime, but because later growth layers contribute disproportionately to total biomass, isotopic signatures primarily reflect the final period of marine feeding prior to freshwater return (Espinasse et al., 2020; Satterfield & Finney, 2002). Since state and federal agencies have collected and archived Chinook salmon scales for decades as part of routine monitoring, these collections represent an untapped record of the marine foraging history of Chinook salmon.

This study uses stable isotope analysis of archived scales from fall, winter, and spring run Central Valley Chinook salmon across eleven return years (2013–2023) to ask: were there detectable changes in marine isotopic niche structure prior to the clinical emergence of TDC in 2020? We test the hypothesis that trophic diversity declined in the years preceding and during the TDC period, reflecting a narrowing of the marine prey base. We measure this decline using isotopic niche size (Bayesian standard ellipse area, SEA_B) and trophic variability (within-cohort $\delta^{15}N$ standard deviation). We predict that (1) isotopic niche contracted prior to and during the documented TDC period across all three runs, with the most severe contraction in winter run, the most thiamine deficient; (2) within-cohort trophic variability (SD of $\delta^{15}N$) was more strongly related to egg thiamine concentration than overall niche size (SEA_B); and (3) isotopic niche contraction

preceded the first measurement of low egg thiamine, indicating that archived scales could have provided advance warning of population-level vulnerability to TDC.

2 MATERIALS AND METHODS

We analyzed carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope signatures from archived Chinook salmon (*Oncorhynchus tshawytscha*) scales collected across multiple hatcheries and years. We targeted age 3 fish exclusively, as this is the most dominant age class returning to Central Valley hatcheries and standardizes the number of ocean years across individuals, enabling consistent cohort reconstruction. Our study period spanned eleven return years (2013–2023), capturing conditions before the detection of Thiamine Deficiency Complex (TDC) in 2020. We expected that this longer timeframe would also capture variability associated with major oceanographic phenomena affecting the California Current, including the strong 2014–2016 El Niño event, subsequent La Niña periods, and shifts between positive and negative PDO phases.

2.1 SAMPLE SOURCES AND SELECTION

Fall run Chinook salmon were sourced from Coleman National Fish Hatchery, winter run from Livingston Stone National Fish Hatchery, and spring run from Feather River Fish Hatchery (Figure 1; Table 1). We aimed for a minimum of 30 fish per cohort. Some cohorts ended up with sample sizes below or above the target because scale availability varied among groups, and additional losses occurred due to archive constraints, damaged scales or insufficient scale mass.

Table 1: Sample sizes (n) and origin for fall, winter, and spring run Chinook salmon cohorts by return year (2013–2023).

	ORIGIN	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	TOTAL
Fall Run	Coleman National Fish Hatchery	30	29	30	29	30	30	39	28	30	29	28	332
Winter Run	Carcass fish collected at Livingston National Fish Hatchery	30	29	27	18	30	28	38	29	28	25	50	332
Spring Run	Feather River Fish Hatchery	30	27	30	30	29	28	30	30	38	30	30	332



Figure 1: Sample origin map.

2.2 SAMPLE COLLECTION

2.2.1 Overview

Scales were collected by two groups: UC Davis researchers and the California Department of Fish and Wildlife (CDFW) as part of their ongoing salmon monitoring programs. In 2020, during the onset of TDC, UC Davis researchers began collecting a variety of tissue samples from Central

Valley hatcheries, including scales. Fall and spring run scales from 2020–2023 were collected by UC Davis researchers; all other samples were obtained from CDFW archives.

2.2.2 Field Collection Method

Scales were collected using two methods: direct scale scraping and excision of a skin section containing scales. For direct scale scraping, scales were collected from freshly spawned individuals at the hatcheries. The mucous layer was removed by running the back of a paring knife along the body with the grain of the scales, then wiping the knife clean with a paper towel moistened with deionized (DI) water. We then removed scales using a knife and scraping against the grain between the posterior dorsal fin insertion and the anterior anal fin insertion, approximately 2–3 rows above the lateral line. Scales from this part of the fish are among the first formed and exhibit complete, well-defined annuli (Clutter & Whitesel, 1956; Eaton, 2015). We placed collected scales on waterproof paper, dried them, and stored them in coin envelopes at room temperature.

Other samples were obtained from the California Department of Fish and Wildlife (CDFW) scale archive. For these samples, CDFW staff excised a section of skin from between the dorsal fin and lateral line, placed it on waterproof paper, and stored it in a coin envelope.

2.3 SCALE EXTRACTION AND PREPARATION

2.3.1 Extraction

Scales arrived in three forms: skin sections in envelopes, loose scraped scales in envelopes, or previously mounted on glass slides. We rehydrated skin sections in DI water for approximately 10 minutes, then removed scales with forceps. Loose scales were often adhered together with dried mucous, so we soaked them in DI water and separated them with forceps. Some scales had been

previously cleaned by CDFW with Simple Green All Purpose cleaner and mounted between glass slides for age estimation. We extracted these scales from their mounts using a scalpel and forceps. Lowe-Webb et al. (in prep) found no significant effect of Simple Green cleaning on carbon or nitrogen isotope values.

2.3.2 Selection Criteria

We visually inspected all scales for damage and resorption using a Leica EZ4W stereomicroscope (Leica Microsystems, Wetzlar, Germany). During their freshwater spawning migration, Chinook salmon cease feeding and rely on endogenous energy reserves (Welch & Parsons, 1993). During this fasting period, salmon resorb minerals, primarily calcium and phosphorus, from their scales and bones to meet the physiological demands of sexual maturation (Kacem et al., 2013). This resorption erodes the scales' margins and in extreme cases the inner surface as well, potentially altering isotopic values (MacLellan & Gillespie, 2015). Due to this, we selected the most intact scales for analysis.

2.3.3 Whole Scale Analysis

We analyzed scales whole to target the recent marine foraging period rather than subsectioning them to isolate individual annuli. The collagen basal plate builds up in layers. Each new lamella forms beneath older layers and spreads across the underside of the scale (Hutchinson & Trueman, 2006; Trueman & Moore, 2007). This new lamella covers an area proportional to the fish's body size at the time of deposition, so the majority of the collagen mass reflects the most recent growth. In Atlantic salmon (*Salmo salar*), roughly 75% of the collagen in the central, juvenile portion of the scale can be replaced or overprinted by collagen formed later during the marine phase. This shifts the isotopic signal toward the last season of growth (Hutchinson & Trueman, 2006). In another study, whole-scale and last-annulus $\delta^{13}\text{C}$ values were nearly identical, consistent

with whole-scale $\delta^{13}\text{C}$ being dominated by the final growing season and showing minimal freshwater influence (Espinasse et al., 2020). Pacific salmon complete more than 99% of somatic growth in the ocean (Welch & Parsons, 1993), with the largest increases in size and weight occurring during the final year at sea (Satterfield & Finney, 2002). Individual annuli contain very little material, and splitting scales would have pushed many samples below recommended mass thresholds for reliable Elemental Analyzer coupled to Isotope Ratio Mass Spectrometry (EA-IRMS) elemental and isotope measurements. Since the majority of biomass, and scale collagen, is accrued during the marine phase, whole-scale analysis best represents recent marine foraging, which is why we analyzed scales whole rather than subsectioning the outermost annuli.

2.3.4 Scale Cleaning

We cleaned scales by sonication in 5 mL of room temperature DI water for 2.5 minutes using a Cole-Parmer UC-100 ultrasonic cleaner to remove adhered paper, tissue, or mucous (methods developed by Lowe-Webb et al. in prep). We then dried the scales at room temperature on a sterile towel until fully dry. We placed dried scales in 8 × 5 mm pressed tin capsules and weighed them to the nearest 0.01 mg with a Mettler Toledo Semi-MicroBalance. Scale masses ranged from 0.14 to 1.88 mg. If a scale fell below the minimum analytical mass, we substituted a larger scale from the same fish.

2.4 STABLE ISOTOPE ANALYSIS

We measured carbon and nitrogen stable isotope ratios using a Costech ECS 4010 elemental analyzer interfaced with a Thermo Delta V Advantage continuous flow isotopic ratio mass spectrometer at the Center for Archaeology, Materials, and Applied Spectroscopy (CAMAS) Stable Isotope Laboratory at Idaho State University's Pocatello campus. Isotope ratios are

expressed in δ -notation ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$; parts per thousand, ‰) relative to the Vienna Pee Dee Belemnite (V-PDB) and atmospheric N_2 standards, respectively, and calculated as:

$$\delta_x = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000 .$$

where x is ^{13}C or ^{15}N and R is the ratio of the heavy to light isotope ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$). Scale samples ranged in mass from 0.14 to 1.88 mg. Replicate analyses of internal standards distributed throughout each analytical run yielded precision of $\pm 0.2\text{‰}$ for both $\delta^{13}\text{C}$ (SD = 0.064‰) and $\delta^{15}\text{N}$ (SD = 0.196‰), and $\pm 0.5\%$ of the measured value for %C and %N.

2.5 STATISTICAL ANALYSES

A total of 1,008 scale samples were analyzed across three runs (fall, winter, spring) and eleven return years (2013–2023). Five samples were removed following quality control flags assigned by the isotope analysis facility, indicating potential analytical error, yielding 1,003 QC-passing samples. We then screened for statistical outliers within each run $\times$ year cohort using Tukey's (1977) outer-fence rule ($k = 3 \times \text{IQR}$) applied separately to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. We flagged any value more than $3 \times \text{IQR}$ below the first quartile or above the third quartile, and we excluded any sample flagged on either isotope axis from all subsequent analyses. This threshold is more conservative than the conventional inner-fence rule ($k = 1.5$) and is expected to flag fewer than 1 in 400,000 observations under a normal distribution; in practice it targets values that are analytically implausible rather than biologically extreme. Seven samples (0.7% of QC-passing samples) were flagged across six cohorts, including one with a $\delta^{13}\text{C}$ value of -22.5‰ , more than $20 \times$ the cohort IQR below Q1 and inconsistent with marine Chinook foraging ecology. After exclusion, the final dataset comprised 996 samples: fall run ($n = 332$, $\delta^{13}\text{C} = -13.98 \pm 0.37\text{‰}$, $\delta^{15}\text{N} = 14.51 \pm 0.58\text{‰}$), winter run ($n = 332$, $\delta^{13}\text{C} = -13.59 \pm 0.43\text{‰}$, $\delta^{15}\text{N} = 15.40 \pm 0.54\text{‰}$), and spring run ($n = 332$, $\delta^{13}\text{C} =$

$-13.85 \pm 0.36\text{‰}$, $\delta^{15}\text{N} = 14.79 \pm 0.66\text{‰}$; all values mean $\pm$ SD). Cohort sample sizes ranged from 18 to 50 individuals. Sensitivity analyses confirmed that all directional conclusions are unchanged when the seven IQR-flagged samples are retained (SI Appendix, Section S.1).

We conducted all analyses in R version 4.5.1 (R Core Team, 2025) within RStudio 2025.9.9.418 (Posit Team, 2025). We performed data manipulation using the *tidyverse* suite of packages version 2.0.0 (Wickham et al., 2019). We produced figures using the *ggplot2* package (Wickham, 2016). We conducted multivariate analyses with the *vegan* package (Oksanen et al., 2017), and isotopic niche analyses with the Stable Isotope Bayesian Ellipses in R (SIBER) package version 2.1.9 (Jackson et al., 2011; Jackson & Parnell, 2015).

2.5.1 Isotopic Centroid Analysis

We calculated isotopic centroids for each run $\times$ year cohort as the arithmetic mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. We quantified pairwise differences between cohort centroids using Euclidean distance (D) in bivariate $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space.

$$D = \sqrt{(\delta^{13}\text{C}_2 - \delta^{13}\text{C}_1)^2 + (\delta^{15}\text{N}_2 - \delta^{15}\text{N}_1)^2}$$

We used distance matrices to characterize both within-run (interannual) and between-run differences in isotopic niche position (Layman et al., 2007). These distances summarize simultaneous shifts in both the prey origin ($\delta^{13}\text{C}$) and trophic position ($\delta^{15}\text{N}$).

2.5.2 Multivariate Tests of Cohort Differences

We tested differences in multivariate isotope space ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) among run $\times$ year cohorts using permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) implemented via the *adonis2()* function in *vegan* with Euclidean distance and 999 permutations (seed = 42). The

model tested the effects of run, year (as a factor), and their interaction on individual-level multivariate isotope composition:

$$isotope\ matrix \sim run \times year$$

Since PERMANOVA can be sensitive to heterogeneity in multivariate dispersion among groups (Anderson, 2006), we tested homogeneity of group dispersions using *betadisper()*, which calculates distances from individual observations to their group centroid in multivariate space. We evaluated significance of dispersion differences using permutation tests (999 permutations) via *permutest()*. Where dispersion heterogeneity is significant, PERMANOVA results should be interpreted as reflecting differences in both niche position (centroid location) and niche breadth (spread around centroids), rather than position alone (Anderson, 2006).

2.5.3 Isotopic Niche Size (Standard Ellipse Area)

We estimated isotopic niche size for each run $\times$ year cohort using the Stable Isotope Bayesian Ellipses in R (SIBER) framework (Jackson et al., 2011). SIBER fits bivariate normal distributions to $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ data and estimates the standard ellipse area (SEA), which is the bivariate analogue of standard deviation and encloses approximately 40% of the data. Unlike convex hull approaches (Layman et al., 2007), standard ellipses are relatively insensitive to sample size, making them appropriate for comparisons among groups with unequal sample sizes (Jackson et al., 2011; Syväranta et al., 2013).

We created separate SIBER objects for each run of Chinook salmon (fall, winter, spring), with years treated as groups within each run. We generated Bayesian estimates of the standard ellipse area (SEA_B) via Markov Chain Monte Carlo (MCMC) sampling to produce posterior distributions of niche size that naturally incorporate uncertainty from the sampling process. The

MCMC sampling parameters were: 40,000 iterations, a burn-in of 10,000 iterations, a thinning interval of 5, and 4 chains. We specified vague priors following Jackson et al. (2011): an Inverse Wishart prior on the covariance matrix Σ with scale matrix $R = I_2$ (the 2×2 identity matrix) and $k = 2$ degrees of freedom, and a normal prior on the means μ with precision $\tau = 1.0 \times 10^{-3}$. We summarized posterior distributions of SEA_B by their mean, median, mode, standard deviation, and 95% credible intervals (2.5th and 97.5th percentiles).

2.5.4 Temporal Trends and Correlations

To assess temporal trends in isotopic niche size and trophic position, we calculated Spearman rank correlations between year and mean SEA_B , and between year and mean $\delta^{15}N$, separately for each run. We used Pearson correlations to examine the relationship between mean $\delta^{15}N$ and SEA_B across run $\times$ year cohorts. We calculated within-cohort $\delta^{15}N$ standard deviation for each cohort as a complementary metric to SEA_B , as it isolates the trophic dimension of niche variation by removing the influence of $\delta^{13}C$ (Jackson et al., 2011). This metric is hereafter referred to as trophic variability, reflecting its interpretation as the spread of trophic positions within a cohort. Where egg thiamine concentration data were available (2020–2023), we used Pearson and Spearman correlations and linear regressions to assess the relationship between isotopic niche metrics (SEA_B and SD of $\delta^{15}N$) and mean egg thiamine concentration (nmol/g). We conducted an analysis of covariance (ANCOVA) to test whether the relationship between SEA_B and egg thiamine differed after accounting for run identity.

3 RESULTS

3.1 DISTINCT MARINE FORAGING NICHES AMONG RUNS

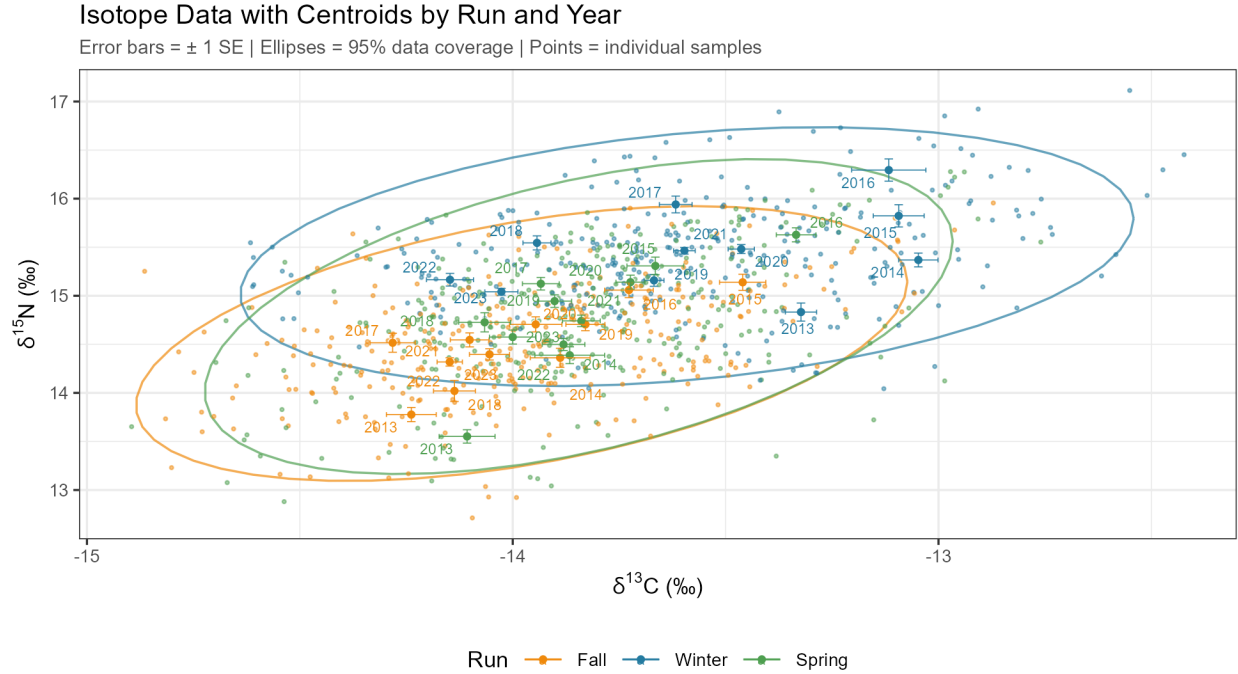


Figure 2: Isotopic niche space by run.

Stable isotope bivariate plot ($\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$, ‰) for fall (orange, $n = 332$), winter (blue, $n = 332$), and spring (green, $n = 332$) run Chinook salmon scales (2013–2023). Bayesian standard ellipses represent 95% credible intervals for each run. Cross-hatch symbols indicate run-year cohort centroids (mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$); error bars represent ± 1 standard error. More negative $\delta^{13}\text{C}$ values reflect pelagic foraging; less negative values indicate nearshore or benthic foraging. Higher $\delta^{15}\text{N}$ values reflect feeding at higher trophic levels. Cohort sample sizes ranged from 18–50 individuals.

Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope values differed across runs (Figure 2). The cross hatches (centroids) represent the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values (‰) for each run-year cohort. Winter run exhibited consistently higher $\delta^{15}\text{N}$ values compared to fall and spring runs. Fall run presented the lowest mean $\delta^{15}\text{N}$ values, while spring run had intermediate $\delta^{15}\text{N}$ values. Standard ellipse areas (SEA_B) (95% credible intervals) varied among runs and years. Mean SEA_B values were largest in fall run (0.377‰^2), intermediate in spring run (0.371‰^2), and smallest in winter run (0.285‰^2 ; Table 2).

