

ARTICLE

Implications of increased spatial and trophic overlap between juvenile Pacific salmon and Sablefish in the northern California Current

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Abstract

Objective: The study was designed to assess long-term variability in the distribution of juvenile Pacific salmon *Oncorhynchus* spp. and Sablefish *Anoplopoma fimbria*. The study also evaluated whether Sablefish and Pacific salmon shared food resources and looked to characterize Sablefish during an understudied period of their life cycle.

Methods: To meet the objectives, the study used data from 26 years of surface trawls conducted in Oregon and Washington coastal waters (1998–2023). Spatial-temporal models were used to measure changes in abundance and distribution of Pacific salmon and Sablefish along with covariates of ocean temperature. The study evaluated trophic characteristics of Pacific salmon and Sablefish from 2020 for differences. The temporal variation in size and diets of Sablefish were also analyzed, along with energy density of fish caught in 2020.

Result: The spatial-temporal model demonstrated that there has been a nearshore expansion of juvenile Sablefish over the past 26 years that was correlated with increased ocean temperature. The nearshore expansion of Sablefish resulted in increased spatial and trophic overlap with juvenile Pacific salmon. While feeding in nearshore waters, juvenile Sablefish demonstrated competitive feeding advantages over juvenile Pacific salmon during a critical phase of salmonid early marine life history. Juvenile Sablefish exhibited significant ontogenetic diet and energetic shifts, and even the smallest (68–80 mm fork length) were piscivorous.

Conclusions: If juvenile Sablefish numbers continue to increase relative to Pacific salmon, they could exert more competitive pressure, especially if food resources become limited. Pacific salmon may experience adverse effects from competition, regardless of whether or not juvenile Sablefish, which have recently expanded into nearshore waters, successfully recruit to the adult population.

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KEYWORDS

climate change, competition, Pacific salmon, juvenile Sablefish, juvenile salmon, trophic overlap

INTRODUCTION

Novel interactions between managed species in the nearshore marine environment are increasing as a result of changes in atmospheric and ocean processes, which can have implications for fisheries management and conservation (Poloczanska et al. 2016). Ecosystem management of multiple species requires understanding complex ecological interactions in order to ensure that there are sustainable resources for managed populations while accounting for climate-driven changes (Weiskopf et al. 2020). Competitive interactions can adversely affect the growth and survival rates of marine fishes in their early-life history stages. When food availability is limited, whether locally or broadly, the individuals that are better adapted to obtain and utilize resources tend to have a competitive advantage and are more likely to grow faster and survive (Akinori et al. 2003; Le Pape and Bonhommeau 2015; Fennie et al. 2023).

The epipelagic zone of the northern California Current (NCC) is a highly productive system, primarily due to the spring and summer upwelling of nutrient-rich waters into the nearshore. Many larval and juvenile fishes utilize these productive upper surface waters of the epipelagic zone to feed and grow (Brodeur et al. 2019). Juvenile Pacific salmon *Oncorhynchus* spp. from the Columbia River enter the ocean in spring and summer and spend weeks to several months feeding and growing in the near-surface waters of coastal Oregon and Washington (Weitkamp 2010; Tomaro et al. 2012). The growth of juvenile Coho Salmon *Oncorhynchus kisutch* and Chinook Salmon *O. tshawytscha* during their early marine phase is critical to their survival to adults (Pearcy 1992; Duffy and Beauchamp 2011; Burke et al. 2013; Miller et al. 2014). While numerous populations of commercially important Pacific salmon in the NCC are stable or increasing, many are in decline and are listed as threatened or endangered under the Endangered Species Act. Another commercially important fish species in the California Current is Sablefish *Anoplopoma fimbria*, a marine demersal fish whose early-life history stages rear in the offshore surface waters of the California Current in winter through summer (McFarlane and Beamish 1983; Moser et al. 1994). Interannual variation in Sablefish recruitment in the California Current has been linked to oceanographic conditions during the egg and larval stages along with prey abundance and early growth (McFarlane

Impact statement

Juvenile Sablefish have expanded into nearshore coastal waters in correlation with warmer ocean temperatures. This expansion placed them in direct competition with juvenile Pacific salmon, where Sablefish exhibited higher feeding capabilities and were at times much more numerous.

and Beamish 1983; Kendall and Matarese 1987; Schirripa and Colbert 2006; Sogard 2011; Tolimieri et al. 2018; Haltuch et al. 2019).