3.1.1 Mean $\delta^{15}\text{N}$ by return year

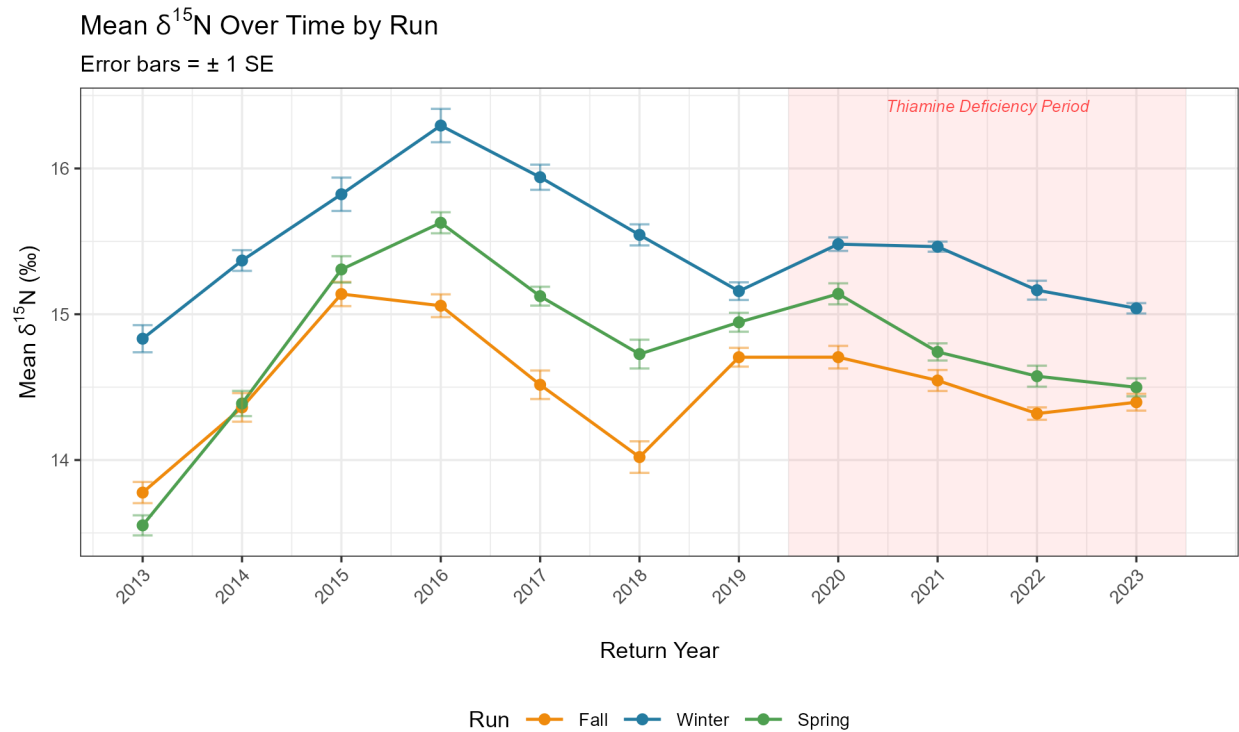


Figure 3: Mean $\delta^{15}\text{N}$ by run and year.

Time series of mean $\delta^{15}\text{N}$ (‰) for fall (orange, $n = 332$), winter (blue, $n = 332$), and spring (green, $n = 332$) run Chinook salmon (2013–2023). Error bars represent ± 1 standard error.

Winter run had consistently higher $\delta^{15}\text{N}$ values (mean: 15.46‰). Spring run exhibited intermediate values (mean $\delta^{15}\text{N} = 14.78$ ‰). Fall run exhibited the lowest mean $\delta^{15}\text{N}$ (mean = 14.50‰). Interannual variability was observed within each run with fall run being the most variable, followed by spring and winter run. All three runs differed significantly in mean $\delta^{15}\text{N}$ (pairwise Welch t-tests, Bonferroni corrected; all $p < 10^{-7}$).

3.2 THIAMINE DEFICIENCY COMPLEX

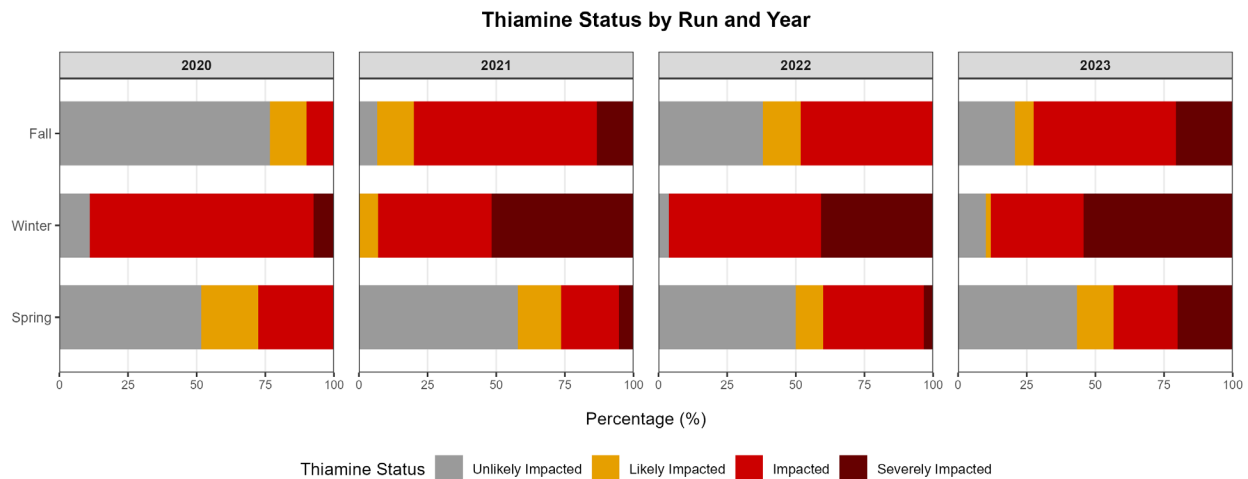


Figure 4: Egg thiamine status by run and year.

Proportional egg thiamine status classification by run and return year (2020–2023). Horizontal stacked bars show the proportion of sampled females classified as unlikely impacted (grey; >7.7 nmol/g), likely impacted (yellow; 5.9–7.7 nmol/g), impacted (red; 2.7–5.9 nmol/g), or severely impacted (dark red; <2.7 nmol/g) by thiamine deficiency complex (TDC). Note that 2020 fall run egg thiamine values were not matched to individual fish with scale isotope data; scale-based dietary assignment protocols were not yet established in the first sampling year. Cohort sample sizes ranged from $n = 27$ to $n = 59$. Egg thiamine concentrations were sourced from EDI <https://doi.org/10.6073/pasta/ce132c1ef916900b5b50650388aa2266> (Ward et al., 2025).

Winter run Chinook salmon were the most affected by thiamine deficiency across all four years. Each year of the study, 89–100% of sampled winter run fish were impacted by thiamine deficiency (Figure 4). In 2021, 100% of the winter run Chinook salmon were thiamine deficient, with 93% falling into the "impacted" or "severely impacted" categories. The proportion of winter run fish that were "severely impacted" by TDC increased from 7% in 2020 to 52% in 2021 and reached a peak in 2023 with 54% of winter run fish classifying as severely impacted by TDC. Even during their "best" year (2020), 89% of winter run fish were affected by TDC.

Fall run fish were intermediate but erratic. In 2020, only 23% of fall run fish were affected by thiamine deficiency, with just 10% in the "impacted" or "severely impacted" categories and 77% classified as "unlikely impacted". Conditions worsened dramatically by 2021, when 93% of fish were affected by TDC, with 80% in the impacted or severely impacted categories. There was an improvement in 2022 (only 48% impacted or severely impacted and 38% unlikely impacted), but

conditions worsened again in 2023 (72% impacted or severely impacted). Of all run types, fall run showed the greatest interannual variability, with the "impacted or severely impacted" category swinging by as much as 70 percentage points across years.

Spring run fish were the least affected but show a worsening trend. In 2020 and 2021, roughly half of spring run fish were classified as "unlikely impacted" (52% and 58%). However, the proportion of fish in the two most severe categories ("impacted" and "severely impacted") increased from 28% in 2020 to 43% in 2023, driven primarily by a jump in "severely impacted" fish from 0% (2020) to 20% (2023).

The prevalence and severity of thiamine deficiency are escalating. Across all runs, the proportion of fish classified as "severely impacted" tended to increase over time, even when the overall proportion affected stayed relatively stable. For winter run fish, in 2020 there were only 7% that were "severely impacted". However, in 2023, this metric increased to 54%. For spring run fish, in 2020, 0% registered as "severely impacted". In 2023, 20% of spring run fish were severely impacted by TDC. This suggests the condition is worsening, not just increasing.

3.3 ISOTOPIC NICHE SIZE (SEA_B) AND TROPHIC VARIABILITY (SD OF $\Delta^{15}N$) CONTRACTED ACROSS RUNS, MOST SEVERELY IN WINTER RUN [HYPOTHESIS 1]

3.3.1 Fall Run

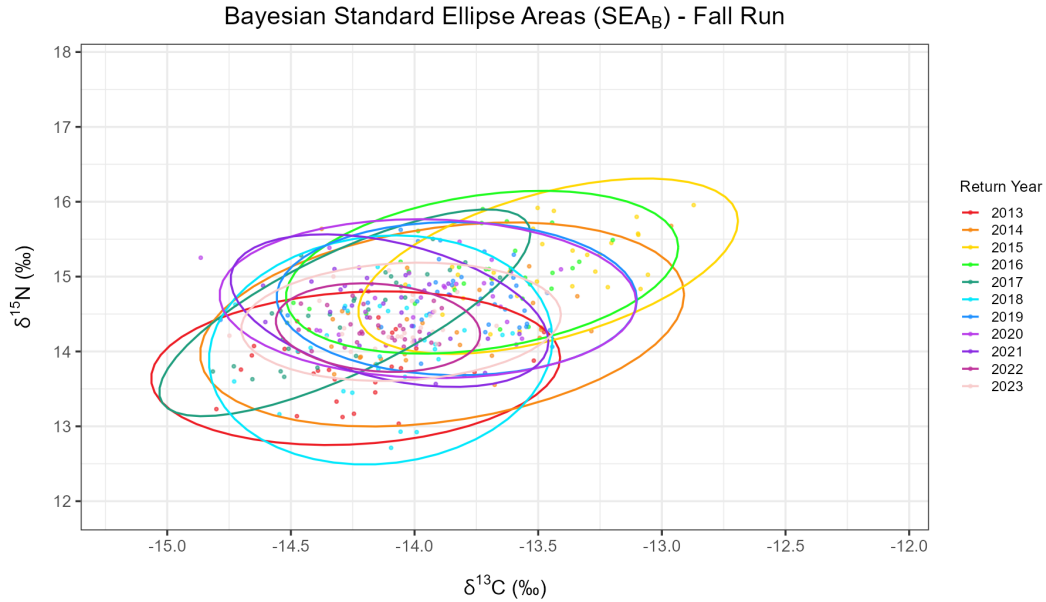


Figure 5: Fall run isotopic niche space by year. Stable isotope bivariate plot ($\delta^{13}C$ vs. $\delta^{15}N$, ‰) for fall run Chinook salmon scales (2013–2023). Bayesian standard ellipses represent 95% credible intervals for each return year; colors indicate return year. Sample sizes ranged from 28–39 individuals per cohort.

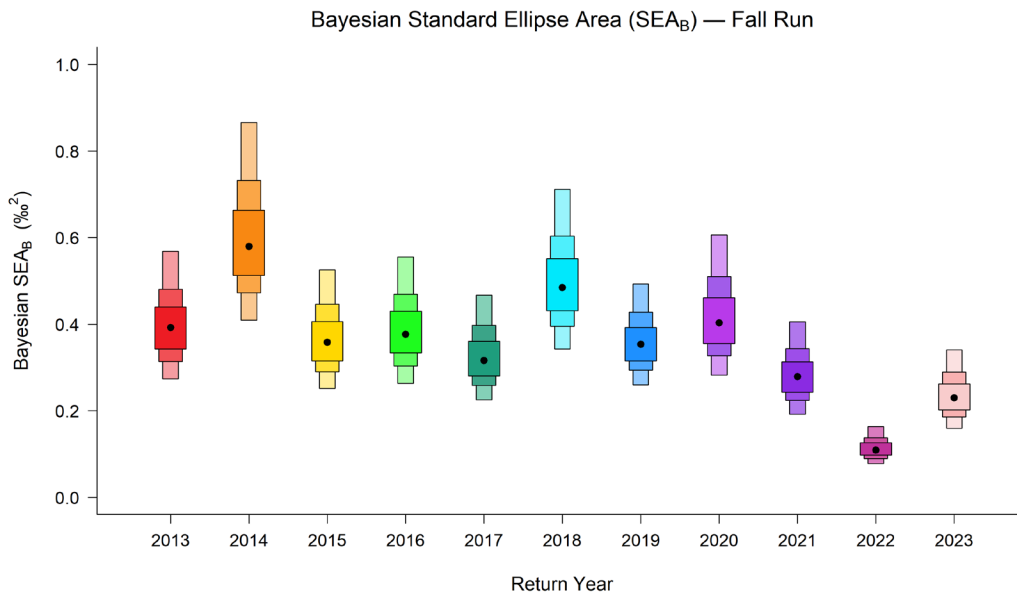


Figure 6: Fall run SEA_B posterior distributions by year. Posterior density distributions of Bayesian standard ellipse area (SEA_B , ‰^2) for fall run Chinook salmon (2013–2023), one panel per return year ($n = 28 - 39$ per cohort). Shaded regions represent 50%, 75%, and 95% credible intervals. Black circles indicate the modal SEA_B value for each cohort.

Fall run had the most stability in ellipse area with a coefficient of variation of 35.5% (Table 2). Fall run had the largest mean niche area among all runs ($0.377\%{}^2$; Table 2). 2014 exhibited the largest ellipse area ($0.625\%{}^2$), followed by 2018 ($0.518\%{}^2$; Figure 5–Figure 6; SI Appendix, Table S.3.1). The smallest SEA_B for fall run was in 2022 at $0.118\%{}^2$. This is an 81% decrease in SEA_B from the peak in 2014 ($0.625\%{}^2$) and a 60% decrease in ellipse area from just the year before (SEA_B 2021 = $0.294\%{}^2$). This marks the sharpest year to year decrease in niche size for this study.

3.3.2 Winter Run

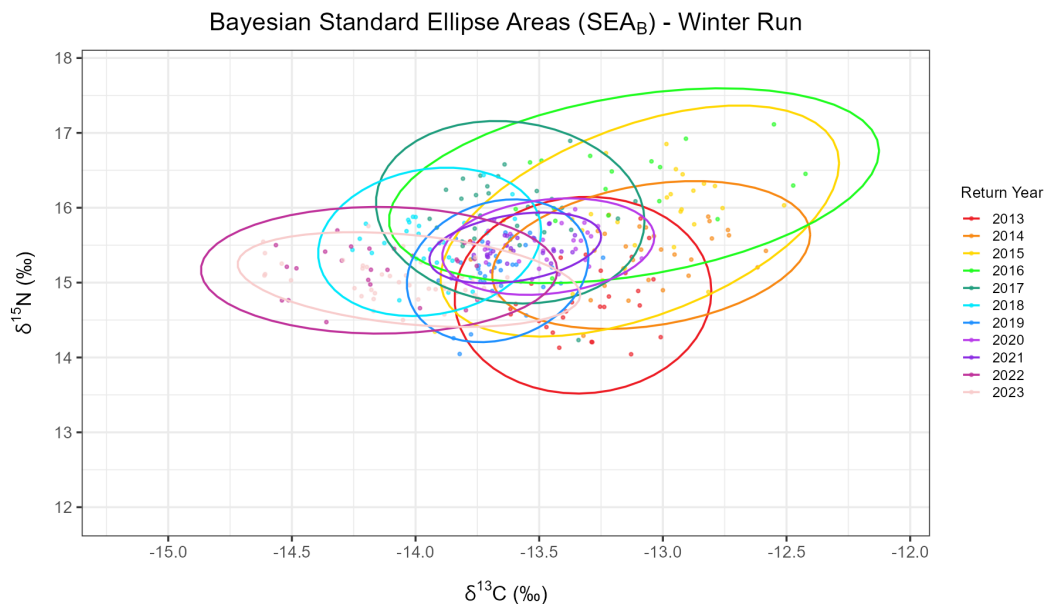


Figure 7: Winter run isotopic niche space by year.

Stable isotope bivariate plot ($\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$, ‰) for winter run Chinook salmon scales (2013–2023). Bayesian standard ellipses represent 95% credible intervals for each return year; colors indicate year. Cohort sample sizes ranged from 18–50 individuals per year.

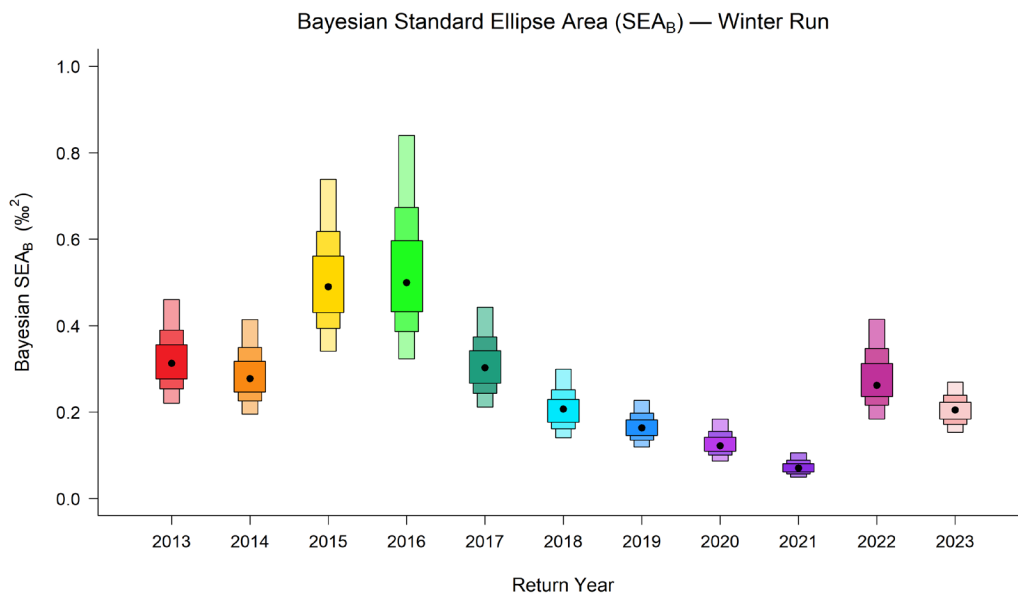


Figure 8: Winter run SEA_B posterior distributions by year.

Posterior density distributions of Bayesian standard ellipse area (SEA_B , ‰^2) for winter run Chinook salmon (2013–2023), one panel per return year ($n = 18\text{--}50$ per cohort). Shaded regions represent 50%, 75%, and 95% credible intervals. Black circles indicate the modal SEA_B value for each cohort.

Winter run Chinook salmon were the most variable in SEA_B (coefficient of variation = 53.1%)

(Table 2) This indicates substantial year to year variability relative to the mean niche area (Figure 7–

Figure 8). Mean SEA_B increased from $0.333\%{}^2$ in 2013 to a maximum of $0.562\%{}^2$ in 2016. From 2016 to 2021, SEA_B declined progressively, reaching a minimum of $0.076\%{}^2$ in 2021 (SI Appendix, Table S.3.1). This represents an approximately 87% reduction in mean ellipse area from the 2016 maximum. Winter run's ellipse area for 2021 is the lowest in this study. Following 2021, SEA_B increased to $0.293\%{}^2$ in 2022 and declined to $0.210\%{}^2$ in 2023. A Spearman correlation between year and SEA_B indicated a strong monotonic decline from 2016–2021 ($\rho = -1.00$, $p = 0.0028$).

3.3.3 Spring Run

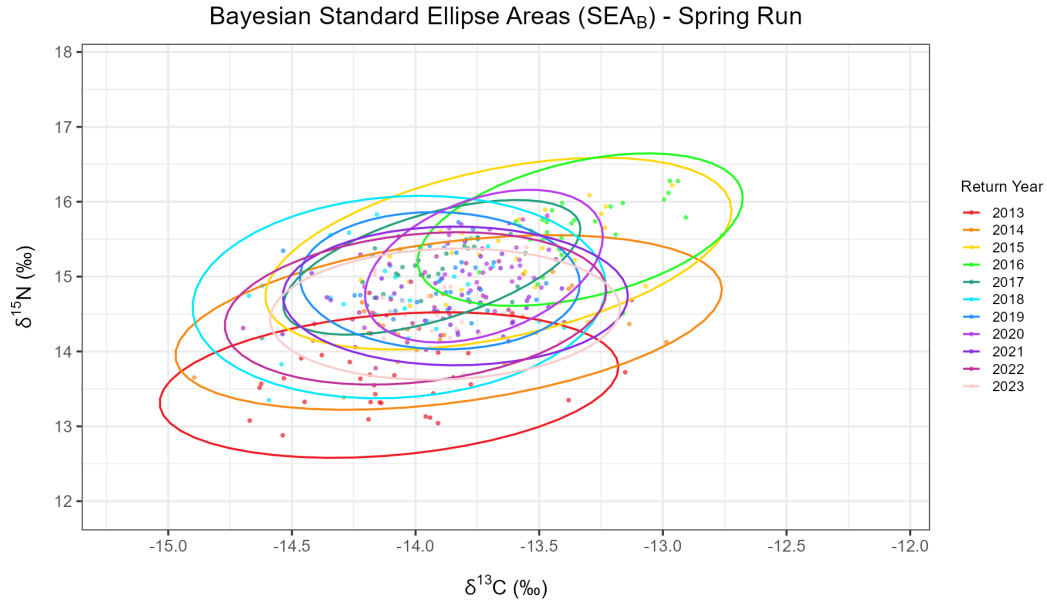


Figure 9: Spring run isotopic niche space by year.

Stable isotope bivariate plot ($\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$, ‰) for spring run Chinook salmon scales (2013–2023). Bayesian standard ellipses represent 95% credible intervals for each return year; colors indicate year. Cohort sample sizes ranged from 27–38 individuals per year.

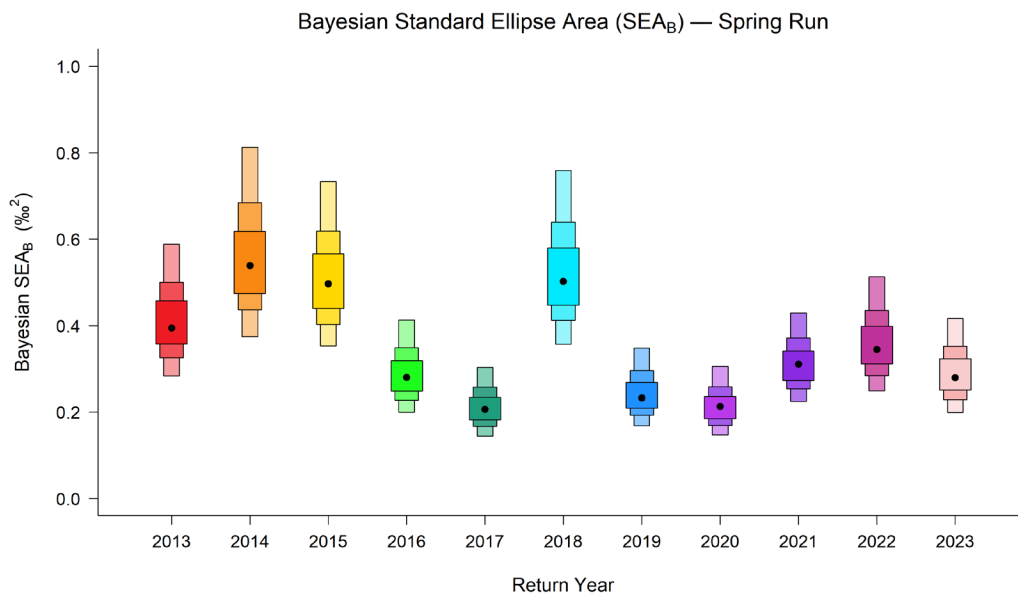


Figure 10: Spring run SEA_B posterior distributions by year.

Posterior density distributions of Bayesian standard ellipse area (SEA_B , ‰^2) for spring run Chinook salmon (2013–2023), one panel per return year ($n = 27\text{--}38$ per cohort). Shaded regions represent 50%, 75%, and 95% credible intervals. Black circles indicate the modal SEA_B value for each cohort.

Spring run exhibited interannual variability in SEA_B across the study period (2013–2023)

(coefficient of variation = 35.7%; Table 2). The largest mean SEA_B values occurred in 2014

(0.582‰²) and 2018 (0.545‰²) (SI Appendix, Table S.3.1). Beginning in 2019, SEA_B values dropped sharply and remained low throughout 2023 (Figure 10). Mean SEA_B during that time was 0.294‰², compared to the previous mean of 0.434‰² for 2013–2018. This represents an approximate 32% reduction in ellipse area after the drop in 2019.

3.3.4 Variability and Stability Pre/Post TDC

Table 2: Descriptive statistics for Bayesian standard ellipse area (SEA_B, ‰²) by run and study period (pre-TDC: 2013–2019; post-TDC: 2020–2023; full study: 2013–2023). CV = coefficient of variation (SD/mean × 100%).

RUN	PERIOD	YEARS	MEAN SEA _B	SD	COEFFICIENT OF VARIATION (CV%)	N
Fall	Pre-TDC	2013–2019	0.435	0.100	23.1%	7
Fall	Post-TDC	2020–2023	0.273	0.131	47.9%	4
Fall	Full Study	2013–2023	0.376	0.134	35.5%	11
Winter	Pre-TDC	2013–2019	0.347	0.147	42.5%	7
Winter	Post-TDC	2020–2023	0.178	0.094	53.1%	4
Winter	Full Study	2013–2023	0.285	0.152	53.1%	11
Spring	Pre-TDC	2013–2019	0.408	0.151	36.9%	7
Spring	Post-TDC	2020–2023	0.304	0.063	20.6%	4
Spring	Full Study	2013–2023	0.371	0.132	35.7%	11

Winter run fish exhibited the highest interannual variability in isotopic niche size (CV = 53.1%), followed by spring run (CV = 35.7%) and fall run (CV = 35.5%), which was the most temporally stable (Table 2). Spring and Winter both became less variable during TDC (SD dropped), suggesting convergence on a narrower, more constrained niche. Fall run became more variable during TDC.

3.3.5 Comparison of Ellipse Area (SEA_B) Among Runs

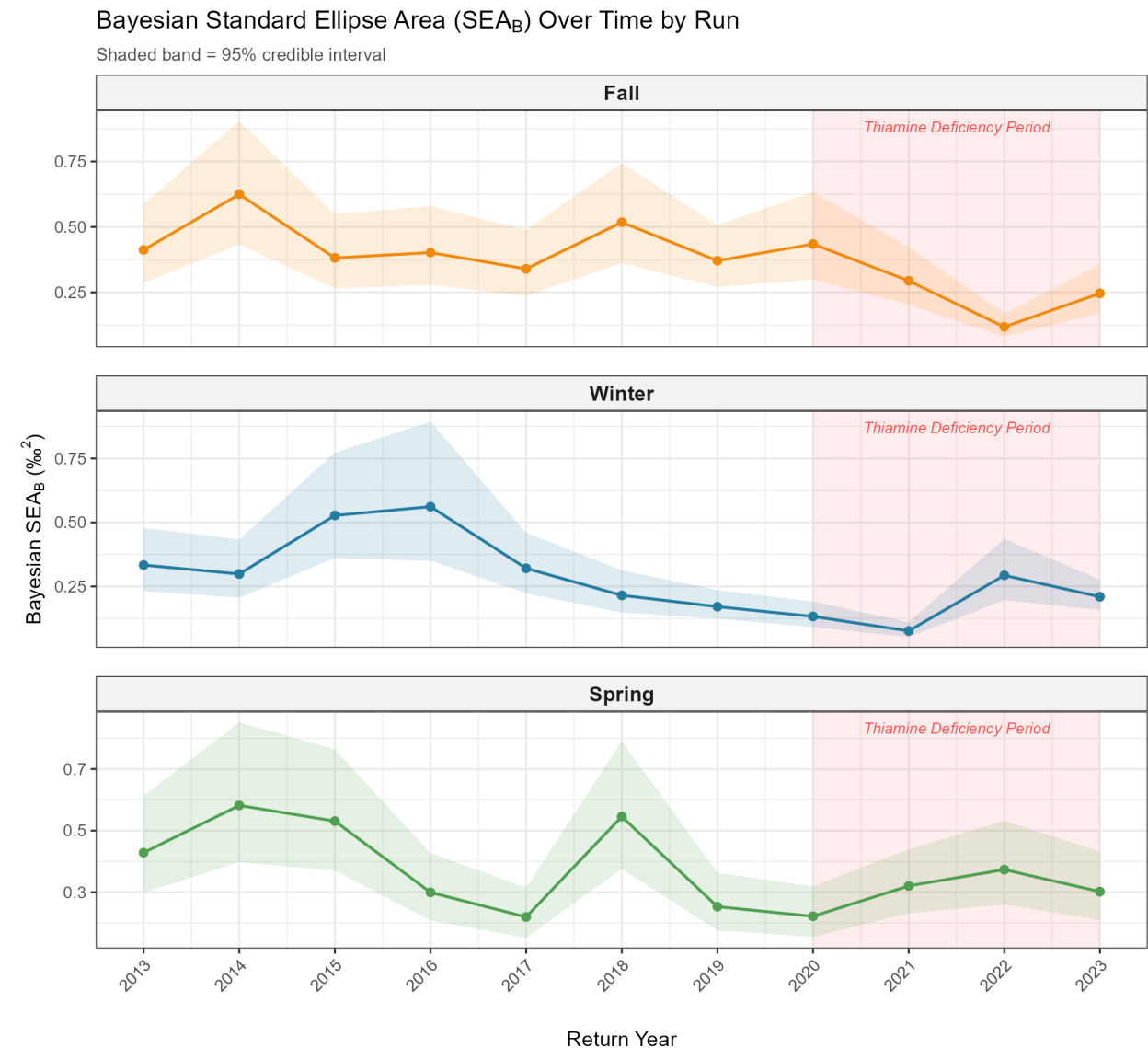


Figure 11: Mean SEA_B by run and year.

Time series of mean Bayesian standard ellipse area (SEA_B , $\% ^2$) for fall (orange), winter (blue), and spring (green) run Chinook salmon (2013–2023). Points represent annual cohort mean SEA_B values; error bars represent 95% credible intervals. Fall run: $n = 28$ –39 per cohort; winter run: $n = 18$ –50 per cohort; spring run: $n = 27$ –38 per cohort.

Fall run exhibited the largest mean ellipse area among observed years ($0.377\% ^2$) (Table 2) with spring close behind at $0.370\% ^2$. Winter run had the smallest SEA_B values, particularly during 2019–2021 (0.076 – $0.171\% ^2$). A Spearman correlation restricted to the period of niche contraction (2016–2021) indicated a strong and statistically significant declining trend in SEA_B for winter run ($\rho = -1.00$, $p = 0.0028$) (SI Appendix, Table S.3.1). Winter run experienced the largest proportional

decline between pre-TDC and TDC periods (-48.7%). After the onset of thiamine deficiency in 2020, isotopic niche size declined across all runs: winter run declined 49%, fall run 37%, and spring run 26%. Spring and winter both became less variable during TDC (SD dropped), suggesting a convergence on a narrower, more constrained niche. All three runs experienced substantial declines in SEA_B from their peak values to the low observed during the TDC period: winter run declined 86.5% from 2016 to 2021, fall run declined 77.2% from 2018 to 2022, and spring run declined 61.9% from 2014 to 2020 (SI Appendix, Table S.3.1).

3.3.6 Isotopic Niche Area (SEA_B) Before and During TDC

Isotopic Niche Area Before and After Thiamine Deficiency was Documented

Niche area = Bayesian Standard Ellipse Area per run–year | Darker = pre-thiamine deficiency; cross-hatched = thiamine deficiency per
 ◆ = group mean; Letters: Tukey-adjusted pairwise comparisons ($\alpha = 0.05$); groups sharing a letter are not significantly different

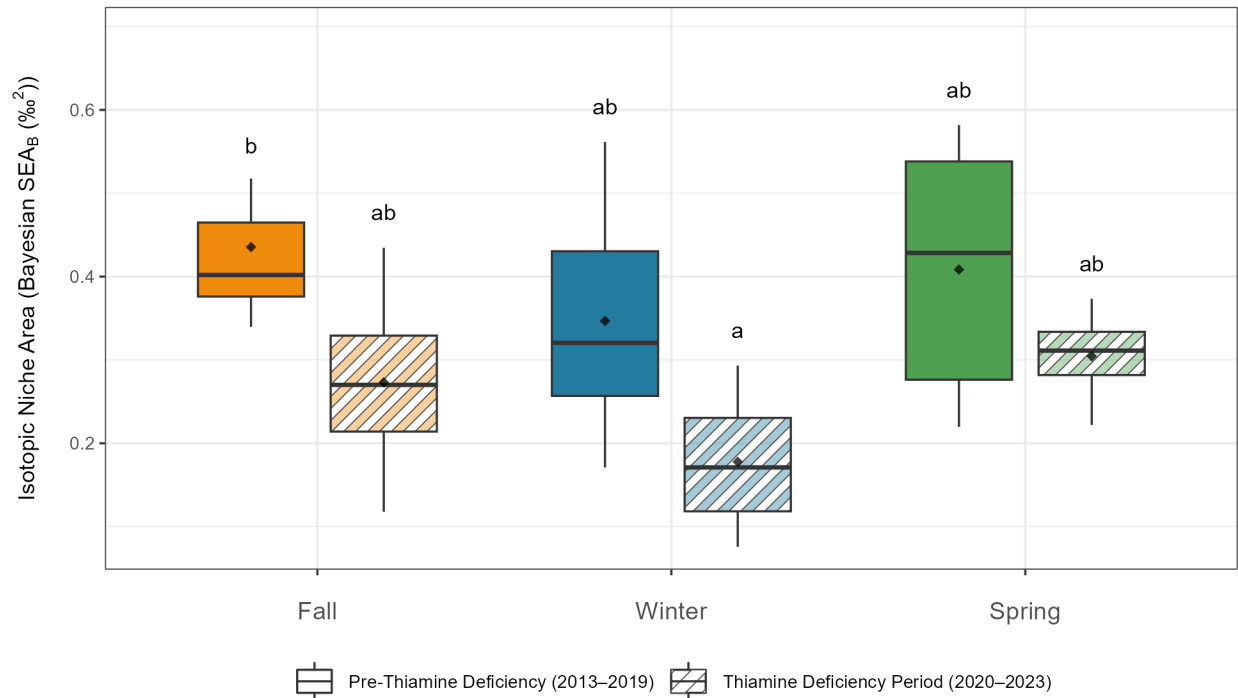


Figure 12: Isotopic niche area (Bayesian Standard Ellipse Area, SEA_B) before and during the thiamine deficiency period. Comparison of SEA_B between pre-thiamine deficiency (2013–2019) and thiamine deficiency period (2020–2023) for fall, winter, and spring run Chinook salmon. Boxplots summarize the distribution of annual posterior mean SEA_B values within each period (pre-thiamine deficiency: $n = 7$ years; thiamine deficiency period: $n = 4$ years); diamonds indicate period means. Colored boxes represent pre-thiamine deficiency values (run-specific colors); cross-hatched boxes represent thiamine deficiency period values. Letters denote Tukey-adjusted pairwise comparisons among all six run $\times$ period groups (linear model: $SEA_B \sim \text{run} \times \text{period}$; $\alpha = 0.05$); groups sharing a letter are not significantly different.

Isotopic niche area (SEA_B) declined across all three runs during the thiamine deficiency period, although the signal was weaker than the decline observed for trophic variability (Figure 12). Across runs, the thiamine deficiency period was associated with a significant reduction in niche area ($SEA_B = -0.162 \text{ ‰}^2$, $SE = 0.078$, $p = 0.047$), indicating a broad contraction in dietary niche space. However, the magnitude of decline did not differ among runs, and no individual run exhibited a statistically significant pre-to-thiamine deficiency period change after Tukey correction.

Of the 15 pairwise contrasts examined, only one reached significance: Fall run pre-thiamine deficiency vs. Winter run thiamine deficiency period (Tukey-adjusted $p = 0.029$). These represent the two most extreme groups in the dataset, and the result suggests that only the largest contrast between groups was detectable given the available sample size. Spring run pre-thiamine deficiency and Winter run thiamine deficiency period showed a similar trend but fell short of significance ($p = 0.063$). The compact letter display illustrates the limited resolution of these comparisons. Five of the six groups shared the same statistical grouping ("b" or "ab"), while Winter run thiamine deficiency period occupied the lowest end of the distribution ("a") and Fall run pre-thiamine deficiency occupied the highest ("b") (Figure 12).

Despite the limited statistical separation among groups, all three runs showed substantial reductions in mean niche area during the thiamine deficiency period. SEA_B declined by 37% in fall run (0.435 to 0.273 $\% \text{ } ^2$), 49% in winter run (0.347 to 0.178 $\% \text{ } ^2$), and 26% in spring run (0.408 to 0.304 $\% \text{ } ^2$). The consistency of these declines across runs suggests a system-wide contraction in dietary niche space associated with the emergence of thiamine deficiency. However, high interannual variability in SEA_B and the small number of thiamine deficiency period years ($n = 4$) limited the ability to resolve run-specific differences after correcting for multiple comparisons.

3.3.7 Within-Cohort $\delta^{15}\text{N}$ Variability Declined Over Time

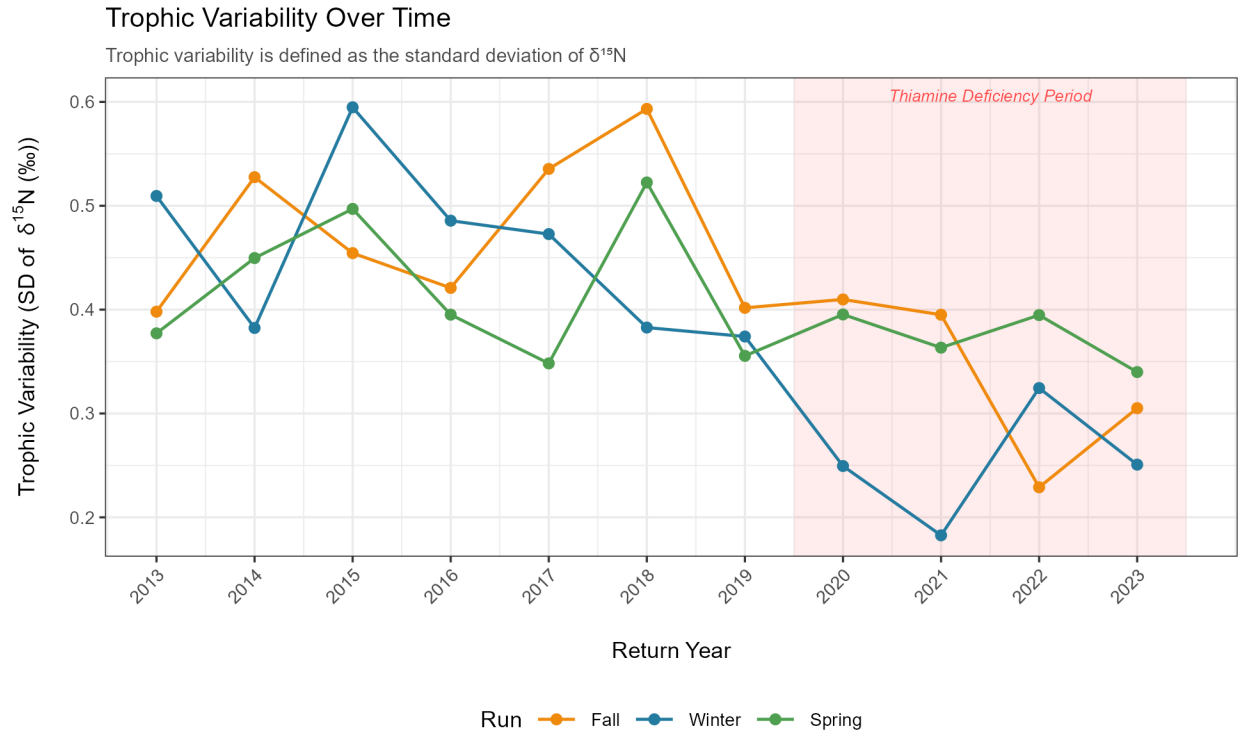


Figure 13: Within-cohort $\delta^{15}\text{N}$ standard deviation by run and year.
Time series of within-cohort $\delta^{15}\text{N}$ standard deviation (‰) for fall (orange), winter (blue), and spring (green) run Chinook salmon (2013–2023). Each point represents one run-year cohort (fall: $n = 28\text{--}39$; winter: $n = 18\text{--}50$; spring: $n = 27\text{--}38$).