The distribution, size, and diets of juvenile Coho and Chinook salmon during their early marine residence have been well studied in the NCC. Juvenile Pacific salmon typically reside in the top 10–20 m of the epipelagic zone of the ocean (Emmett et al. 2004), enter the ocean in spring (Weitkamp et al. 2012), and are generally captured less than 25 nm from shore on the shelf (Peterson et al. 2010; Daly et al. 2012). Juvenile Coho and Chinook Salmon diets primarily consist of juvenile fish, krill, and crab megalopae (Brodeur et al. 2007; Miller et al. 2010; Hertz et al. 2015; Dale et al. 2017). In contrast, adult Sablefish release pelagic eggs, typically near the edge of the continental shelf during winter, with larvae rising to the surface waters in late winter to early spring where they are obligate neustonic dwellers 5–370 km from shore (Kendall and Matarese 1987; Shenker 1988; Tolimieri et al. 2018). By fall, some portion of juvenile Sablefish move inshore and then become demersal and move back offshore (Brodeur and Pearcy 1986; Brodeur et al. 2004). Diets of surface-caught juvenile Sablefish consist of a mixture of juvenile fish, crab larvae, krill, and gelatinous zooplankton with low to moderate diet overlap with Pacific salmon (Brodeur and Pearcy 1992; Sigler et al. 2001; Miller and Brodeur 2007). Juvenile (>35 mm SL) Sablefish grow approximately 2 mm/day during this phase of their life (Boehlert and Yoklavich 1985; Kendall and Matarese 1987) and have one of the fastest growth rates recorded for juvenile fish (Shenker and Olla 1986; Sogard and Olla 2001). While in the neuston, juvenile Sablefish feed consistently at maximum consumption if prey are available and exhibit an aggressive foraging strategy (Sogard and Olla 2002).

Ultimately, while both juvenile Pacific salmon and Sablefish utilize the epipelagic waters of the NCC while

young, spatial overlap has historically been low due to their distinct nearshore (Pacific salmon) and offshore (Sablefish) distributions. However, there has been an increase in juvenile Sablefish within nearshore areas when juvenile Pacific salmon are first entering the ocean, leading to greater spatial overlap with juvenile Pacific salmon. As such, the main objectives of this study were to (1) develop spatial-temporal models for juvenile Pacific salmon and Sablefish that estimate changes in abundance for each taxon, (2) relate variability in distribution and abundance to covariates of local and basin-scale ocean temperature, (3) evaluate if juvenile Sablefish and Pacific salmon share food resources where they overlap spatially and/or if they exhibit any significant feeding interactions as evidence of direct competition or even predation (Holt 1977), and (4) characterize temporal variation in size, diet, and energy density of juvenile Sablefish during a little known period of their life history.

METHODS

Data collection

Surface trawl surveys were conducted during the latter part of June for 26 years (1998–2023) in Oregon and Washington coastal waters as part of the Juvenile Salmon and Ocean Ecosystem Survey (JSOES) by the Estuarine and Ocean Ecology Program of the National Marine Fisheries Service (NMFS) and Oregon State University (Figure 1; Figure S1 in the Supplement

available separately online). Sampling stations were spaced 3–5 km apart starting inshore at 30–40 m bottom depth and continuing offshore to the continental shelf break at ~180 m bottom depth. Established transects ran perpendicular to the coast and were spaced ~30–50 km apart, primarily located between 44–48.5°N and 124–125°W. At each station, temperature was measured with a conductivity-temperature-depth profiler to within 5 m of the bottom or a depth of 200 m. Additionally, at each station, a Nordic 264 pelagic rope trawl, with a mouth opening that was 28 m wide and 20 m deep and a 0.8-cm cod-end liner, was towed at the surface during daylight hours for 30 min at a ship speed of ~6 km/h (3.2 knots). All sampled Pacific salmon and Sablefish were identified and quantified, and up to 50 individuals per haul were measured to the nearest millimeter fork length. Juvenile Pacific salmon were individually tagged and frozen, and a subsample of the Sablefish caught in 2016, 2020–2021, and 2023 were bulk-frozen at sea. More limited surveys occurred in May and September in the same region. To examine the size of age-0 Sablefish throughout their first marine summer, length data from May, June, and September JSOES surveys were utilized. For all other analyses, only June survey data was used. In the laboratory, the Pacific salmon and Sablefish were individually weighed to the nearest gram and stomachs were removed, frozen, and analyzed. Chinook Salmon were classified by length into the life-history stages of subyearling and yearling using size criteria from Percy and Fisher (1990), and all juvenile Coho Salmon were classified as yearling based on known life-history strategies.

Spatial analysis of juvenile Pacific salmon and Sablefish

Given the potential competition between Sablefish and juvenile Pacific salmon, the goal was to determine whether the data supported an increase in juvenile Sablefish abundance during the survey period (1998–2023) and whether there was spatial correlation between the species in space and time. Because the data from the JSOES survey were spatially and temporally unbalanced (Figure 1), the Vector Autoregressive Spatio-Temporal Model (VAST; Thorson 2019) package in R was used to make inferences about missing stations and years that could bias the derived variables, such as indices of abundance (Maunder et al. 2020). The VAST model divided the survey domain into a set of spatial cells with a known area and then estimated the encounter rate and positive catch for each cell given the observed catches. Specifically, the statistical distribution of the model