3.3.8 Trophic Variability (SD of $\delta^{15}\text{N}$)- Before and During TDC

Trophic Variability Before and After Thiamine Deficiency was Documented

Trophic variability = SD of $\delta^{15}\text{N}$ per run-year | Darker = pre-thiamine deficiency; cross-hatched = thiamine deficiency period;
 ◆ = group mean; Letters: Tukey-adjusted pairwise comparisons ($\alpha = 0.05$); groups sharing a letter are not significantly different

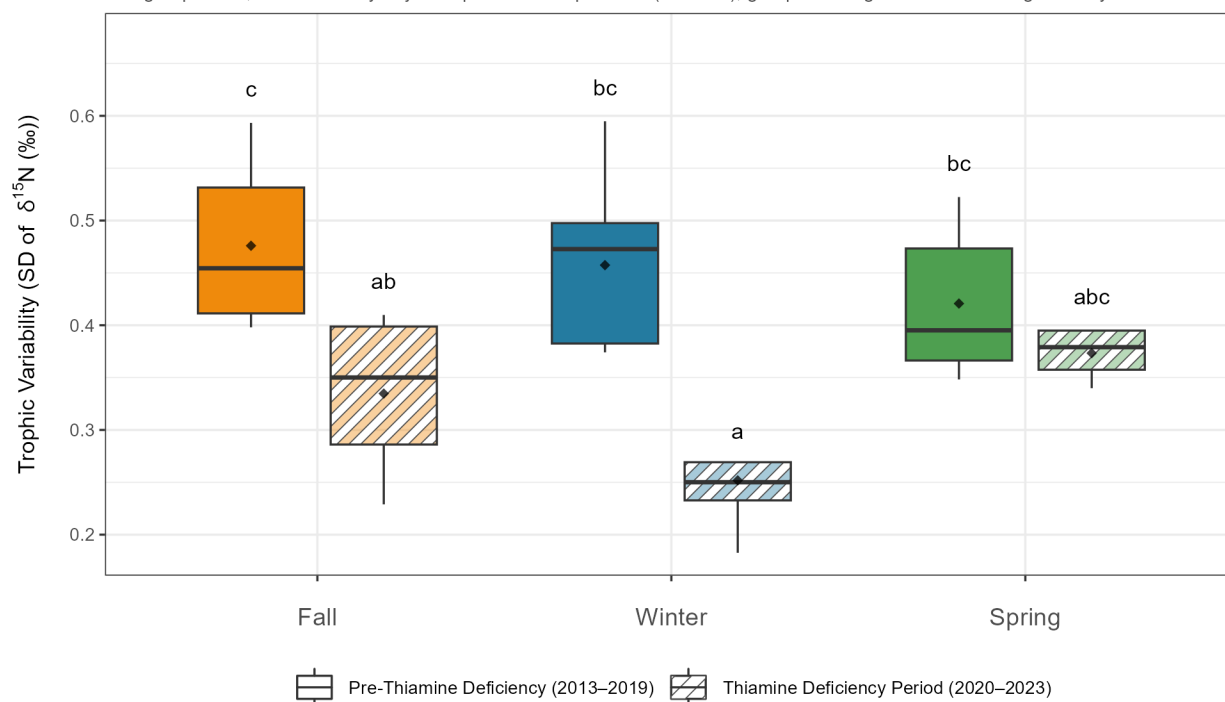


Figure 14: Trophic variability (within-cohort SD of $\delta^{15}\text{N}$) before and during the thiamine deficiency period. Comparison of within-cohort $\delta^{15}\text{N}$ variability between pre-TDC (2013–2019) and TDC (2020–2023) periods for fall, winter, and spring run Chinook salmon. Boxplots summarize the distribution of annual values within each period (pre-TDC: $n = 7$ years; TDC: $n = 4$ years); diamonds indicate period means. Colored boxes represent pre-TDC values (run-specific colors); cross-hatched boxes represent TDC values. Letters above each box indicate Tukey-adjusted pairwise comparisons among all six run $\times$ period groups (linear model: SD of $\delta^{15}\text{N} \sim \text{run} \times \text{period}$; $\alpha = 0.05$); groups sharing a letter are not significantly different.

Table 3: Mean $\delta^{15}\text{N}$ (‰) and within-cohort standard deviation (SD) by run and study period (pre-TDC: 2013–2019; post-TDC: 2020–2023; full study: 2013–2023).

RUN	PERIOD	YEARS	MEAN $\Delta^{15}\text{N}$	MEAN SD	N
Fall	Pre-TDC	2013–2019	14.511	0.476	7
Fall	Post-TDC	2020–2023	14.492	0.335	4
Fall	Full Study	2013–2023	14.504	0.425	11
Winter	Pre-TDC	2013–2019	15.566	0.457	7
Winter	Post-TDC	2020–2023	15.288	0.252	4
Winter	Full Study	2013–2023	15.465	0.383	11
Spring	Pre-TDC	2013–2019	14.810	0.421	7
Spring	Post-TDC	2020–2023	14.739	0.373	4
Spring	Full Study	2013–2023	14.784	0.403	11

Within-cohort $\delta^{15}\text{N}$ standard deviation varied both across runs and over time (Figure 13). A

linear model including run, period, and their interaction explained 55.6% of variance in within-

cohort $\delta^{15}\text{N}$ standard deviation ($F_{5,27} = 6.77$, $p < 0.001$). The TDC period was associated with a significant overall reduction in trophic variability ($\beta = -0.141$ ‰, $\text{SE} = 0.045$, $p = 0.004$). The run $\times$ period interaction was not significant (Winter $\times$ TDC: $p = 0.319$; Spring $\times$ TDC: $p = 0.151$), indicating the data do not support a statistically distinguishable difference in the magnitude of decline across runs at this sample size. Tukey-adjusted pairwise comparisons nevertheless revealed run-specific patterns in whether pre-to-TDC declines reached significance (Figure 13).

Winter run exhibited a pronounced decline in nitrogen variability over the study period, with a Spearman correlation indicating a significant monotonic decrease ($\rho = -0.82$, $p = 0.002$). From 2015 to 2021, the decline was perfectly monotonic ($\rho = -1.00$, $p < 0.001$), with standard deviation decreasing by 69% from 0.595‰ to 0.183‰. Standard deviation rebounded partially in 2022 (0.325‰) before declining again in 2023 (0.251‰). $\delta^{15}\text{N}$ variability was declining before the discovery of thiamine deficiency in 2020. Mean $\delta^{15}\text{N}$ standard deviation during the TDC period (2020–2023) was 0.252‰, compared to 0.457‰ during the pre-TDC period (2013–2019), representing a 45% decline (Table 3, Figure 14). This pre-to-TDC decline was statistically significant (Tukey-adjusted $p = 0.001$).

Fall run had the highest mean trophic variability ($\text{SD} = 0.425$ ‰) across the study period (2013–2023) (Figure 13). From 2013–2023, there was a marginally non-significant declining trend in nitrogen variability for fall run ($\rho = -0.58$, $p = 0.060$). Standard deviation was most variable during the pre-TDC period, ranging from 0.398‰ (2013) to 0.593‰ (2018), and declined to a minimum of 0.229‰ in 2022, the lowest single-year value observed for fall run. Mean standard deviation declined 30% from pre-TDC (0.476‰) to TDC (0.335‰) (Table 3, Figure 14). This decline was statistically significant (Tukey-adjusted $p = 0.042$).

Spring run showed no significant trend in nitrogen/trophic variability over time ($p = -0.43$, $p = 0.19$). Spring run had intermediate year to year variation in $\delta^{15}\text{N}$ from 2013–2023 (Mean $\text{SD}=0.403\text{‰}$) (Table 3). Standard deviation fluctuated between 0.340‰ and 0.522‰ across the study period with no consistent directional pattern. The decline from pre-TDC (0.421‰) to TDC (0.373‰) was modest (11%) relative to winter and fall runs (Figure 14). Consistent with this pattern, the pre-to-TDC difference for spring run was not statistically significant (Tukey-adjusted $p = 0.894$).

3.4 WITHIN-COHORT $\Delta^{15}\text{N}$ VARIABILITY BETTER PREDICTS EGG THIAMINE THAN SEA_B [HYPOTHESIS 2]

3.4.1 Ellipse Area (SEA_B) Does Not Predict Egg Thiamine Concentration

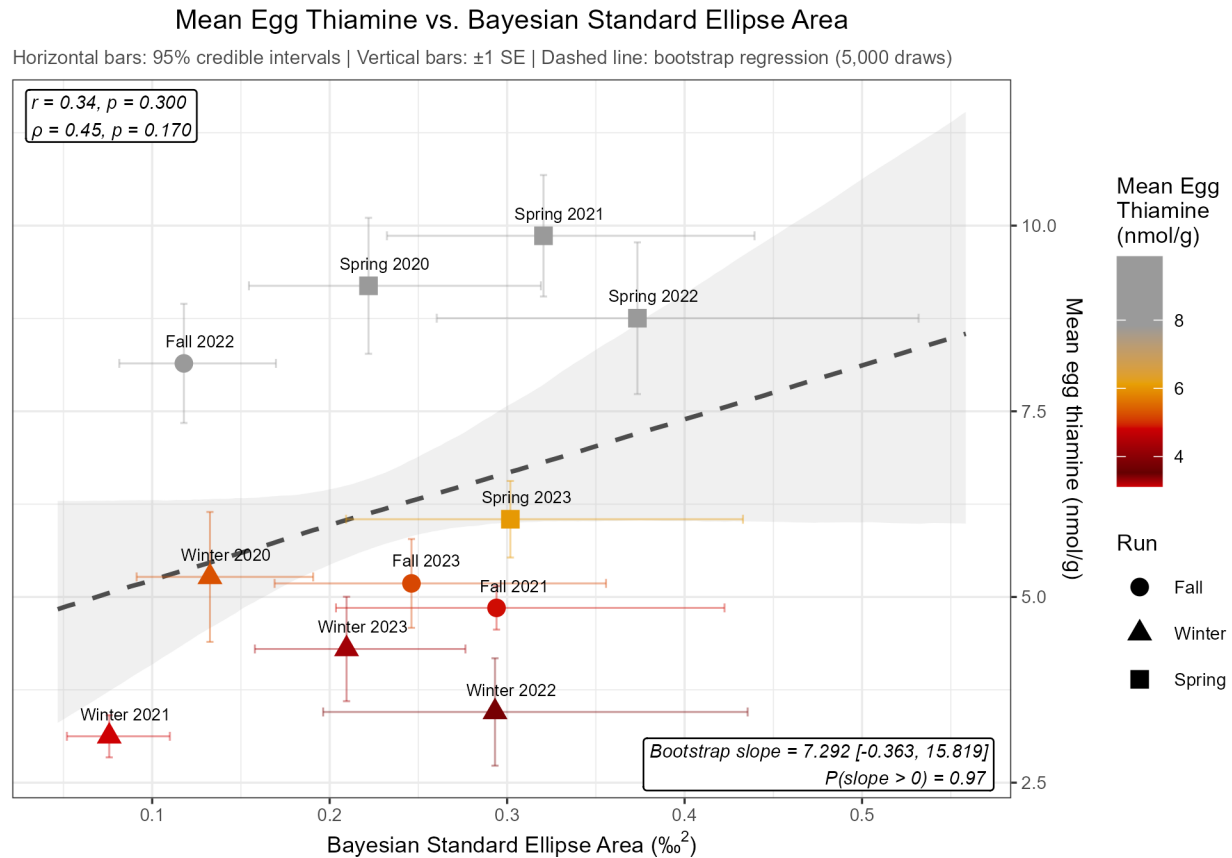


Figure 15: SEA_B versus egg thiamine concentration.

Mean egg thiamine concentration (nmol/g) plotted against Bayesian standard ellipse area (SEA_B , %²) for fall (circles), winter (triangles), and spring (squares) run Chinook salmon cohorts (2020–2023, $n = 11$ cohorts). Points are colored by thiamine status category: severely impacted (dark red; < 2.7 nmol/g), impacted (red; 2.7–5.9 nmol/g), likely impacted (yellow; 5.9–7.7 nmol/g), and unlikely impacted (grey; > 7.7 nmol/g). Points are labeled by run and return year. Horizontal error bars show 95% Bayesian credible intervals for SEA_B ; vertical error bars show ± 1 SE for mean egg thiamine. The dashed line and shaded ribbon show the median and 95% interval of a bootstrap regression (5,000 draws) that propagates uncertainty from both the SEA_B posterior distributions and thiamine standard errors into the slope estimate. The bottom-right inset reports the bootstrap slope with 95% bootstrap confidence interval and the posterior probability that the slope is positive. The top-left annotation reports Pearson r and Spearman ρ computed on point estimates. Egg thiamine data were unavailable prior to 2020.

To assess whether isotopic niche size was associated with thiamine level, mean SEA_B was plotted against mean egg thiamine concentration (nmol/g) for each cohort where egg thiamine data was available (2020–2023; $n = 11$; Figure 15). Egg thiamine data were unavailable prior to the documentation of thiamine deficiency, limiting this analysis to the thiamine deficiency period.

Because SEA_B is derived from a Bayesian model with posterior uncertainty on each point, and egg thiamine is a group mean with measurement error, a bootstrap regression (5,000 draws) was used to propagate both sources of uncertainty into the slope estimate rather than treating point estimates as exact. Each draw sampled one SEA_B value per cohort from its posterior distribution and added Gaussian noise to thiamine values proportional to their standard errors before fitting a regression line.

The bootstrap yielded a positive slope of 7.29 nmol/g per ‰² (95% bootstrap CI: -0.36 to 15.82), with 97% of draws producing a positive slope ($P(\text{slope} > 0) = 0.97$), indicating a consistent positive trend across all uncertainty realizations. However, the confidence interval includes zero, meaning the relationship does not meet the conventional threshold for statistical significance given the small sample size. Point-estimate correlations were similarly weak and non-significant (Pearson $r = 0.34$, $p = 0.30$; Spearman $\rho = 0.45$, $p = 0.17$), suggesting that the current sample size ($n = 11$, limited to 2020–2023) is insufficient to confirm the relationship statistically.

Since each run occupied distinct regions of the plot, with winter run cohorts clustering at lower egg thiamine values (3.1–5.3 nmol/g) and spring run cohorts at higher values (6.0–9.9 nmol/g), run identity is a likely confounding factor in this relationship. However, with only 11 observations, models formally accounting for run identity are underpowered and their results are not reported. In contrast, within-cohort trophic variability (SD of $\delta^{15}\text{N}$) showed a stronger association with egg thiamine (Pearson $r = 0.51$, $p = 0.10$; Spearman $\rho = 0.45$, $p = 0.17$; $n = 11$), though this also did not reach significance at the available sample size.

3.4.2 Trophic variability (SD of $\delta^{15}\text{N}$) is a Stronger Correlate of Egg Thiamine Than SEA_B

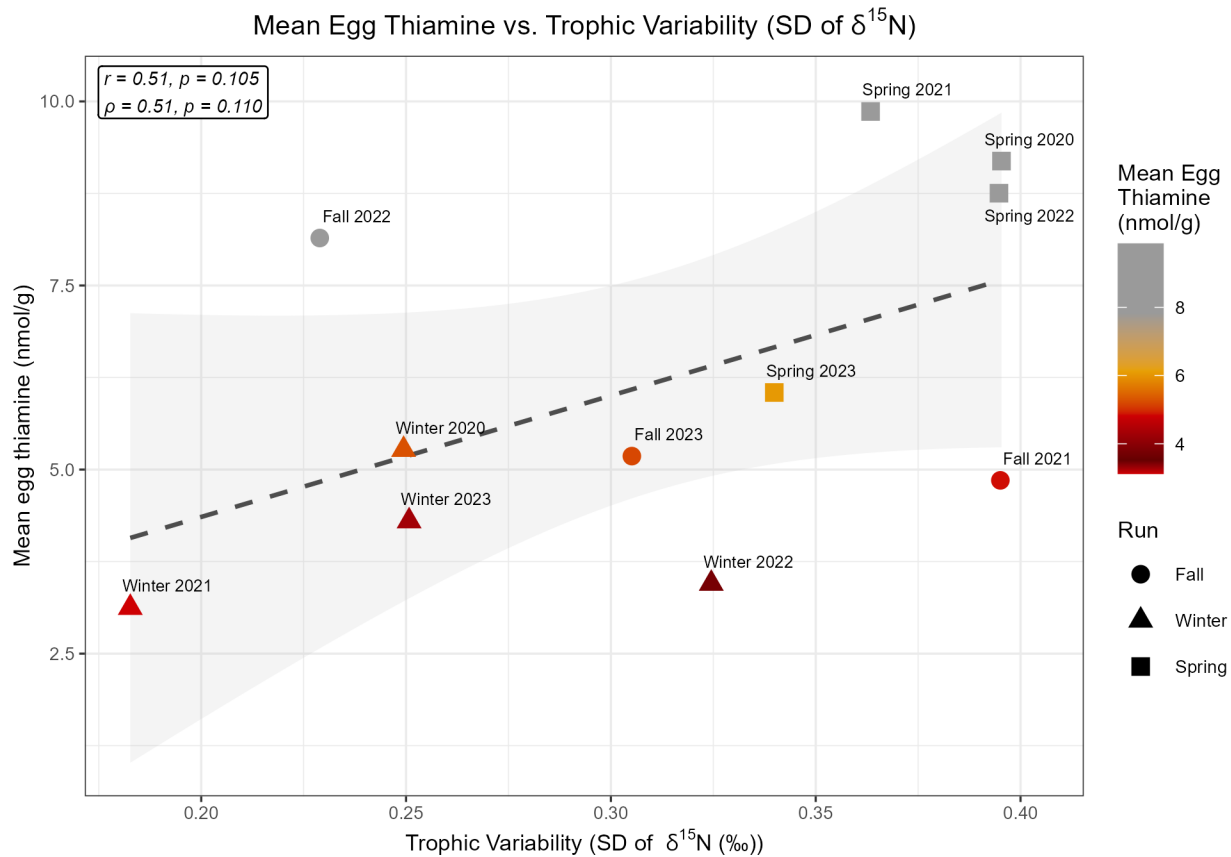


Figure 16: Trophic variability versus egg thiamine concentration.

Trophic variability (Within-cohort $\delta^{15}\text{N}$ standard deviation (‰)) plotted against mean egg thiamine concentration (nmol/g) for fall (circles), winter (triangles) and spring (squares). Chinook salmon cohorts from 2020–2023 ($n = 11$ cohorts). Points are colored by mean egg thiamine concentration, with colors corresponding to thiamine status categories: severely impacted (dark red; <2.7 nmol/g), impacted (red; 2.7 – 5.9 nmol/g), likely impacted (yellow; 5.9 – 7.7 nmol/g), and unlikely impacted (grey; >7.7 nmol/g). Points are labeled by run and return year. The dashed grey line shows the fitted linear regression between trophic variability (SD of $\delta^{15}\text{N}$) and mean egg thiamine concentration, and the shaded grey ribbon shows the 95% confidence interval around the regression line. The inset reports Pearson's correlation coefficient (r) and associated p -value, followed by Spearman's rank correlation coefficient (ρ) and associated p -value, computed on point estimates. Egg thiamine data were unavailable prior to 2020.

To assess whether trophic-level dietary diversity was associated with thiamine status, within-cohort $\delta^{15}\text{N}$ standard deviation was plotted against mean egg thiamine concentration for each run-year cohort with available egg thiamine data (2020–2023; $n = 11$; Figure 16). A positive trend was observed: cohorts with greater nitrogen variability tended to have higher egg thiamine concentrations. The Pearson correlation was moderate but did not reach statistical significance ($r = 0.51$, $p = 0.105$; Spearman $\rho = 0.51$, $p = 0.11$). The linear regression explained approximately 27%

of the variance in SD of $\delta^{15}\text{N}$ ($R^2 = 0.265$, $F(1,9) = 3.24$, $p = 0.11$), compared to 12% explained by the SEA_B -egg thiamine relationship ($R^2 = 0.118$, $p = 0.30$; Figure 15). When uncertainty in SEA_B estimates was propagated via bootstrap regression, the positive trend between SEA_B and egg thiamine was consistent across 97% of draws ($P(\text{slope} > 0) = 0.97$), but the bootstrap confidence interval included zero (95% CI: -0.36 to 15.82), reinforcing that SD of $\delta^{15}\text{N}$ is the more reliable correlate of egg thiamine concentration among the two metrics examined.

3.5 ISOTOPIC CONTRACTION PRECEDED THE FIRST DOCUMENTED THIAMINE DEFICIT [HYPOTHESIS 3]

The first measurements of egg thiamine concentration in Central Valley Chinook salmon were made in 2020, the year TDC was clinically detected and identified (Foott, 2020; Mantua et al., 2021). Hypothesis 3 predicted that detectable contraction in isotopic niche size and trophic variability preceded that first measurement. The scale record supports this prediction across all three runs, with the clearest signal in winter run.

Winter run SEA_B reached its maximum value in 2016 (0.562‰^2) and then declined steadily to 0.171‰^2 by 2019, representing a 70% reduction that occurred entirely before TDC monitoring began (Figure 8, SI Appendix, Table S.3.1). By the start of egg thiamine sampling in 2020 ($\text{SEA}_B = 0.133\text{‰}^2$), winter declined by 76% compared to its 2016 isotopic niche size. The decline from 2016 to 2021 was perfectly monotonic ($\rho = -1.00$, $p = 0.0028$) and began three years before the first egg thiamine measurements were collected. Winter run $\delta^{15}\text{N}$ variability showed the same pattern. Between 2015 and 2021, trophic variability (SD of $\delta^{15}\text{N}$) declined from 0.595‰ to 0.183‰ , a 69% reduction that also followed a perfectly monotonic trajectory ($\rho = -1.00$, $p < 0.001$; Figure 14). This decline in trophic variability began five years before the first egg thiamine measurement.

Spring run showed a more abrupt shift. SEA_B dropped from 0.545‰^2 in 2018 to 0.253‰^2 in 2019, a 54% decline in a single year occurring before TDC was identified (SI Appendix, Table S.3.1, Figure 9–10). Mean SEA_B averaged 0.434‰^2 from 2013–2018 but only 0.294‰^2 from 2019–2023, a 32% reduction driven largely by the sharp contraction observed in 2019. Fall run exhibited weaker evidence of pre-TDC change. trophic variability (SD of $\delta^{15}\text{N}$) declined marginally across 2013–2023 ($\rho = -0.58$, $p = 0.060$; Figure 14), with lower values appearing in 2017 and 2019 ahead of further decline during TDC.

Taken together, the scale record contained detectable signals of dietary contraction one to four years before any egg thiamine measurements were available. The clearest signals emerged in winter run, the run that would later exhibit the most severe thiamine deficiency, and in spring run immediately before TDC was first recognized. These results suggest that archived scales can reveal shifts in trophic structure before deficiency becomes apparent through direct monitoring. As a result, scale isotopes may serve as an early warning indicator of population-level vulnerability to thiamine deficiency, complementing egg thiamine surveillance rather than replacing it.

4 DISCUSSION

4.1 OVERVIEW

Stable isotope analysis of archived Chinook salmon scales reveals a consistent directional shift in marine foraging ecology across fall, winter, and spring runs for 2013–2023. All three runs show sustained contraction in isotopic niche size and declines in trophic variability, pointing to reduced dietary diversity during the marine phase. Among the metrics evaluated, trophic variability (SD of $\delta^{15}\text{N}$) consistently captured these changes more effectively than isotopic niche area (SEA_B), suggesting that contraction along the trophic axis was more closely linked to thiamine status than overall isotopic niche area. The three runs are genetically and ecologically distinct, with different ocean entry timing, geographic distributions, and migratory pathways. These differences expose each run to partially distinct foraging environments. Thus, the simultaneous contraction in diet across fall, winter, and spring run indicates a shared external driver rather than just run level responses. This pattern points to a broad, ecosystem scale shift in the marine food web.

The simplest explanation for this collective reduction in diet diversity is a restructuring of the California Current prey community toward northern anchovy dominance. This single forage species increasingly displaced a historically diverse prey assemblage (Thompson et al., 2019). As the numbers of anchovy increased, all three runs of Chinook salmon converged on a narrower, less thiamine replete diet. These contractions began before TDC was first documented in 2020, with the most pronounced changes occurring in the years immediately preceding its emergence. It is likely that thiamine deficiency was already present in some cohorts before 2020 but went undetected until the mass mortality event. Stable isotope analysis of archived scales identified a shift in marine diet, followed by a narrowing of dietary breadth that increased population vulnerability and ultimately led to thiamine deficiency.

Archived scale collections offer a way to detect these changes as they develop. Incorporating stable isotope monitoring into existing scale collection programs could provide an annual measure of diet diversity and overall population health. Together, these results demonstrate that archived scales serve as both a retrospective record and an early warning tool, capable of providing insight on population health trends before they manifest as mortality.

Chinook salmon are a cultural, ecological, and economic keystone in California. State and federal agencies invest millions of dollars each year to support and guarantee the survival of these populations. Most monitoring efforts focus heavily on freshwater systems, where stressors are immediate and measurable. High temperatures, reduced flows, dam barriers, and habitat degradation are well documented and actively managed. What happens to Chinook salmon once they enter the ocean, where they spend the majority of their lives and acquire more than 99% of their somatic growth (Welch & Parsons, 1993), remains far less understood.

4.2 CHANGING OCEAN FOOD WEBS

The isotopic contraction observed across all runs temporally aligns with a major disruption in the California Current. Beginning in fall 2013, a large warm temperature anomaly developed in the upper ocean of the Gulf of Alaska and spread broadly (Di Lorenzo & Mantua, 2016; Thompson et al., 2019). A strong El Niño in 2015–2016 extended these conditions throughout the water column, making it the warmest three-year interval in the system since 1920 (Thompson et al., 2019). This 2014–2016 Pacific marine heatwave was the largest recorded in the northeast Pacific, lasting over 700 days and elevating sea surface temperatures by more than 2°C above the mean (Gentemann et al., 2017). Marine heatwaves of this kind are projected to become more frequent and intense (Jacox et al., 2022), placing this event within a longer-term warming trend.

This event reorganized the ecosystem. Upwelling regions compressed shoreward, reducing the extent of cool, productive surface waters. As this habitat narrowed, krill declined and became less concentrated along the coast (Santora et al., 2020). Unlike krill, anchovy thrived during this reorganization. Northern anchovy recruitment surged in central California during 2015–2016 (Santora et al., 2020). Prior to 2015, anchovy had been depleted for over a decade. Anchovy (age 1+) biomass increased rapidly after 2015, reaching ~2.1 million metric tons by 2021, roughly 30–40 times higher than pre-2015 levels, and remained elevated through 2022 due to strong recruitment in 2015, 2019, and 2020 (Hinchliffe et al., 2025).

This increase diverges from the long-standing pattern linking anchovy to cool conditions and sardine to warm conditions (Chavez et al., 2003). Anchovy recruitment instead peaked under the warmest conditions on record (Thompson et al., 2019), indicating that previous thermal relationships no longer predict anchovy dynamics. This departure contrasts with the sardine–anchovy cycles documented in the Santa Barbara Basin sedimentary record for at least 2,000 years, in which anchovy dominated during cool, productive periods and sardine during warm, stratified conditions (Chavez et al., 2003; Checkley et al., 2017).

The unexpected success of anchovy under these warm conditions is not fully resolved, but several mechanisms have been proposed. Stratified conditions may have allowed larval prey to accumulate, improving survival (Lasker, 1985; Thompson et al., 2019). Anchovy also benefit from shorter, more efficient food chains during boom periods, including recent conditions (Swalethorp et al., 2023). In addition, the shoreward compression of upwelling habitat likely concentrated nutrients, plankton, and larvae into a narrower coastal band, increasing encounter rates between first-feeding larvae and their prey and reducing starvation mortality during the critical first-feeding period (Hinchliffe et al., 2025; Santora et al., 2020).

As anchovy expanded in both abundance and range, they became the dominant forage species across much of the California Current (Santora et al., 2020; Thompson et al., 2022).

Anchovy booms of this length are not unusual. The system has shifted between multi-decadal anchovy booms and busts for decades to millennia, and the current increase, now about a decade long, is shorter than the ~25-year boom from the 1960s to 1980s (Swailethorp et al., 2023). What is unusual is that this boom occurred under warm conditions, indicating that warming has altered the historical temperature–forage relationship. Anchovy dominance has reshaped predator diets across the system. Multiple pelagic predators converged on anchovy after 2015, including tuna, swordfish, seabirds, and sea lions (Portner et al., 2025).

This shift reflects a simpler prey field, not the disappearance of alternative prey. Most other forage species remained available at moderate to high abundance. Rockfish recruitment remained high through and after the heatwave, and other groundfish and squid populations persisted near typical levels (Thompson et al., 2022). Krill are the main exception, with below-average abundance through 2021, potentially due to grazing pressure from high anchovy biomass, though direct evidence is limited (Thompson et al., 2019). The system is therefore not prey-limited but dominated by a single species.

For Chinook salmon, the relevant consequence of anchovy dominance is not absolute prey scarcity but reduced dietary diversity combined with a specific biochemical cost associated with anchovy consumption (thiaminase). Central California Chinook salmon diet diversity has declined since 1955, with recent diets dominated by northern anchovy, euphausiids, and sardine (Thayer et al., 2017). A diet dominated by a single prey species reduces dietary buffering: when multiple prey are available, declines in one can be offset by increased consumption of others, stabilizing

predator energy intake and dampening the transmission of prey population variability to predator condition and reproductive success (Portner et al., 2025).

Anchovy are a particularly problematic dominant prey from a thiamine standpoint. Among the key forage taxa available to Chinook salmon in the ocean, anchovy have the highest thiaminase activity and the lowest thiamine content (Harder et al., 2018; Honeyfield et al., 2005; Mantua et al., 2025). Thiaminase I is an enzyme that degrades thiamine through a base-exchange reaction, catalytically cleaving the vitamin in the gut of consumers before it can be absorbed (Wolfe et al., 2023). Thus, a diet simultaneously low in thiamine and high in thiaminase activity creates a compounding depletion pathway (Harder et al., 2018; Honeyfield et al., 2005). A diet dominated by anchovy therefore both reduces thiamine intake and increases thiamine degradation. Furthermore, the high lipid content of anchovy may further amplify this effect by increasing oxidative stress and subsequently drawing down thiamine reserves (Keinänen et al., 2012; Mantua et al., 2025). Krill, juvenile rockfish, and herring, by contrast, provide thiamine and do not carry significant thiaminase loads. A Chinook salmon diet dominated by anchovy therefore simultaneously increases thiaminase exposure and reduces dietary thiamine intake. Sustained reliance on such a diet across the last feeding season would be expected to progressively deplete egg thiamine concentrations, exactly the pattern observed in the TDC data (Figure 4).

4.3 ARCHIVED SCALES AS A RETROSPECTIVE RECORD OF MARINE DIET

Understanding whether dietary changes preceded the emergence of TDC requires a retrospective record of marine feeding ecology. Fish scales provide one such tool. Scales have been collected for fisheries work for well over a century (Baltz, 1990; DeVries & Frie, 1996). In the late 1800s, scale annuli (annual growth rings) were established as a practical and rapid way to determine fish age and growth and to help distinguish stocks (Hoffbauer, 1898; Van Oosten, 1928).

Today, Chinook salmon scales are routinely collected by state and federal agencies as part of long-term monitoring programs. These collections have traditionally been used for age determinations and population reconstruction; however, they also represent an underutilized archive of biochemical information. The stable isotopes embedded in scale collagen record the assimilated diet of the fish during the most recent period of ocean growth (Hutchinson & Trueman, 2006; Tzadik et al., 2017). Applied systematically, stable isotope analysis of archived scales can reconstruct marine foraging patterns and trophic history at the population level across decades, without any new sampling infrastructure.

Given the substantial financial investment in salmon monitoring and recovery, integrating stable isotope analysis into existing sampling programs may provide additional ecological insight with little additional cost. Stable isotope analysis of fish scales does not require advanced materials or specialized training, and per-sample costs are low.

If anchovy dominance progressively narrowed the diets of foraging Chinook salmon, that narrowing should be detectable isotopically. A population feeding across diverse prey spanning a range of trophic levels will produce high $\delta^{15}\text{N}$ variability and broad isotopic ellipses in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space. A population converging on a single dominant prey will show the opposite: contracted ellipses and reduced trophic variability. The central question this study asks is whether archived scales from returning Chinook salmon show that pattern, and whether it preceded the clinical emergence of TDC.

4.4 DISTINCT MARINE FORAGING NICHES AMONG CHINOOK SALMON RUNS

A foundational result of this study is the consistent separation among fall, winter, and spring run Chinook salmon in isotopic space (Figure 2). Each run occupied a distinct region of the

$\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bivariate plane, and this separation was stable across all eleven years of the study. This spatial separation amongst runs indicates that each run occupies a unique marine foraging niche. The three runs are more different from one another isotopically than any single run varies across years: mean between-run centroid distance was 0.910‰, compared to 0.671‰ for within-run variation across years (SI Appendix, Table S.2.1). A PERMANOVA found a statistically significant difference between runs. Run explained 64.5% of isotopic variation ($R^2 = 0.645$) (PERMANOVA: $F = 54.74$, $p = 0.001$), indicating extremely strong and statistically robust separation of marine trophic niches among fall, spring, and winter runs.

When comparing run to run, fall and winter run were the most isotopically dissimilar (mean centroid distance 1.145‰). The most similar were fall and spring runs (0.660‰; SI Appendix, Table S.2.2). Winter run consistently had the highest $\delta^{15}\text{N}$ values (mean: 15.46‰), suggesting feeding at the highest trophic levels. Fall run had the lowest mean $\delta^{15}\text{N}$ (14.50‰), and spring run was intermediate (14.78‰; Figure 3). These differences in mean $\delta^{15}\text{N}$ likely reflect genuine ecological divergence: winter and spring runs have slightly different geographic distributions relative to fall run (Jensen et al., 2023; R. C. Johnson et al., 2016), and their earlier ocean entry timing and different migratory corridors expose them to distinct prey communities during the critical marine growth period (Hertz et al., 2015).

The persistence of isotopic niche separation across years (despite the interannual variability in oceanographic conditions) supports that these are real ecological differences, not sampling artifacts. This consistent run separation also provides a stable baseline for interpreting temporal trends: year to year changes in niche size or trophic diversity can be evaluated within a run specific reference frame, rather than being conflated by the large isotopic differences that exist between runs.

All three runs experienced substantial declines in Bayesian standard ellipse area (SEA_B) over the study period, with the most pronounced contraction during or immediately preceding the TDC period (2020–2023; Figure 11). These contractions were not uniform: the magnitude, timing, and direction of niche contraction varied by run in ways that reveal differences in the mechanisms involved and each population's relative vulnerability. Critically, this contraction preceded the clinical emergence of thiamine deficiency by several years, suggesting isotopic monitoring could serve as an early warning tool.

4.5 ISOTOPIC NICHE CONTRACTION ACROSS RUNS

4.5.1 Winter Run

Winter run Chinook salmon had the earliest and most extreme isotopic contraction. SEA_B peaked in 2016 (0.562‰^2), then declined progressively and nearly without interruption for five years, reaching a minimum of 0.076‰^2 in 2021, an 87% reduction from the 2016 peak and the lowest ellipse area observed for any cohort in this study (SI Appendix, Table S.3.1, Figure 7). The contraction from 2016–2019 is particularly striking: over just three years SEA_B declined approximately 70% (from 0.562‰^2 in 2016 to 0.171‰^2 in 2019), right before thiamine deficiency complex was first documented. This sharp reduction in ellipse area implies a strong constraint on dietary or isotopic inputs during this time. This may suggest diminished prey diversity, reduced habitat breadth and reliance on a limited subset of forage species during this time. Trophic variability (within-cohort SD of $\delta^{15}\text{N}$) is used here as a complementary metric to SEA_B because it isolates the trophic dimension of niche area specifically by eliminating the influence from $\delta^{13}\text{C}$ on ellipse area.

The bulk of this contraction in ellipse area occurred before thiamine deficiency was detected. Egg thiamine concentrations were not measured in California Chinook salmon until

2020, meaning there is no pre-2020 thiamine baseline for comparison. However, the temporal pattern in the isotopic record is unmistakable: by the time thiamine deficiency was first documented in winter run Chinook salmon in 2020, their isotopic niche had already contracted by approximately 76% from its 2016 maximum. The dietary restructuring of the California current ecosystem that produced the conditions for TDC was well underway years before the clinical signal appeared. Isotopic niche metrics could function as leading indicators of population level vulnerability like thiamine deficiency risk, which was detectable from archived scales years before egg thiamine sampling revealed a problem.

Following the 2021 minimum, SEA_B nearly quadrupled in 2022 (0.293‰^2), suggesting a partial recovery of dietary diversity (Figure 8). This recovery may reflect improved upwelling conditions during the winter run's primary feeding window (January–April) in early 2022 (Harvey et al., 2023). However, the improvement was short-lived: ellipse area declined again in 2023 (0.210‰^2), and TDC prevalence continued to worsen, the proportion of winter run females classified as "severely impacted" reached 54% in 2023, up from 7% in 2020 (Figure 4). The rebound in isotopic diversity did not translate into a rapid recovery of thiamine status, suggesting that either the improvement was insufficient in magnitude or duration, or that there is a lag between dietary improvement and egg thiamine accumulation. Notably, within run nitrogen variability (SD of $\delta^{15}\text{N}$) showed a more muted recovery in 2022 (0.325‰ , 71% of the pre-TDC mean) than SEA_B (84% of pre-TDC mean), suggesting that while winter run fish ranged more broadly in isotopic space in 2022, trophic-level dietary diversity, the dimension more linked to thiamine status, did not recover proportionally. This dissociation between overall niche expansion and trophic diversity recovery may help explain why egg thiamine concentrations remained critically low despite the apparent improvement in niche size.

4.5.2 Fall Run

Fall run had the broadest mean isotopic niche of the three runs (mean $SEA_B = 0.376\text{‰}^2$), the lowest mean $\delta^{15}N$ ($\sim 14.50\text{‰}$) and was the most temporally stable prior to the TDC period (coefficient of variation = 23.1% for 2013–2019; Table 2, Table 3). Unlike winter run, fall run did not exhibit a monotonic decline over the study period (Figure 6). Instead, niche size remained relatively elevated through 2018 (0.518‰^2) and even rebounded in 2020 (0.435‰^2), suggesting that fall run maintained some dietary flexibility during the early TDC period (SI Appendix, Table S.3.1). This is consistent with fall run's broader geographic range and later ocean entry timing (Satterthwaite et al., 2014), which may have provided access to a more diverse prey field during the critical pre-spawning feeding period.