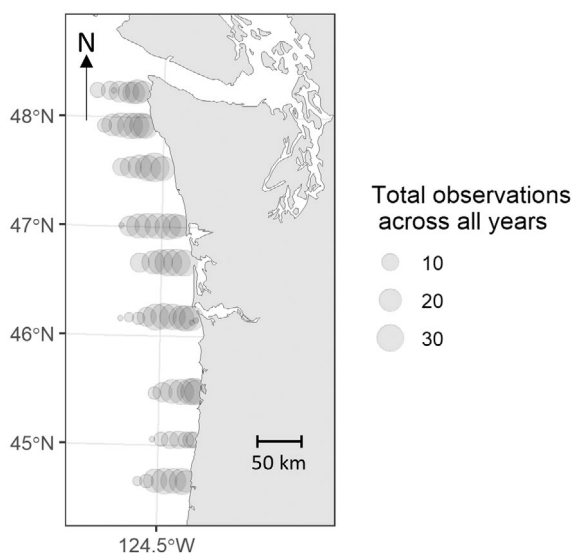


FIGURE 1 Stations sampled along the Washington and Oregon coast during the National Marine Fisheries Service's surface trawl surveys in June 1998–2023 by total trawl observations.

included a Bernoulli probability for the presence/absence of fish at a sampling location (i.e., encounter probability) and a lognormal distribution for the positive catches. The annual index of abundance was the product of the estimated encounter rate multiplied by the estimated fish densities (numbers divided by area) in each cell integrated over the survey domain.

Comparisons between species over space and time were defined by the covariance matrix for the encounter and positive catch processes. While a full rank model would have estimated 10 parameters for each process (one variance parameter for each fish and six correlation parameters in the off-diagonal of the covariance matrix), data limitations necessitated a reduced rank model. The four fish species were grouped into three categories for the spatial and spatiotemporal deviations of the two processes, reducing the number of estimated parameters for each covariance matrix from 10 to 9. Temporal differences in the spatiotemporal processes describing encounter rates and positive catches were assumed to be independent and identically distributed, which introduced an additional variance parameter.

Environmental covariates may bias the indices of abundance, as well as correlation between fish species in space and time (Maunder et al. 2006, 2020). Within the JSOES survey, basin- and local-scale temperature covariates were expected to influence encounter rates and positive catches (Henderson et al. 2017). The basin-scale temperature was derived from the anomaly of the average sea surface temperature in the northeast Pacific Ocean (SSTarc) for May as described by Johnstone and Mantua (2014) for the month of May (Figure S2), and it was assumed to affect encounter rates consistently across all observations within a year. Conversely, the 3-m station temperature, which varied across stations, was presumed to influence fish densities based on localized habitat differences. May SSTarc was chosen to represent ocean conditions prior to the capture of Pacific salmon and Sablefish in June, aiming to identify if large-scale oceanographic conditions impacted their distribution. Various functional relationships for the covariates were explored. For both SSTarc and 3-m station temperature, a species-specific, first-order linear response provided the most reasonable estimates of fish densities without causing large deviations in the model predictions. In the encounter model, the intercept (average expected encounter rate) for each species was assumed to be independent, fixed, and constant across all years.

Several additional data transformations were applied: (1) to enhance interpretability of the range parameter describing spatial decorrelation, coordinate data were transformed from latitude and longitude to Universal Transverse Mercator Zone 10; (2) the density of catches in kilometers squared was calculated by multiplying the

towed distance in kilometers by 0.028 km, the width of the Nordic trawl net (NMFS 2008), and was \log_{10} transformed; and (3) GPS coordinates were mapped to a single station for Gaussian Markov Random Fields calculation using the INLA package (Lindgren and Rue 2015), with the number of knot locations fixed at 68—one for each station (Figure S3). Reviews of the approximation of the Gaussian Markov Random Fields used to describe the spatial and spatiotemporal deviation for the modeled processes, the optimization of the marginal likelihood to estimate the parameters of the model using Template Model Builder, and the step-wise decision making process for applying the VAST model to observations were found in Lindgren and Rue 2015, Kristensen et al. 2016, and Thorson 2019, respectively. The R-script used to create the model is available at https://github.com/bchasco/juv_Sablefish.

Diet analyses between juvenile Pacific salmon and Sablefish in 2020

To compare trophic characteristics between juvenile Pacific salmon and Sablefish in 2020, the diets of all retained juvenile Sablefish and yearling Chinook Salmon were analyzed (see Table 1 for sample size), while a subsample of up to 10 Coho Salmon and 10 subyearling Chinook Salmon diets from each station were analyzed. Stomach contents were identified to the lowest possible taxonomic category, counted, and weighed to the nearest 0.001 g. Length of freshly consumed fish prey (up to six per taxa per stomach) were measured to the nearest 1 mm. Diet composition was calculated as percent weight of prey consumed by an individual fish, then averaged by predator at the station sampled, followed by an overall average of the stations. For the Sablefish, there were distinct size-based diet differences, so their diets were separated into two groups before the diets were averaged at the station. See further details in methods on Sablefish ontogenetic diet differences and the cluster analysis in Figure S4. The diet data was averaged by station prior to analysis due to the high station level autocorrelation in recently consumed prey items (Weitkamp and Sturdevant 2008). Prey were grouped into 18 prey categories, where the taxa or group taxa made up greater than 5% of the diets by weight of prey consumed (see Table 1). Station average diet composition by weight of prey consumed by juvenile Sablefish and juvenile Pacific salmon were evaluated visually via nonmetric multidimensional scaling ordination using a pairwise Bray–Curtis similarity matrix. The via nonmetric multidimensional scaling ordination analysis was completed using the *vegan*, *mass*, *permute*, and *labdsv* packages in