Despite their apparent resilience, fall run experienced a dramatic collapse in niche size. From 2021 to 2022, SEA_B declined 0.294‰^2 to 0.118‰^2 , a 60% drop in a single year, the largest proportional single-year decline observed for any run in this study. By 2022, fall run SEA_B had declined 77.2% from its 2018 peak. This pattern suggests a threshold effect (Scheffer et al., 2001): fall run maintained dietary diversity longer than winter or spring run, but once conditions deteriorated sufficiently, driven by sustained anchovy dominance in the late 2010s and early 2020s (Harvey et al., 2023; Swalethorp et al., 2023; Thompson et al., 2022), the niche collapsed abruptly rather than gradually. TDC prevalence in fall run was correspondingly erratic: severe in 2021 (93% affected), partially improved in 2022 (48% in the two most severe categories), then worsening again in 2023 (72%) (Figure 4). The isotopic variability during TDC ($CV = 47.9\%$) was higher than the pre-TDC period (23.1%), reflecting this boom-bust pattern.

4.5.3 Spring Run

Spring run demonstrated interannual variability in ellipse area across the study period (2013–2023) (Figure 9–Figure 10; SI Appendix, Table S.3.1). They occupied an intermediate position in both niche size and thiamine deficiency vulnerability. Niche size was broad in 2014 (0.582‰^2) and 2018 (0.545‰^2), both of which are years marked by weak or neutral ENSO forcing, which has historically supported diverse prey communities in the California Current (Thompson et al., 2019). Niche size declined substantially beginning in 2019. Mean SEA_B during 2013–2018 was 0.434‰^2 , compared to 0.294‰^2 during 2019–2023, a 32% reduction (SI Appendix, Table S.3.1, Figure 10). As with winter run, this contraction began before 2020, suggesting the dietary shift that accompanied or preceded TDC was already underway before thiamine sampling could detect it.

Nitrogen variability (SD of $\delta^{15}\text{N}$) declined from 0.421‰ (pre-TDC) to 0.373‰ (TDC period), an 11% reduction, smaller than the declines observed in winter (–45%) and fall (–30%) runs but consistent with spring run's moderate worsening trajectory. TDC prevalence in spring run was the lowest of the three runs but still showed a clear decline. The proportion of severely impacted fish increased from 0% in 2020 to 20.0% in 2023. The combined proportion of impacted and severely impacted fish rose from 27.6% to 43.3% over the same period (Figure 4). The broad niche sizes observed for spring run in 2014 and 2018, followed by sustained contraction, are consistent with a run whose dietary diversity is sensitive to interannual oceanographic conditions and is currently under sustained pressure from prey community change.

4.5.4 Run Comparison

The three runs differ substantially in the timing, magnitude, and pattern of isotopic contraction, but all show the same directional trend. Winter run experienced the earliest and most severe contraction, with a near-monotonic decline beginning in 2016 and a 87% reduction in SEA_B

by 2021. Spring run showed a more gradual decline, with broad niches in neutral ENSO years and sustained contraction beginning in 2019. Fall run was the most stable prior to the TDC period but underwent the sharpest single-year collapse, a 60% drop in SEA_B between 2021 and 2022, consistent with a threshold response rather than a gradual transition. Across all three runs, trophic variability (SD of $\delta^{15}N$) declined during the TDC period, suggesting a convergence on a narrower, more constrained dietary niche. The fact that three genetically and ecologically distinct runs, exposed to partially different foraging environments, all show this directional shift points to a shared ecosystem-scale driver rather than run-specific anomalies.

The narrowing patterns in isotopic niche size (SEA_B) and trophic variability (SD of $\delta^{15}N$) coincide with the dramatic increase in northern anchovy (*Engraulis mordax*) abundance along the California coast during the late 2010s and especially the early 2020s. Figure 17 illustrates the geographic expansion of anchovy in fisheries catches from 2017 to 2021, a shift that transformed the prey landscape available to foraging Chinook salmon. Diet studies of adult Chinook salmon in the central California Current during this period found that stomach contents were overwhelmingly composed of anchovy, reaching 98% of gut content biomass in 2020, 89% in 2021, and 100% in 2022, compared to historical samples where anchovy averaged 49% and alternative prey such as krill, juvenile rockfish, squid, and herring were consistently represented (Mantua et al., 2025).

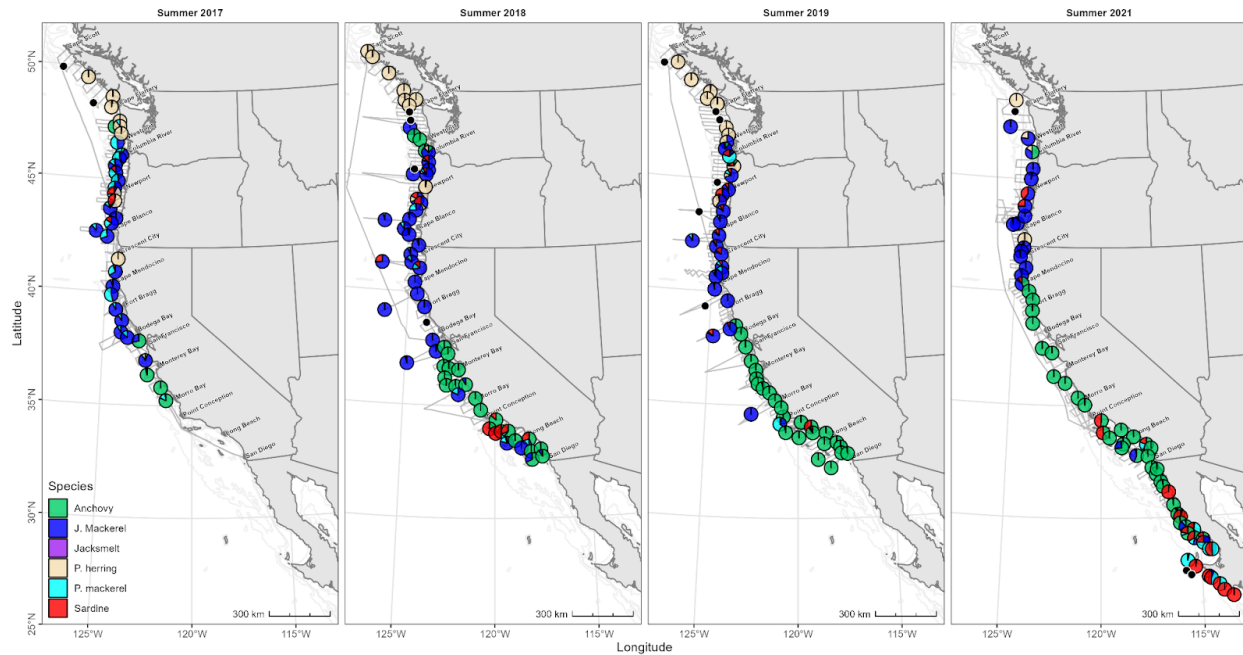


Figure 17: Anchovy increase along the California coast, 2017–2021. Geographic distribution of anchovy in California coastal fisheries catches (2017–2021). Pie charts indicate catch composition by area, with green representing northern anchovy and blue representing jack mackerel. Figure from Mantua et al., 2025.

The isotopic data are consistent with this mechanism. The contraction of SEA_B and the decline in within run $\delta^{15}N$ standard deviation both reflect dietary narrowing, a convergence on fewer prey types spanning a narrower range of trophic levels. The association between trophic variability and egg thiamine concentration ($r = 0.51$, $p = 0.11$; Figure 16), while falling short of conventional significance thresholds given the limited number of annual observations available, accounts for 27% of the variance in egg thiamine and aligns with the anchovy-dominance hypothesis. As more individuals within a cohort converge on anchovy, the spread of $\delta^{15}N$ values across the cohort decreases. When diet is diverse and individuals are feeding on krill, squid, juvenile rockfish, and other prey, the cohort spans a wide range of trophic positions, producing high $\delta^{15}N$ variability and broad isotopic ellipses. When diet narrows due to anchovy dominance, that trophic variability collapses: individuals cluster at similar isotopic values, the ellipse contracts, and SD of $\delta^{15}N$ declines. Lower SD of $\delta^{15}N$ therefore signals fewer individuals foraging on krill,

squid, or juvenile fish, which means less dietary thiamine and greater thiaminase exposure at the population level.

4.6 $\Delta^{15}\text{N}$ VARIABILITY AND SEA_B AS CORRELATES OF EGG THIAMINE

A notable analytical result of this study is the differing performance of SEA_B and $\delta^{15}\text{N}$ standard deviation as indicators of TDC related dietary change. Bootstrap regression propagating uncertainty from both SEA_B posterior distributions and thiamine measurement error yielded a consistently positive slope (7.29 nmol/g per ‰², 95% CI: -0.36 to 15.82; $P(\text{slope} > 0) = 0.97$), but the confidence interval included zero, indicating the relationship did not reach statistical significance at the available sample size ($n = 11$; Pearson $r = 0.34$, $p = 0.30$; Figure 15). These results indicate that overall isotopic niche size is not strongly associated with thiamine status, though the consistently positive direction across bootstrap draws leaves open the possibility of a real relationship that the current dataset is underpowered in confirming. In contrast, $\delta^{15}\text{N}$ standard deviation showed a moderate positive association with egg thiamine concentration ($r = 0.51$, $p = 0.11$; $R^2 = 0.265$; Figure 16). Although this relationship was not statistically significant, SD of $\delta^{15}\text{N}$ explained approximately twice as much variation in egg thiamine as SEA_B ($\approx 27\%$ vs. $\approx 12\%$ based on point-estimate OLS; bootstrap analysis of SEA_B confirmed the positive direction but not significance), indicating that trophic variability shows a stronger relationship with egg thiamine than overall isotopic niche area.

This contrast between SEA_B and SD of $\delta^{15}\text{N}$ reflects the fundamental difference in what each parameter captures. SEA_B integrates variation across both isotopic axes, which makes it sensitive to spatial differences in where individual fish were foraging, particularly the nearshore vs. offshore gradient in $\delta^{13}\text{C}$ (Bearhop et al., 2004; Hertz et al., 2015; S. P. Johnson & Schindler, 2012). In a cohort feeding predominantly on anchovy, for example, two fish eating the same prey at the

same trophic level could have very different $\delta^{13}\text{C}$ values depending on whether that prey originated from nearshore or offshore habitats. This can produce a wide, thin ellipse characterized by substantial carbon variation but little trophic variation, a pattern especially apparent in spring run fish (Figure 9). This spatial carbon variation inflates SEA_B without reflecting any meaningful difference in diet or thiamine exposure, weakening its relationship with TDC.

The stronger statistical signal in trophic variability (SD of $\delta^{15}\text{N}$; $R^2 = 0.556$, multiple significant pairwise comparisons) relative to isotopic niche area (SEA_B ; one significant pairwise comparison) suggests that the nitrogen dimension of isotopic space contracted more consistently during the thiamine deficiency period than the carbon dimension. While $\delta^{13}\text{C}$ variability also declined across runs (fall: 20%, winter: 10%, spring: 17%), the reductions were smaller in magnitude and less consistent than those in $\delta^{15}\text{N}$ (fall: 30%, winter: 45%, spring: 11%), particularly for winter run where $\delta^{13}\text{C}$ variability partially rebounded in 2022–2023. This mixed carbon signal likely diluted the period effect in SEA_B , which integrates both isotopic dimensions simultaneously.

4.7 ISOTOPIC CONTRACTION PRECEDED DOCUMENTED TDC

The protocols for responding to TDC in hatchery fish are now established: since TDC was first detected in 2020, fertilized eggs have been treated with thiamine baths at the time of fertilization, a protocol piloted by CDFW Fish Health Lab staff (CDFW, unpublished), along with prespawn thiamine injections to adult females (Bell, 2022; Mantua et al., 2025). An earlier warning of increasing population-level vulnerability changes whether agencies are prepared when they need to be. Without a warning, agencies have little time to respond, as happened in 2020 when a cohort arrived 89% impacted by thiamine deficiency complex.

The temporal link between isotopic niche contraction and the emergence of thiamine deficiency is among the more consequential findings of this study. In winter run, SEA_B began declining in 2017, three years before thiamine deficiency complex was first documented, and by 2019 the niche had already contracted approximately 70% from its 2016 peak. Spring run shows a similar pattern: SEA_B dropped sharply in 2019, a full year before thiamine data were first available. By the time TDC was formally documented in Central Valley Chinook salmon in 2020, all runs were already severely affected, with 89% of sampled winter run females that first year classified as impacted (Mantua et al., 2025). Had the $\delta^{13}C$ and $\delta^{15}N$ isotopes in those scales been analyzed, a clear and progressive narrowing of the marine diet would have been visible for winter run as early as 2017, and for spring and fall run by 2019, years before TDC was ever detected.

If trophic variability (SD of $\delta^{15}N$) in a cohort's scales fell below an empirically established threshold, hatchery managers would have advance indication to prepare supplementation resources and protocols for the future cohort. For wild fish, which have no direct treatment options currently available, the primary benefit of earlier warning would be enhanced monitoring, allowing agencies to focus spawning surveys and redd assessments in high-risk years, providing earlier detection of fry mortality and TDC symptoms in natural redds (Mantua et al., 2025). If stable isotope signatures, particularly SD of $\delta^{15}N$, were monitored annually from routinely collected scales, they could provide advance notice that a cohort's marine diet has been narrowing and that elevated vulnerability should be anticipated.

This study shows that food web simplification driven by oceanographic change can be detected in archived biological tissues before it manifests as a population-level health issue. That lead time is a management opportunity. The simultaneous contraction of isotopic niche area across three genetically and ecologically distinct Chinook salmon runs points to an ecosystem-

scale driver rather than a population-specific anomaly. Fall, winter, and spring run differ in ocean entry timing, geographic distribution, and life history, yet all show the same directional trend. The most straightforward explanation is a shared restructuring of the California Current prey community toward anchovy dominance. This kind of food web simplification reduces predator resilience: when salmon lack dietary alternatives, a bad anchovy year becomes a bad salmon year. Stable isotope monitoring of archived or newly collected scales, focused on trophic variability as a dietary breadth index, could provide an annual read on whether prey conditions that support diverse and thiamine replete diets are present for each run. Most agencies already collect scales from returning adults at weirs, traps, and hatcheries; adding a modest stable isotope analysis component to existing protocols could yield substantial management insight at relatively low cost.

5 CONCLUSION

This study extends a growing body of work demonstrating that stable isotope analysis of archived Chinook salmon scales can serve as a retrospective window into marine foraging history (Lowe-Webb et al., in prep; S. P. Johnson & Schindler, 2012; Satterfield & Finney, 2002), and applies that approach to a new question: whether multi-year trends in isotopic niche size and trophic diversity are associated with the emergence of thiamine deficiency in Central Valley Chinook salmon. All three runs examined experienced sustained contraction in isotopic niche area during or preceding the documented TDC period, with winter run showing the most extreme and earliest decline. Trophic variability (SD of $\delta^{15}\text{N}$) showed a stronger directional association with egg thiamine concentration than SEA_B , suggesting that trophic narrowing is a more relevant signal of thiamine deficiency risk than general niche contraction (SEA_B). Most importantly, the isotopic decline preceded clinical detection of TDC by several years in winter and spring runs. This temporal lead suggests that isotopes in scales may function as early-warning indicators of thiamine deficiency

risk. Integrating routine stable isotope analysis into existing scale sampling protocols could provide agencies with a cost-effective, retrospective, and potentially predictive tool for monitoring the marine dietary conditions driving one of the most significant emerging threats to California's Chinook salmon populations.

REFERENCES

- Amcoff, P., Börjeson, H., Landergren, P., Vallin, L., & Norrgren, L. (1999). Thiamine (vitamin B1) concentrations in salmon (*Salmo salar*), brown trout (*Salmo trutta*) and cod (*Gadus morhua*) from the Baltic Sea. *Ambio*, 28, 48–54.
- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26(1), 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62(1), 245–253. <https://doi.org/10.1111/j.1541-0420.2005.00440.x>
- Baltz, D. M. (1990). Autecology. In C. B. Schreck & P. B. Moyle (Eds.), *Methods for Fish Biology* (pp. 585–607). American Fisheries Society.
- Bearhop, S., Adams, C. E., Waldron, S., Fuller, R. A., & Macleod, H. (2004). Determining trophic niche width: A novel approach using stable isotope analysis. *Journal of Animal Ecology*, 73(5), 1007–1012. <https://doi.org/10.1111/j.0021-8790.2004.00861.x>
- Bell, H. N. (2022). *Assessment of the effects of thiamine deficiency on the survival, physiology, and behavior of early life-stage winter-run chinook salmon* (Master's Thesis) [UC Davis]. <https://escholarship.org/uc/item/465026qq>
- Cederholm, C. J., Johnson, D. H., Bilby, R. E., Dominguez, L. G., Garrett, A. M., Graeber, W. H., Greda, E. L., Kunze, M. D., Marcot, B. G., Palmisano, J. F., Plotnikoff, R. W., Pearcy, W. G., Simenstad, C. A., & Trotter, P. C. (2000). *Pacific salmon and wildlife: Ecological contexts, relationships, and implications for management* [Special Edition Technical Report]. Washington Department of Fish and Wildlife. <https://wdfw.wa.gov/sites/default/files/publications/00063/wdfw00063.pdf>

- Chavez, F. P., Ryan, J., Lluch-Cota, S. E., & Niquen, M. (2003). From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science*, 299, 217–221.
<https://doi.org/10.1126/science.1075880>
- Checkley, D. M., Asch, R. G., & Rykaczewski, R. R. (2017). Climate, Anchovy, and Sardine. *Annual Review of Marine Science*, 9(1), 469–493. <https://doi.org/10.1146/annurev-marine-122414-033819>
- Checkley, D. M., & Barth, J. A. (2009). Patterns and processes in the California Current System. *Progress in Oceanography*, 83(1–4), 49–64. <https://doi.org/10.1016/j.pocean.2009.07.028>
- Clutter, R., & Whitesel, L. (1956). *Collection and Interpretation of Sockeye Salmon Scales* (Vol. 9). International Pacific Salmon Fisheries Commission Bulletin.
- DeNiro, M. J., & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, 42(5), 495–506.
[https://doi.org/10.1016/0016-7037\(78\)90199-0](https://doi.org/10.1016/0016-7037(78)90199-0)
- DeNiro, M. J., & Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, 45(3), 341–351.
[https://doi.org/10.1016/0016-7037\(81\)90244-1](https://doi.org/10.1016/0016-7037(81)90244-1)
- DeVries, R., & Frie, R. (1996). Determination of age and growth. In B. R. Murphy & D. W. Willis (Eds.), *Fisheries Techniques* (2nd edition, pp. 483–512). American Fisheries Society.
- Di Lorenzo, E., & Mantua, N. J. (2016). Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nature Climate Change*, 6(11), 1042–1047.
<https://doi.org/10.1038/nclimate3082>

- Eaton, S. M. (2015). *Salmon Age, Sex, and Length (ASL) Sampling Procedures for the Arctic-Yukon-Kuskokwim Region*. (Regional Information Report Nos. 3A15-04). Alaska Department of Fish and Game Divisions of Sport Fish and Commercial Fisheries.
- Espinasse, B., Hunt, B. P. V., Finney, B. P., Fryer, J. K., Bugaev, A. V., & Pakhomov, E. A. (2020). Using stable isotopes to infer stock-specific high-seas distribution of maturing sockeye salmon in the North Pacific. *Ecology and Evolution*, 10(23), 13555–13570.
<https://doi.org/10.1002/ece3.7022>
- Fisher, J. P., Fitzsimons, J. D., Combs, G. F., & Spitsbergen, J. M. (1996). Naturally Occurring Thiamine Deficiency Causing Reproductive Failure in Finger Lakes Atlantic Salmon and Great Lakes Lake Trout. *Transactions of the American Fisheries Society*, 125(2), 167–178.
[https://doi.org/10.1577/1548-8659\(1996\)125%3C0167:NOTDCR%3E2.3.CO;2](https://doi.org/10.1577/1548-8659(1996)125%3C0167:NOTDCR%3E2.3.CO;2)
- Fitzsimons, J. D., Brown, S. B., Honeyfield, D. C., & Hnath, J. G. (1999). A review of early mortality syndrome (EMS) in Great Lakes salmonids: Relationship with thiamine deficiency. *Ambio*, 28(1), 9–15. <https://www.jstor.org/stable/4314842>
- Fitzsimons, J. D., Williston, B., Amcoff, P., Balk, L., Pecor, C., Ketola, H. G., Hinterkopf, J. P., & Honeyfield, D. C. (2005). The effect of thiamine injection on upstream migration, survival, and thiamine status of putative thiamine-deficient coho salmon. *Journal of Aquatic Animal Health*, 17, 48–58. <https://doi.org/https://doi.org/10.1577/H04-003.1>
- Foott, J. S. (2020). *Fall-run chinook fry loss not associated with infectious agent*. U.S. Fish and Wildlife Service.
- Free, C. M., Anderson, S. C., Hellmers, E. A., Muhling, B. A., Navarro, M. O., Richerson, K., Rogers, L. A., Satterthwaite, W. H., Thompson, A. R., Burt, J. M., Gaines, S. D., Marshall, K. N., White, J. W., & Bellquist, L. F. (2023). Impact of the 2014–2016 marine heatwave on US and

- Canada West Coast fisheries: Surprises and lessons from key case studies. *Fish and Fisheries*, 24(4), 652–674. <https://doi.org/10.1111/faf.12753>
- Futia, M. H., Hallenbeck, S., Noyes, A. D., Honeyfield, D. C., Eckerlin, G. E., & Rinchard, J. (2017). Thiamine deficiency and the effectiveness of thiamine treatments through broodstock injections and egg immersion on Lake Ontario steelhead trout. *Journal of Great Lakes Research*, 43(2), 352–358. <https://doi.org/10.1016/j.jglr.2017.01.001>
- Gentemann, C. L., Fewings, M. R., & García-Reyes, M. (2017). Satellite sea surface temperatures along the West Coast of the United States during the 2014–2016 northeast Pacific marine heat wave. *Geophysical Research Letters*, 44(1), 312–319. <https://doi.org/10.1002/2016GL071039>
- Gerstung, E. R. (1971). *A report to the California State Water Resources Control Board on the fish and wildlife resources of the American River to be affected by the Auburn Dam and Reservoir and the Folsom South Canal and measures proposed to maintain these resources*. California Department of Fish and Game.
- Harder, A. M., Ardren, W. R., Evans, A. N., Futia, M. H., Kraft, C. E., Marsden, J. E., Richter, C. A., Rinchard, J., Tillitt, D. E., & Christie, M. R. (2018). Thiamine deficiency in fishes: Causes, consequences, and potential solutions. *Reviews in Fish Biology and Fisheries*, 28(4), 865–886. <https://doi.org/10.1007/s11160-018-9538-x>
- Harvey, C., Leising, A., Tolimieri, N., & Williams, G. (2023). *2022–2023 California Current Ecosystem status report*. NOAA California Current Integrated Ecosystem Assessment Team (CCIEA).
- Healey, M. C. (1991). Life history of chinook salmon (*Oncorhynchus tshawytscha*). In C. Groot & L. Margolis (Eds.), *Pacific Salmon Life Histories* (pp. 311–393). UBC Press.

- Hertz, E., Trudel, M., Brodeur, R., Daly, E., Eisner, L., Farley Jr, E., Harding, J., MacFarlane, R., Mazumder, S., Moss, J., Murphy, J., & Mazumder, A. (2015). Continental-scale variability in the feeding ecology of juvenile Chinook salmon along the coastal Northeast Pacific Ocean. *Marine Ecology Progress Series*, 537, 247–263. <https://doi.org/10.3354/meps11440>
- Hinchliffe, C., Kuriyama, P. T., Punt, A. E., Field, J. C., Thompson, A. R., Santora, J. A., Muhling, B. A., Koenigstein, S., Hernvann, P.-Y., & Tommasi, D. (2025). Long-term population trend of northern anchovy (*Engraulis mordax*) in the California Current system. *ICES Journal of Marine Science*, 82(1). <https://doi.org/10.1093/icesjms/fsae177>
- Hobson, K. A., & Wassenaar, L. I. (2008). Tracking Animal Migration with Stable Isotopes. In *Tracking Animal Migration with Stable Isotopes* (1st ed.). Elsevier. <https://doi.org/10.1016/C2017-0-01125-4>
- Hoffbauer, C. (1898). Die Altersbestimmung des Karpfens an seiner Schuppe [Age determination of carp using its scales]. *Allgemeine Fischerei-Zeitung*, 23, 341–343.
- Honeyfield, D. C., Hinterkopf, J. P., Fitzsimons, J. D., Tillitt, D. E., Zajicek, J. L., & Brown, S. B. (2005). Development of thiamine deficiencies and early mortality syndrome in lake trout by feeding experimental and feral fish diets containing thiaminase. *Journal of Aquatic Animal Health*, 17(1), 4–12. <https://doi.org/10.1577/H03-078.1>
- Hutchinson, J. J., & Trueman, C. N. (2006). Stable isotope analyses of collagen in fish scales: Limitations set by scale architecture. *Journal of Fish Biology*, 69(6), 1874–1880. <https://doi.org/10.1111/j.1095-8649.2006.01234.x>
- Jackson, A., Inger, R., Parnell, A., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R: Bayesian isotopic

- niche metrics. *Journal of Animal Ecology*, 80(3), 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>
- Jackson, A., & Parnell, A. (2015). *SIBER: Stable Isotope Bayesian Ellipses in R* (p. 2.1.9) [Dataset]. <https://doi.org/10.32614/CRAN.package.SIBER>
- Jacox, M. G., Alexander, M. A., Amaya, D., Becker, E., Bograd, S. J., Brodie, S., Hazen, E. L., Pozo Buil, M., & Tommasi, D. (2022). Global seasonal forecasts of marine heatwaves. *Nature*, 604(7906), 486–490. <https://doi.org/10.1038/s41586-022-04573-9>
- Jacox, M. G., Alexander, M. A., Mantua, N. J., Scott, J. D., Hervieux, G., Webb, R. S., & Werner, F. E. (2018). Forcing of multiyear extreme ocean temperatures that impacted california current living marine resources in 2016. *Bulletin of the American Meteorological Society*, 99(1), S27–S33. <https://doi.org/10.1175/BAMS-D-17-0119.1>
- Jensen, A. J., Kelly, R. P., Satterthwaite, W. H., Ward, E. J., Moran, P., & Shelton, A. O. (2023). Modeling ocean distributions and abundances of natural- and hatchery-origin Chinook salmon stocks with integrated genetic and tagging data. *PeerJ*, 11, e16487. <https://doi.org/10.7717/peerj.16487>
- Johnson, R. C., Garza, J. C., MacFarlane, R. B., Grimes, C. B., Phillis, C. C., Koch, P. L., Weber, P. K., & Carr, M. H. (2016). Isotopes and genes reveal freshwater origins of Chinook salmon *Oncorhynchus tshawytscha* aggregations in California’s coastal ocean. *Marine Ecology Progress Series*, 548. <https://doi.org/10.3354/meps11623>
- Johnson, S. P., & Schindler, D. E. (2012). Four decades of foraging history: Stock-specific variation in the carbon and nitrogen stable isotope signatures of Alaskan sockeye salmon. *Marine Ecology Progress Series*, 460, 155–167. <https://doi.org/10.3354/meps09772>

- Julienne, J., & Morse, H. (2021, April 28). *CDFW Takes Proactive Measures to Increase Salmon Smolt Survival*. <https://cdfgnews.wordpress.com/2021/04/28/cdfw-takes-proactive-measures-to-increase-salmon-smolt-survival/>
- Kacem, A., Baglinière, J.-L., & Meunier, F. (2013). Resorption of scales in Atlantic salmon (*Salmo salar*) during its anadromous migration: A quantitative study. *Cybiuim: International Journal of Ichthyology*, 37, 199–206.
- Keinänen, M., Uddström, A., Mikkonen, J., Casini, M., Pönni, J., Myllylä, T., Aro, E., & Vuorinen, P. J. (2012). The thiamine deficiency syndrome M74, a reproductive disorder of Atlantic salmon (*Salmo salar*) feeding in the Baltic Sea, is related to the fat and thiamine content of prey fish. *ICES Journal of Marine Science*, 69(4), 516–528.
<https://doi.org/10.1093/icesjms/fss041>
- Ketola, H. G., Chiotti, T. L., Rathman, R. S., Fitzsimons, J. D., Honeyfield, D. C., Van Dusen, P. J., & Lewis, G. E. (2005). Thiamine Status of Cayuga Lake Rainbow Trout and Its Influence on Spawning Migration. *North American Journal of Fisheries Management*, 25(4), 1281–1287.
<https://doi.org/10.1577/M04-173.1>
- Koski, P., Pakarinen, M., Nakari, T., Soivio, A., & Hartikainen, K. (1999). Treatment with thiamine hydrochloride and astaxanthine for the prevention of yolk-sac mortality in Baltic salmon fry (M74 syndrome). *Diseases of Aquatic Organisms*, 37, 209–220.
<https://doi.org/https://doi.org/10.3354/dao037209>
- Kwak, K. (2021). *Thiamine mononitrate supplementation during fertilization for Chinook salmon at CDFW anadromous hatcheries*. California Department of Fish and Wildlife, Fish Health Laboratory.

- Ladago, B. J., Futia, M. H., Ardren, W. R., Honeyfield, D. C., Kelsey, K. P., Kozel, C. L., Riley, S. C., Rinchard, J., Tillitt, D. E., Zajicek, J. L., & Marsden, J. E. (2020). Thiamine concentrations in lake trout and Atlantic salmon eggs during 14 years following the invasion of alewife in Lake Champlain. *Journal of Great Lakes Research*, 46(5), 1340–1348.
<https://doi.org/10.1016/j.jglr.2020.06.018>
- Lasker, R. (1985). What limits clupeoid production? *Canadian Journal of Fisheries and Aquatic Sciences*, 42(S1), 31–38. <https://doi.org/10.1139/f85-261>
- Layman, C. A., Arrington, D. A., Montaña, C. G., & Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, 88(1), 42–48.
[https://doi.org/10.1890/0012-9658\(2007\)88%5B42:CSIRPF%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88%5B42:CSIRPF%5D2.0.CO;2)
- Lerner, J. E., & Hunt, B. P. V. (2025). Compound-Specific Stable Isotope Analysis Reveals Population-Specific Differences in Chinook Salmon Trophic Level and Basal Resource Use in the Northeast Pacific. *Fisheries Oceanography*, n/a(n/a), fog.70024.
<https://doi.org/10.1111/fog.70024>
- Lindley, S. T., Schick, R. S., Mora, E., Adams, P. B., Anderson, J. J., Greene, S., Hanson, C., May, B. P., McEwan, D., MacFarlane, R. B., & others. (2007). Framework for assessing viability of threatened and endangered Chinook salmon and steelhead in the Sacramento–San Joaquin basin. *San Francisco Estuary and Watershed Science*, 5(1).
- Litz, M. N. C., Miller, J. A., Copeman, L. A., Teel, D. J., Weitkamp, L. A., Daly, E. A., & Claiborne, A. M. (2017). Ontogenetic shifts in the diets of juvenile Chinook Salmon: New insight from stable isotopes and fatty acids. *Environmental Biology of Fishes*, 100(4), 337–360.
<https://doi.org/10.1007/s10641-016-0542-5>

- Mantua, N. J., Bell, H., Todgham, A. E., Daniels, M. E., Rinchard, J., Ludwig, J. M., Field, J. C., Lindley, S. T., Rowland, F. E., Richter, C. A., Walters, D., Finney, B., Distajo, H. A. R., Tillitt, D., Honeyfield, D. C., Lipscomb, T., Kwak, K., Kindopp, J., Cocherell, D., ... Johnson, R. C. (2025). Widespread thiamine deficiency in California salmon linked to an anchovy-dominated marine prey base. *Proceedings of the National Academy of Sciences*, 122(26), e2426011122. <https://doi.org/10.1073/pnas.2426011122>
- Mantua, N. J., Johnson, R., Field, J., Lindley, S., Williams, T., Todgham, A., Fangue, N., Jeffres, C., Bell, H., Cocherell, D., Rinchard, J., Tillitt, D., Finney, B., Honeyfield, D., Lipscomb, T., Foott, S., Kwak, K., Adkison, M., Kormos, B., ... Ruiz-Cooley, I. (2021). *Mechanisms, impacts, and mitigation for thiamine deficiency and early life stage mortality in California's Central Valley Chinook salmon* (No. 17; pp. 92–93). North Pacific Anadromous Fish Commission. <https://doi.org/10.23849/npafctr17/92.93>.
- Minagawa, M., & Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta*, 48(5), 1135–1140. [https://doi.org/10.1016/0016-7037\(84\)90204-7](https://doi.org/10.1016/0016-7037(84)90204-7)
- Moyle, P., Samuel, P. J., & Lusardi, R. (2017). *SOS II: Fish in hot water*. California Trout.
- NMFS. (1994). *Endangered and Threatened Species; Status of Sacramento River Winter-Run Chinook Salmon* (Federal Register, Vol. 59, Issue 2, pp. 440–450). <https://www.federalregister.gov/documents/1994/01/04/93-31089/endangered-and-threatened-species-status-of-sacramento-river-winter--run-chinook-salmon>
- NMFS. (1999). *Endangered and Threatened Species; Threatened Status for Two Chinook Salmon Evolutionarily Significant Units (ESUs) and Change in Status for One Chinook Salmon ESU* (Federal Register, Vol. 64, Issue 179, p. 50394).

<https://www.federalregister.gov/documents/1999/09/16/99-24060/endangered-and-threatened-species-threatened-status-for-two-chinook-salmon-evolutionarily-significant>

NMFS. (2014). *Recovery plan for the evolutionarily significant units of sacramento river winter-run chinook salmon and central valley spring-run chinook salmon and the distinct population segment of california central valley steelhead*. California Central Valley Area Office.

https://s3.amazonaws.com/media.fisheries.noaa.gov/dam-migration/central_valley_salmonids_recovery_plan-accessible.pdf

NOAA Fisheries. (2023, January 30). *River Temperatures and Survival of Endangered California Winter-Run Chinook Salmon in the 2021 Drought* | NOAA Fisheries. (West Coast). NOAA.

<https://www.fisheries.noaa.gov/west-coast/climate/river-temperatures-and-survival-endangered-california-winter-run-chinook-salmon>

Office of the Federal Register, N. A. and R. A. (1999). *Endangered and Threatened Species; Threatened Status for Two Chinook Salmon Evolutionarily Significant Units (ESUs) in California* (Federal Register, Vol. 64, p. 50394). Office of the Federal Register, National Archives and Records Administration. <https://www.govinfo.gov/app/details/FR-1999-09-16/99-24051>

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2017). *vegan: Community Ecology Package*. <https://CRAN.R-project.org/package=vegan>

Portner, E. J., Muhling, B. A., Preti, A., Snodgrass, O. E., Richards, T. M., Nickels, C. F., Dewar, H., Hazen, E. L., & Choy, C. A. (2025). Resource partitioning among pelagic predators remains stable despite annual variability in diet composition. *Journal of Animal Ecology*, 1365-2656.70032. <https://doi.org/10.1111/1365-2656.70032>

- Posit Team. (2025). *RStudio: Integrated development environment for R*. Posit Software, PBC.
<http://www.posit.co/>
- Post, D. M. (2002). Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology*, 83(3), 703–718. [https://doi.org/10.1890/0012-9658\(2002\)083%5B0703:USITET%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083%5B0703:USITET%5D2.0.CO;2)
- R Core Team. (2025). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Ralston, S., Field, J. C., & Sakuma, K. M. (2015). Long-term variation in a central California pelagic forage assemblage. *Journal of Marine Systems, California Current System – Predators and the Preyscape*, 146, 26–37. <https://doi.org/10.1016/j.jmarsys.2014.06.013>
- Reed, A. N., Rowland, F. E., Krajcik, J. A., & Tillitt, D. E. (2023). Thiamine Supplementation Improves Survival and Body Condition of Hatchery-Reared Steelhead (*Oncorhynchus mykiss*) in Oregon. *Veterinary Sciences*, 10(2), 156. <https://doi.org/10.3390/vetsci10020156>
- Riley, S. C., & Evans, A. N. (2008). Phylogenetic and Ecological Characteristics Associated with Thiaminase Activity in Laurentian Great Lakes Fishes. *Transactions of the American Fisheries Society*, 137(1), 147–157. <https://doi.org/10.1577/T06-210.1>
- Rutter, C. (1904). Natural history of the quinnat salmon. *U.S. Fish Commission Bulletin*, 22, 66–141.
- Santora, J. A., Hazen, E., Schroeder, I., Bograd, S., Sakuma, K., & Field, J. (2017). Impacts of ocean climate variability on biodiversity of pelagic forage species in an upwelling ecosystem. *Marine Ecology Progress Series*, 580, 205–220. <https://doi.org/10.3354/meps12278>
- Santora, J. A., Mantua, N. J., Schroeder, I. D., Field, J. C., Hazen, E. L., Bograd, S. J., Sydeman, W. J., Wells, B. K., Calambokidis, J., Saez, L., Lawson, D., & Forney, K. A. (2020). Habitat

- compression and ecosystem shifts as potential links between marine heatwave and record whale entanglements. *Nature Communications*, 11(1), 536.
<https://doi.org/10.1038/s41467-019-14215-w>
- Satterfield, F. R., & Finney, B. P. (2002). Stable isotope analysis of Pacific salmon: Insight into trophic status and oceanographic conditions over the last 30 years. *Progress in Oceanography, Physical and Biological Conditions and Processes in the Northeast Pacific Ocean*, 53(2), 231–246. [https://doi.org/10.1016/S0079-6611\(02\)00032-0](https://doi.org/10.1016/S0079-6611(02)00032-0)
- Satterthwaite, W., Carlson, S., Allen-Moran, S., Vincenzi, S., Bograd, S., & Wells, B. (2014). Match-mismatch dynamics and the relationship between ocean-entry timing and relative ocean recoveries of Central Valley fall run Chinook salmon. *Marine Ecology Progress Series*, 511, 237–248. <https://doi.org/10.3354/meps10934>
- Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591–596. <https://doi.org/10.1038/35098000>
- Stierhoff, K. L., Renfree, J. S., Rojas-González, R. I., Vallarta-Zárate, J. R. F., Zwolinski, J. P., & Demer, D. A. (2023). *Distribution, biomass, and demographics of coastal pelagic fishes in the California Current Ecosystem during summer 2021 based on acoustic-trawl sampling* (NOAA Technical Memorandum NMFS-SWFSC-676). U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.
<https://doi.org/10.25923/77kp-ww39>
- Stone, L. (1883). Account of operations at the McCloud River fish-breeding stations of the United States Fish Commission, from 1872–1882, inclusive. *U.S. Fish Commission Bulletin*, 2(1882), 217–236.