TABLE 1 Diet composition by percent weight of prey (with standard deviation) consumed by small juvenile Sablefish (<120 mm FL), large juvenile Sablefish (>120 mm FL), subyearling Chinook Salmon, yearling Chinook Salmon, and yearling Coho Salmon in June 2020.

Prey category and measurements	Juvenile Sablefish (small)	Juvenile Sablefish (large)	Subyearling Chinook Salmon	Yearling Chinook Salmon	Yearling Coho Salmon
Prey category (% diet composition)					
Gelatinous zooplankton	14.8 ± 30.1	7.4 ± 16.5	0.2 ± 0.6	0	0
Pteropod (sea butterfly <i>Limacina helicina</i>)	5.9 ± 13.2	0.9 ± 4.1	0.3 ± 0.7	0	0
Squid (order Teuthida)	0	1.8 ± 5.8	0.1 ± 0.3	0	0.3 ± 1.2
Copepod	28.9 ± 29.1	4.2 ± 11.9	48.0 ± 34.4	0	7.5 ± 21.7
Amphipod (families Gammaridae, Hyperidae)	0	5.5 ± 18.2	20.2 ± 23.6	9.7 ± 15.9	2.2 ± 6.5
Krill (<i>Euphausia pacifica</i> , <i>Thysanoessa spinifera</i>)	26.0 ± 27.1	25.7 ± 34.2	2.8 ± 9.2	5.3 ± 15.7	17.3 ± 38
Crab zoea (<i>Metacarcinus</i> spp.)	7.0 ± 22.1	0.9 ± 3.2	1.5 ± 3.6	0	0.3 ± 1.5
Crab megalopae (<i>Metacarcinus</i> spp.)	1.5 ± 5	21.2 ± 24.6	9.6 ± 11	2.7 ± 6.4	16.9 ± 22.1
Crab megalopae (non- <i>Metacarcinus</i> spp.)	0.4 ± 1	0.1 ± 0.3	10.4 ± 16.5	0 ± 0.1	3.4 ± 8.4
Other invertebrates (polychaetes, barnacle cyprid, ostracod, mysid, shrimp larvae, insects)	0.9 ± 2.7	0.2 ± 0.6	2.1 ± 6.1	0	2.5 ± 4.9
Pacific Herring <i>Clupea pallasii</i>	0	4.9 ± 19.9	0	4.3 ± 9.3	1.7 ± 4
Smelt (family Osmeridae)	0.2 ± 0.5	0.2 ± 0.8	2.3 ± 7.5	6.6 ± 12.7	7.2 ± 23
Rockfish (<i>Sebastes</i> spp.)	5.9 ± 8.7	15.1 ± 28.7	0	24.0 ± 39.6	24.3 ± 24.1
Sculpin (family Cottidae)	0	0.5 ± 2.1	0.2 ± 0.7	0	0
Lingcod <i>Ophiodon elongatus</i>	0	0	0	2.0 ± 3.4	0.1 ± 0.4
Palefin Sand Lance <i>Ammodytes personatus</i> (formerly known as Pacific Sand Lance)	0	0	0	7.2 ± 14.8	0
Other fish: Pacific Tomcod <i>Microgadus proximus</i> , Northern Ronquil <i>Ronquilus jordani</i> , Quillfish <i>Ptilichthys goodei</i> , flatfish (family Pleuronectidae)	1.5 ± 5	1.5 ± 3.8	0	1.3 ± 3.3	0.2 ± 0.8
Unidentified fish	7.0 ± 15.9	10.1 ± 21.7	2.4 ± 6.1	36.9 ± 33.8	16.1 ± 19.3
Measurements					
Number stomachs examined	53	138	60	75	119
Total stomachs with food	51	130	56	69	106
Mean fork length of predator (mm)	97.1	152.9	106.4	189.9	170.2
Fork length range of predators (mm)	68–118	121–198	75–136	137–268	105–300

R. Dietary overlap between juvenile Sablefish and each of the Pacific salmon was also calculated at the lowest possible taxonomic level using the percent similarity index (PSI):

$$\text{PSI} = \left(1 - 0.5 \sum_{i=1}^n |p_{ik} - p_{jk}| \right) \times 100,$$

where p_{ik} is the proportion by weight of prey item k found in the diet of predator i , p_{jk} is the proportion by weight of prey item k found in the diet of predator j , and n is the total number of prey categories. The index was calculated at the station level where the Pacific salmon co-occurred with Sablefish in time and space, and station PSI values were then averaged together for an overall index for June of 2020. Average PSI values of 0% represent no overlap in diets when the fish were caught together, and 100% represents complete overlap. Overlap values between 0% and 24% indicate low similarity, moderate diet overlap is between 25% and 49%, high is 50–74%, and very high is 75–100% (Buckley et al. 1999).

Standardized stomach fullness was calculated by dividing the stomach content weight by the total fish weight minus the stomach content weight. The prey (standard length in millimeters) to predator (fork length in millimeters) length was calculated as a ratio. Both standardized stomach fullness and prey–predator length ratio were tested for differences between juvenile Sablefish and juvenile Pacific salmon using the Kruskal–Wallis test ($p < 0.05$), as well as the difference in stomach fullness between Pacific salmon at stations where juvenile Sablefish were present or absent. All figures were created using the R package ggplot2.

Length, trophic characteristics, and energy density of juvenile Sablefish

Interannual changes in size of juvenile Sablefish (1998–2023) were tested using the nonparametric Kruskal–Wallis test for each year with significance at $p < 0.05$, which was used due to nonnormally distributed data. To examine interannual and ontogenetic diet differences of juvenile Sablefish, the prey were grouped into four fewer prey categories than the analysis between Pacific salmon and Sablefish (see above). Juvenile smelt (family Osmeridae), Palefin Sand Lance, Lingcod, and sculpin (family Cottidae) were rarely eaten by Sablefish and were all added to the “other fish” category (i.e., rare fish). Diet composition was calculated as percent weight of prey consumed by an individual fish. Diet data were averaged by station prior to analysis.

Juvenile Sablefish diets were analyzed for ontogenetic diet shifts in fish collected in 2020 only, due to the number and size range of the fish retained ($n = 191$). Diets were grouped with fish separated into 10-mm size-bins, with the three smallest size-bins representing too few fish, which were then merged into a single bin (60–89 mm; $n = 11$). Individual diets were averaged at each station by size-bin, followed by an overall average of all stations for each size-bin category. Bray–Curtis similarity matrix on overall averaged size-based diets were performed followed by cluster analysis to visually display the size-based diets (not shown) and similarity profile (SIMPROF) analysis, which identified two significant size categories of small (fish < 120 mm FL) and large (fish ≥ 120 mm FL; SIMPROF: $p < 0.05$; Figure S4). To identify which prey were significantly responsible for the diet differences between the small and large juvenile Sablefish, the individual small and large Sablefish diets were averaged at each station and similarity percentages (SIMPER) analysis was performed ($p < 0.05$).

Interannual diet differences of juvenile Sablefish were also examined between small and large juvenile Sablefish as defined above. Individual diets were averaged at the station level for each size-class in the following years: 2016 ($n = 12$), 2020 ($n = 191$), 2021 ($n = 27$), and 2023 ($n = 61$). A Bray–Curtis similarity matrix was calculated followed by an analysis of similarities (ANOSIM) test to identify any significant interannual diet differences for small and large juvenile Sablefish ($p < 0.05$). The Cluster, SIMPROF, SIMPER, and ANOSIM analyses were carried out using PRIMER6+ software (Clarke 1993).

Energy density was calculated on a subsample of juvenile Sablefish from 2020 ($n = 56$; 77–178 mm FL) using a Parr 6725 semimicro calorimeter (Parr Instruments, Moline, Illinois). To prepare samples for calorimetry, the whole body minus the stomach of each fish was placed into a desiccating oven at approximately 60°C for 72 h, recording the wet weight of the tissue before and the dry weight after desiccation. Dried samples were then pulverized into a homogenous powder before pressing into pellets ranging in size from 17 to 84 mg. Replicates of each fish were analyzed for energy density, and then the replicate values were averaged together. The average percent difference between the replicates was $1.6 \pm 1.3\%$. Standardization occurred every 10 runs using benzoic acid pellets. Energy density was reported as kilojoules per gram wet weight. An ANOVA test was used to identify any size-based energetic differences. Energy densities of the fish were grouped into the small and large size-bins based on the ontogenetic diet differences of the fish (< 20 mm and ≥ 120 mm; $p < 0.05$; Figure S4).