- Suffridge, C. P., Shannon, K. C., Matthews, H., Johnson, R. C., Jeffres, C., Mantua, N. J., Ward, A. E., Holmes, E., Kindopp, J., Aidoo, M., & Colwell, F. S. (2023). Connecting thiamine availability to the microbial community composition in Chinook salmon spawning habitats of the Sacramento River basin. *Applied and Environmental Microbiology*, 90(1), e01760-23. <https://doi.org/10.1128/aem.01760-23>
- Swalethorp, R., Landry, M. R., Semmens, B. X., Ohman, M. D., Aluwihare, L., Chargualaf, D., & Thompson, A. R. (2023). Anchovy boom and bust linked to trophic shifts in larval diet. *Nature Communications*, 14(1), 7412. <https://doi.org/10.1038/s41467-023-42966-0>
- Syväranta, J., Lensu, A., Marjomäki, T. J., Oksanen, S., & Jones, R. I. (2013). An Empirical Evaluation of the Utility of Convex Hull and Standard Ellipse Areas for Assessing Population Niche Widths from Stable Isotope Data. *PLOS ONE*, 8(2), e56094. <https://doi.org/10.1371/journal.pone.0056094>
- Thayer, J., Field, J., & Sydeman, W. (2014). Changes in California Chinook salmon diet over the past 50 years: Relevance to the recent population crash. *Marine Ecology Progress Series*, 498, 249–261. <https://doi.org/10.3354/meps10608>
- Thayer, J., MacCall, A., Davison, P., & Sydeman, W. (2017). California Anchovy Population Remains Low, 2012–2016. *CalCOFI Reports*, 58.
- Thompson, A. R., Bjorkstedt, E. P., Bograd, S. J., Fisher, J. L., Hazen, E. L., Leising, A., Santora, J. A., Satterthwaite, E. V., Sydeman, W. J., Alksne, M., Auth, T. D., Baumann-Pickering, S., Bowlin, N. M., Burke, B. J., Daly, E. A., Dewar, H., Field, J. C., Garfield, N. T., Giddings, A., ... Weber, E. D. (2022). State of the California Current Ecosystem in 2021: Winter is coming? *Frontiers in Marine Science*, 9. <https://doi.org/10.3389/fmars.2022.958727>

- Thompson, A. R., Schroeder, I. D., Bograd, S. J., Hazen, E. L., Jacox, M. G., Leising, A., Wells, B. K., Largier, J., Fisher, J. L., Jacobson, K. C., Zeman, S. M., Bjorkstedt, E. P., Robertson, R. R., Kahru, M., Goericke, R., Peabody, C. E., Baumgartner, T. R., Lavaniegos, B. E., Miranda, L. E., ... Melin, S. R. (2019). State of the California Current 2018–19: A novel anchovy regime and a new marine heatwave? *CalCOFI Reports*, 60, 1–61.
- Trueman, C. N., & Moore, A. (2007). Use of the stable isotope composition of fish scales for monitoring aquatic ecosystems. In *Terrestrial Ecology* (Vol. 1, pp. 145–161). Elsevier.
[https://doi.org/10.1016/S1936-7961\(07\)01010-X](https://doi.org/10.1016/S1936-7961(07)01010-X)
- Trueman, C. N., & St John Glew, K. (2019). Isotopic Tracking of Marine Animal Movement. In K. A. Hobson & L. I. B. T.-T. A. M. with S. I. (Second E. Wassenaar (Eds.), *Tracking Animal Migration with Stable Isotopes* (pp. 137–172). Academic Press.
<https://doi.org/10.1016/B978-0-12-814723-8.00006-4>
- Tukey, J. W. (1977). *Exploratory Data Analysis*. Addison-Wesley.
- Tzadik, O. E., Curtis, J. S., Granneman, J. E., Kurth, B. N., Pusack, T. J., Wallace, A. A., Hollander, D. J., Peebles, E. B., & Stallings, C. D. (2017). Chemical archives in fishes beyond otoliths: A review on the use of other body parts as chronological recorders of microchemical constituents for expanding interpretations of environmental, ecological, and life-history changes. *Limnology and Oceanography: Methods*, 15(3), 238–263.
<https://doi.org/10.1002/lom3.10153>
- Van Oosten, J. (1928). Life history of the lake herring (*Leucichthys artedi* Lesueur) of Lake Huron as revealed from its scales with a critique of the scale method. *Bulletin of the United States Bureau of Fisheries*, 44, 265–428.

Vogel, D. A., & Marine, K. R. (1991). *Guide to Upper Sacramento River Chinook Salmon Life History*.

CH2M HILL.

Ward, A. E., Johnson, R., Williams, T., Mantua, N., Jeffres, C., Rinchard, J., Ludwig, J., Daniels, M., Lipscomb, T., Kastner, A., Crawshaw, P., Novak, G., Hoover, P., Jason, J., Smith, W., Serr, M., Tsao, S., Knabe, A., Brock, P., ... Neal, K. (2025). *Long term egg thiamine monitoring in salmonid populations in California; 2020-2023* [Dataset].

<https://doi.org/10.6073/pasta/ce132c1ef916900b5b50650388aa2266>

Welch, D. W., & Parsons, T. R. (1993). $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ values as indicators of trophic position and competitive overlap for Pacific salmon (*Oncorhynchus* spp.). *Fisheries Oceanography*, 2(1), 11–23. <https://doi.org/10.1111/j.1365-2419.1993.tb00008.x>

Wells, B., Santora, J., Schroeder, I., Mantua, N. J., Sydeman, W., Huff, D., & Field, J. (2016). Marine ecosystem perspectives on Chinook salmon recruitment: A synthesis of empirical and modeling studies from a California upwelling system. *Marine Ecology Progress Series*, 552, 271–284. <https://doi.org/10.3354/meps11757>

Whitfield, K. C., Bourassa, M. W., Adamolekun, B., Bergeron, G., Bettendorff, L., Brown, K. H., Cox, L., Fattal-Valevski, A., Fischer, P. R., Frank, E. L., Hiffler, L., Hlaing, L. M., Jefferds, M. E., Kapner, H., Kounnavong, S., Mousavi, M. P. S., Roth, D. E., Tsaloglou, M., Wieringa, F., & Combs, G. F. (2018). Thiamine deficiency disorders: Diagnosis, prevalence, and a roadmap for global control programs. *Annals of the New York Academy of Sciences*, 1430(1), 3–43. <https://doi.org/10.1111/nyas.13919>

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. <https://ggplot2.tidyverse.org>

- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., ... Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, 4(43), 1686.
<https://doi.org/10.21105/joss.01686>
- Williams, J. G., Anderson, J. J., Greene, S., Hanson, C. H., Lindley, S. T., Low, A. F., May, B., McEwan, D. R., Mohr, M. S., MacFarlane, R. B., & others. (2007). *Monitoring and research needed to manage the recovery of threatened and endangered Chinook and steelhead in the Sacramento-San Joaquin basin*.
- Wolfe, P. C., Tuske, A. M., Tillitt, D. E., Allen, F., & Edwards, K. A. (2023). Understanding and mitigating thiaminase activity in silver carp. *Current Research in Food Science*, 6, 100502.
<https://doi.org/10.1016/j.crfs.2023.100502>
- Yoshiyama, R. M., Fisher, F. W., & Moyle, P. B. (1998). Historical abundance and decline of chinook salmon in the central valley region of california. *North American Journal of Fisheries Management*, 18(3), 487–521. [https://doi.org/10.1577/1548-8675\(1998\)018%3C0487:HAADOC%3E2.0.CO;2](https://doi.org/10.1577/1548-8675(1998)018%3C0487:HAADOC%3E2.0.CO;2)
- Yoshiyama, R. M., Moyle, P. B., Gerstung, E. R., & Fisher, F. W. (2000). Chinook salmon in the California Central Valley: An assessment. *Fisheries*, 25(2), 6–20.

Supplemental Information Appendix

S.1 SENSITIVITY ANALYSIS: IQR OUTLIER EXCLUSION

All primary analyses were repeated on the full dataset with no IQR-based outlier screening ($n = 1003$, vs $n = 996$ after screening; 7 samples flagged). Directional conclusions were preserved in every case. Pre-TDC to TDC declines in $\delta^{15}\text{N}$ standard deviation were within 3 percentage points across all runs (winter -44.9% vs -42.0% ; fall -29.7% vs -31.3% ; spring -11.3% vs -12.2%), and the winter > fall > spring ranking of both $\delta^{15}\text{N}$ variability decline and SEA_B decline was identical in both datasets. Run $\times$ year structure remained significant by PERMANOVA ($p = 0.001$). The single material exception was the fall 2016 cohort, whose SEA_B increased from 0.40 to 2.15‰^2 when one sample with an implausible $\delta^{13}\text{C}$ value of -22.5‰ (more than 20x the cohort interquartile range below the first quartile, inconsistent with marine Chinook foraging) was retained. This is why conservative outlier screening was applied: a single analytical error can inflate a cohort ellipse fivefold. Excluding such values does not alter any temporal or among-run pattern reported in the main text.

Table S.1.1: Samples flagged by $k = 3$ IQR screening and excluded from primary analyses.

LAB_ID	RUN	YEAR	$\Delta^{13}\text{C}$	$\Delta^{15}\text{N}$	FLAGGED_ON
EE16_3190	fall	2016	-22.466	13.757	$\delta^{13}\text{C}$
THICNH20-FR-31575	fall	2020	-16.297	14.662	$\delta^{13}\text{C}$
THICNH20-FR-31660	fall	2020	-17.071	14.392	$\delta^{13}\text{C}$
THICNH23-FR-26	fall	2023	-15.968	14.715	$\delta^{13}\text{C}$
EE17_83132	spring	2017	-15.471	14.236	$\delta^{13}\text{C}$
EE18_7042	winter	2018	-14.640	15.204	$\delta^{13}\text{C}$
THILSH21-WR-80476	winter	2021	-13.916	14.641	$\delta^{15}\text{N}$

Table S.1.2: Cohort statistics for cohorts containing flagged samples.

RUN	YEAR	N	$\Delta^{13}\text{C}$ Q1	$\Delta^{13}\text{C}$ Q3	$\Delta^{13}\text{C}$ IQR	$\Delta^{15}\text{N}$ Q1	$\Delta^{15}\text{N}$ Q3	$\Delta^{15}\text{N}$ IQR	N FLAGGED
Fall	2016	30	-13.949	-13.543	0.406	14.735	15.198	0.463	1
Fall	2020	30	-14.218	-13.696	0.522	14.392	15.012	0.620	2
Fall	2023	29	-14.258	-13.925	0.332	14.193	14.677	0.484	1
Spring	2017	30	-14.076	-13.769	0.307	14.881	15.393	0.512	1
Winter	2018	29	-14.036	-13.851	0.185	15.318	15.796	0.478	1
Winter	2021	29	-13.707	-13.460	0.247	15.369	15.597	0.228	1

Table S.1.3: Pre-TDC vs post-TDC percent decline in within-cohort SD of $\delta^{15}\text{N}$, IQR, and range: cleaned ($n = 996$) vs full ($n = 1,003$) dataset.

RUN	DATASET	PERCENT DECLINE SD	PERCENT DECLINE IQR	PERCENT DECLINE RANGE
Fall	Clean	-29.7	-13.0	-35.2
Fall	Full	-31.3	-17.3	-37.8
Spring	Clean	-11.3	-10.4	-14.9
Spring	Full	-12.2	-11.4	-14.9
Winter	Clean	-44.9	-41.0	-47.2
Winter	Full	-42.0	-40.9	-42.0

Table S.1.4: Pre-TDC vs post-TDC mean SEA_B and percent decline by run: cleaned vs full dataset.

RUN	DATASET	MEAN SEA_B PRE-TDC	MEAN SEA_B TDC	PERCENT DECLINE
Fall	Clean	0.435	0.273	-37.270
Fall	Full	0.685	0.458	-33.047
Spring	Clean	0.408	0.304	-25.462
Spring	Full	0.427	0.305	-28.583
Winter	Clean	0.347	0.178	-48.739
Winter	Full	0.353	0.183	-48.090

Run $\times$ year structure remained significant ($p = 0.001$) in both the cleaned and full datasets (PERMANOVA, Euclidean distance, 999 permutations).

S.2 ISOTOPIC SEPARATION AMONG RUN-YEAR COHORTS

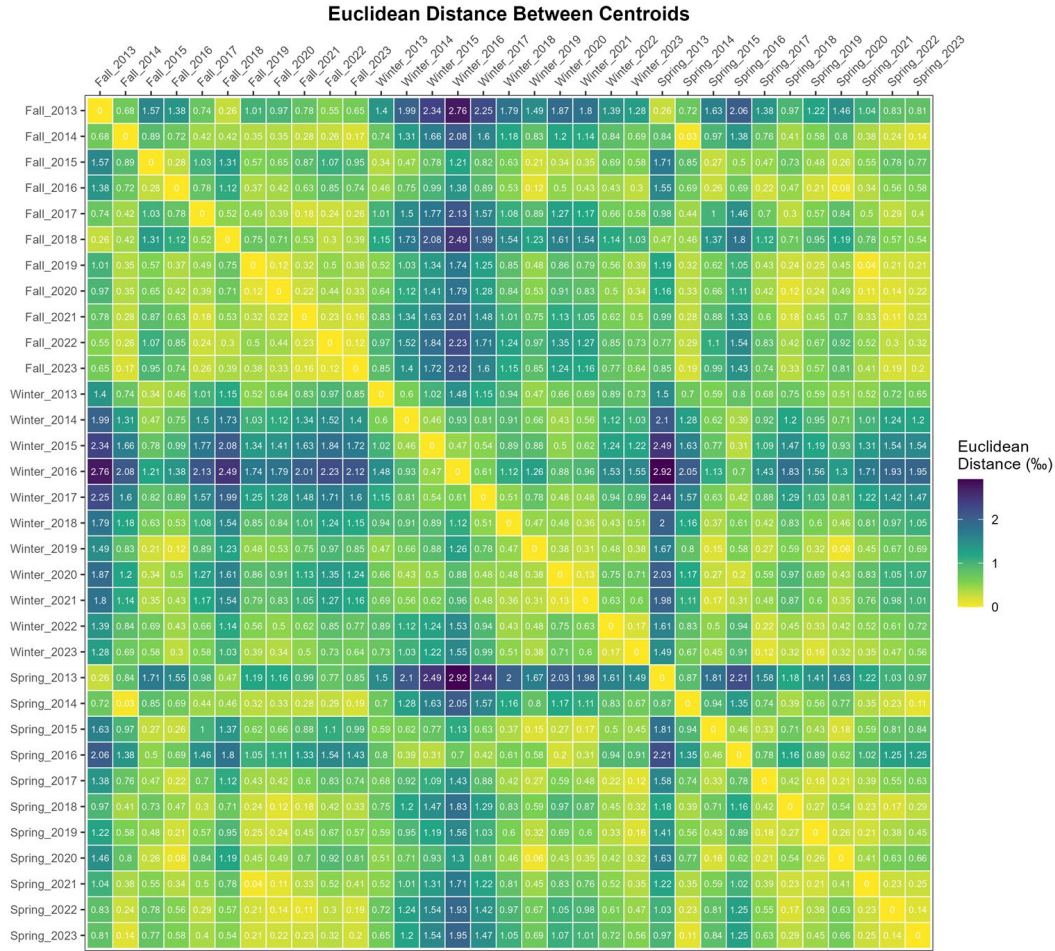


Figure S.2.1: Pairwise isotopic centroid distances among run-year cohorts. Heatmap of pairwise Euclidean distances (‰) between run-year cohort isotopic centroids (2013–2023). Each cell represents the distance between a pair of centroids in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space, calculated as $\text{Distance} = \sqrt{[(\delta^{13}\text{C}_2 - \delta^{13}\text{C}_1)^2 + (\delta^{15}\text{N}_2 - \delta^{15}\text{N}_1)^2]}$. Color scale ranges from yellow (0‰, identical centroids) to dark purple (≥ 2 ‰, maximally separated centroids). Rows and columns are labeled by run and return year.

Pairwise Euclidean distances (D) were calculated between run-year centroids. Euclidean distance summarizes the distance between average $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for each pair. The equation is:

$$D = \sqrt{[(\delta^{13}\text{C}_2 - \delta^{13}\text{C}_1)^2 + (\delta^{15}\text{N}_2 - \delta^{15}\text{N}_1)^2]}.$$

The goal is to see how different or similar each cohort is in isotopic space. The results ranged from 0.035‰ to 2.916‰ (Figure S.2.1, Table S.2.2).

Table S.2.1: Summary statistics for pairwise Euclidean distances (‰) between isotopic centroids, grouped by comparison type (between-run vs. within-run across years). Statistics include mean, standard deviation (SD), minimum, maximum, and number of pairwise comparisons.

COMPARISON TYPE	MEAN DISTANCE	SD DISTANCE	MIN DISTANCE	MAX DISTANCE	N COMPARISONS
Between-run	0.910	0.554	0.035	2.916	363
Within-run (across years)	0.671	0.392	0.112	2.215	165

Table S.2.2: Mean pairwise Euclidean distances (‰) between isotopic centroids for each run pair (fall, winter, and spring run Chinook salmon, 2013–2023). Statistics include mean, standard deviation (SD), minimum, maximum, and number of pairwise comparisons.

RUN PAIR	MEAN DISTANCE	SD DISTANCE	MIN DISTANCE	MAX DISTANCE	N COMPARISONS
Fall vs Winter	1.145	0.551	0.116	2.756	121
Spring vs Winter	0.925	0.563	0.058	2.916	121
Fall vs Spring	0.660	0.430	0.035	2.060	121

Centroid separation was greater between runs than among years within a run. The average difference between centroids of two different runs was 0.910‰. Within a single run (so year to year), the mean difference between centroids was 0.671‰ (Table S.2.2). When comparing run to run, fall and winter run had the largest separation at 1.145‰ mean distance. The most similar were fall and spring with a 0.660‰ mean distance (Table S.2.2). A PERMANOVA found that run grouping explained 64.5% of isotopic variance ($R^2 = 0.645$) (PERMANOVA: $F = 54.74$, $p = 0.001$).

S.3 BAYESIAN STANDARD ELLIPSE AREA (SEA_B) POSTERIOR SUMMARIES

Table S.3.1: Posterior summary statistics for Bayesian standard ellipse area (SEA_B , $\% \text{ }^2$) for all run-year cohorts (2013–2023). Values include the posterior mean, median, standard deviation (SD), and 95% credible interval bounds (q2.5, q97.5). Credible intervals represent the range within which the true SEA_B value falls with 95% posterior probability.

RUN	YEAR	MEAN SEA_B	MEDIAN	SD	Q2.5	Q97.5
Fall	2013	0.412	0.403	0.078	0.287	0.587
Fall	2014	0.625	0.609	0.121	0.433	0.905
Fall	2015	0.381	0.373	0.073	0.265	0.548
Fall	2016	0.402	0.393	0.077	0.278	0.580
Fall	2017	0.340	0.332	0.064	0.237	0.488
Fall	2018	0.518	0.507	0.098	0.361	0.743
Fall	2019	0.371	0.364	0.061	0.270	0.507
Fall	2020	0.435	0.424	0.086	0.299	0.634
Fall	2021	0.294	0.287	0.056	0.204	0.422
Fall	2022	0.118	0.115	0.023	0.081	0.170
Fall	2023	0.246	0.240	0.048	0.169	0.356
Winter	2013	0.333	0.326	0.063	0.232	0.479
Winter	2014	0.299	0.292	0.058	0.206	0.433
Winter	2015	0.527	0.514	0.105	0.361	0.773
Winter	2016	0.562	0.541	0.140	0.350	0.894
Winter	2017	0.321	0.314	0.060	0.223	0.460
Winter	2018	0.215	0.210	0.042	0.148	0.313
Winter	2019	0.171	0.168	0.028	0.124	0.236
Winter	2020	0.133	0.129	0.026	0.091	0.191
Winter	2021	0.076	0.074	0.015	0.052	0.110
Winter	2022	0.293	0.285	0.062	0.196	0.436
Winter	2023	0.210	0.207	0.030	0.158	0.277
Spring	2013	0.428	0.419	0.080	0.298	0.613
Spring	2014	0.582	0.567	0.116	0.398	0.852
Spring	2015	0.531	0.519	0.101	0.370	0.763
Spring	2016	0.299	0.293	0.056	0.209	0.427
Spring	2017	0.220	0.215	0.042	0.152	0.315
Spring	2018	0.545	0.532	0.106	0.376	0.791
Spring	2019	0.253	0.247	0.048	0.176	0.363
Spring	2020	0.222	0.217	0.042	0.155	0.319
Spring	2021	0.320	0.315	0.053	0.232	0.439
Spring	2022	0.373	0.365	0.070	0.260	0.532
Spring	2023	0.302	0.295	0.057	0.209	0.433