RESULTS

Juvenile Pacific salmon and Sablefish catches and VAST spatial–temporal model

Juvenile Sablefish were caught during May, June, and September sampling efforts, but peak catches were observed in June in coastal-shelf waters of central Oregon to northern Washington. The highest catches of juvenile Sablefish were in June of 2020, followed by 2023 and 2013, and in some years, there were no juvenile Sablefish collected (1998–2000, 2002, 2008, 2015, and 2019). Specifically in 2020, juvenile Sablefish were present at 63.8% of the stations sampled and were often caught at the same place as juvenile Pacific salmon (Figures S5–S8). Subyearling Chinook Salmon were caught at 27.7% of the stations sampled in 2020, and at 38.5% of these stations there was at least one juvenile Sablefish concurrently. Yearling Chinook Salmon were sampled at 25.5% of the sample stations, and juvenile Sablefish co-occurred at 41.7% of these stations. Juvenile Coho Salmon occurred at 48.9% of the stations sampled, with juvenile Sablefish at 43.5% of these stations. Within the sampling area of 44.7°N to 48.2°N and 124.0°W to 125.2°W in 2020, Sablefish were approximately four times more numerous than subyearling Chinook Salmon, 32 times more numerous than yearling Chinook Salmon, and 13 times more numerous than Coho Salmon in 2020.

In 2020, juvenile Sablefish had a 3.9-fold increase in the index of abundance compared with the 25-year average of the survey (Figure 2). The highest increases for Pacific salmon were a 2.1-fold increase for subyearling Chinook Salmon in 2010, a 2.0-fold increase for yearling Chinook Salmon in 2008, and a 1.4-fold increase for yearling Coho Salmon in 2003. However, the average coefficient of variation for the Sablefish index (1.72) was much larger than for the Pacific salmon (range = 0.21–0.34), implying more uncertainty in the Sablefish indices relative to the Pacific salmon, though not for all the study years (Figure 2). From 1998 to 2023, juvenile Sablefish exhibited the highest amount of observed and estimated spatiotemporal variability in density across the spatial domain, with no discernable patterns from year to year (Figures S5–S8). Pacific salmon exhibited less spatiotemporal variability, and on average, the highest densities (number/km²) of Pacific salmon were nearshore, with subyearling Chinook Salmon concentrated near the mouth of the Columbia River, yearling Chinook Salmon distributed from the Columbia River north, and yearling Coho Salmon centered more to the north but also some reaching southward (Figure 3; Figures S5–S8). Compared to Pacific salmon, which were consistently present at numerous stations in the survey domain each year, Sablefish were encountered

less frequently. However, when present, Sablefish densities were several times higher than those of the Pacific salmon (Figures 2, 3; Figures S5, S8). During the most recent 4 years, 2020 to 2023, the densities of Sablefish were highest offshore and to the south (Figure 3). Conversely, the subyearling Chinook Salmon densities were highest in the mid-latitudes, yearling Chinook Salmon densities higher nearshore, and yearling Coho Salmon densities were higher in the northern latitudes relative to the southern latitudes (Figure 3).

The VAST models that included covariates for basin-scale and local sea surface temperature produced a more parsimonious fit to the data compared with the models without covariates, which increased the Δ AIC [delta Akaike informatoin criteria] by 12.2). Higher encounter rates of juvenile Sablefish were found at stations with warmer 3-m station temperatures in June (Figure 4). For the encounter rates and densities of the other species categories, the effects of the SST covariates were less conclusive, as they were an order of magnitude smaller, and the sign of the effect often varied between the basin-scale and local covariates (Figure 4).

The larger covariate effects for Sablefish relative to salmonids are evident when comparing the magnitude of the indices of abundance for models with and without covariates. Including environmental covariates did not alter the years in which the maximum index was observed for Sablefish, subyearling Chinook Salmon, and yearling Chinook Salmon (2020, 2010, and 2008, respectively). However, for Coho Salmon, the year of the maximum index shifted from 2003 to 2008 when covariates were included. The relative index of abundance for Sablefish decreased by almost half, from 6.7 to 3.9, compared with the model without temperature covariates. There were no changes in the relative index of abundance between models with temperature covariates for subyearling Chinook Salmon. Finally, there were minimal changes in the relative index of abundance between models without temperature covariates for yearling Chinook Salmon (2.0–2.3), and Coho Salmon (1.4–1.3).

Juvenile Pacific salmon and Sablefish trophic characteristics in June 2020

Overall, juvenile Pacific salmon and Sablefish consumed the same prey types but in different proportions. The top taxa consumed by subyearling Chinook Salmon (average predator length \pm standard deviation [SD] = 106.4 \pm 13.1 mm FL) were copepods, amphipods, and juvenile smelt (Table 1). Top taxa consumed by yearling Chinook Salmon were unidentified fish, juvenile rockfish, and squid (average predator length \pm SD = 189.9 \pm 42.2 mm FL). Top prey of juvenile Coho

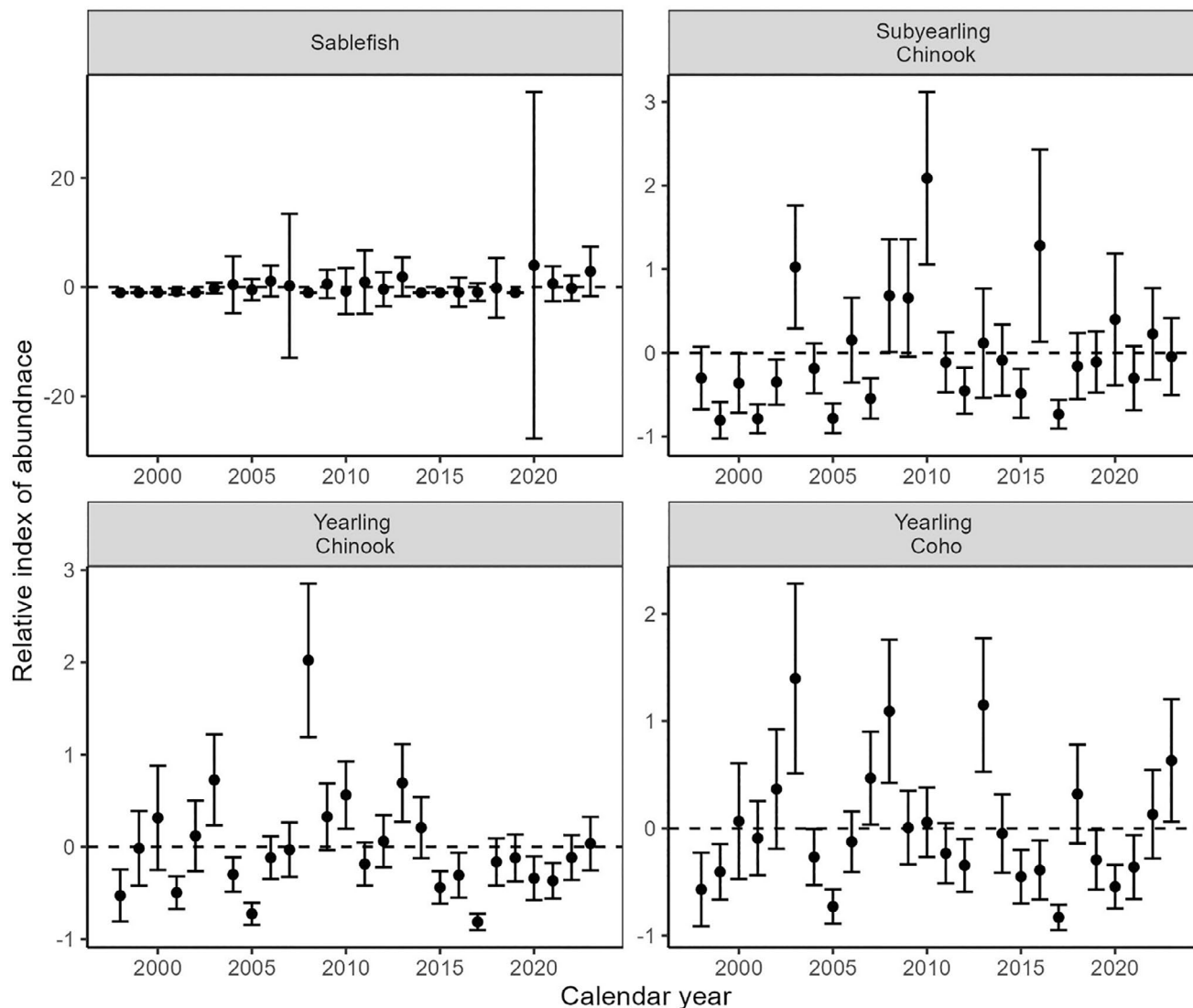


FIGURE 2 Ratio (error bars show 90% CI) between annual and mean indexes of abundance (the product of encounter rates and catch rates integrated over the spatial domain of the survey) for the four species categories from 1998 to 2023. Note the differences in the y-axis scales.

Salmon were juvenile rockfish, krill, and crab megalopae (average predator length \pm SD = 170.2 ± 33.8 mm FL). The top prey consumed by the small Sablefish were copepods, krill, and gelatinous zooplankton (average predator length \pm SD = 97.1 ± 10.9 mm FL), and the top prey consumed by large Sablefish were krill, crab megalopae, and juvenile rockfish in 2020 (average predator length \pm SD = 152.9 ± 13.2 mm FL; Table 1). Coho Salmon and large juvenile Sablefish had the highest diet composition similarity in ordination space due to the consumption of similar types and proportions of prey, followed by modest similarity with yearling Chinook Salmon. The smaller Sablefish had modest diet similarity with subyearling Chinook Salmon and the lowest similarity with the larger yearling Pacific salmon (Figure 5). The PSI results resembled the ordination plot such that average diet overlap between juvenile Sablefish and juvenile Coho

Salmon was moderate (PSI = 32.4%) at the station level and lower between Sablefish and subyearling Chinook Salmon (19.4%) and yearling Chinook Salmon (24.0%).

Sablefish in 2020 had significantly more food in their stomachs than all three Pacific salmon groups (ANOVA; $p < 0.0001$), and length was not a significant covariate. The majority of juvenile Pacific salmon and Sablefish had food in their stomachs. Only 6.7% of subyearling Chinook Salmon, 8.0% of yearling Chinook Salmon, 10.9% of Coho Salmon, and 5.2% of Sablefish had empty stomachs. Subyearling Chinook Salmon had the lowest average stomach fullness \pm SD at $0.76 \pm 0.77\%$, followed by yearling Chinook Salmon at $0.90 \pm 0.83\%$ and Coho Salmon with $1.84 \pm 1.81\%$ average stomach fullness (Figure 6). Juvenile Sablefish average stomach fullness \pm SD was $3.04 \pm 3.70\%$ of their body weight (Figure 6). Over 7% of the juvenile Sablefish had stomach

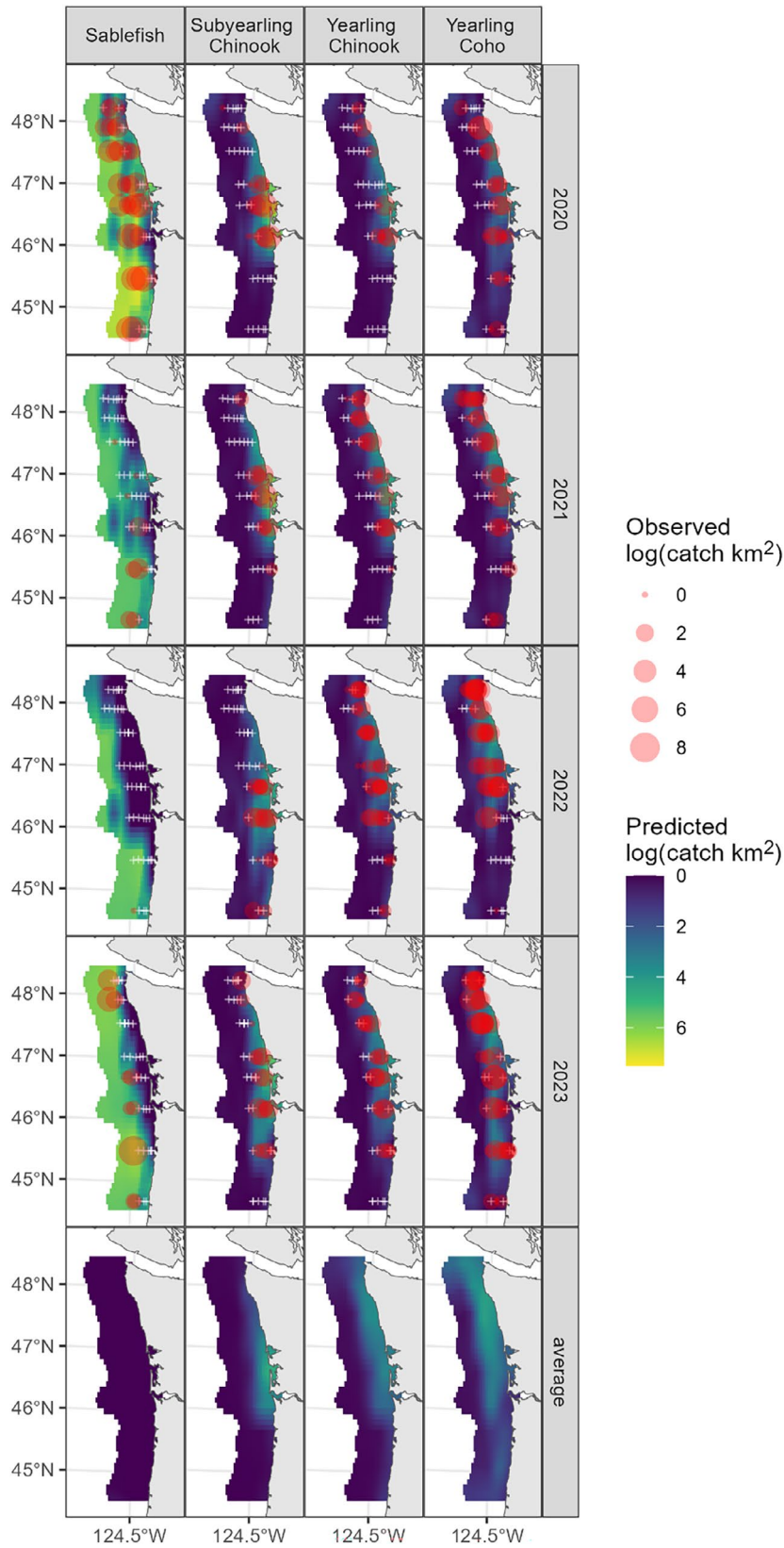


FIGURE 3 Estimated densities of juvenile Sablefish, subyearling Chinook Salmon, yearling Chinook Salmon, and Coho Salmon in an average year and 2020 to 2023. Red points represent locations and size of the log of the observed catches, and plus signs indicate locations where fish were not captured.

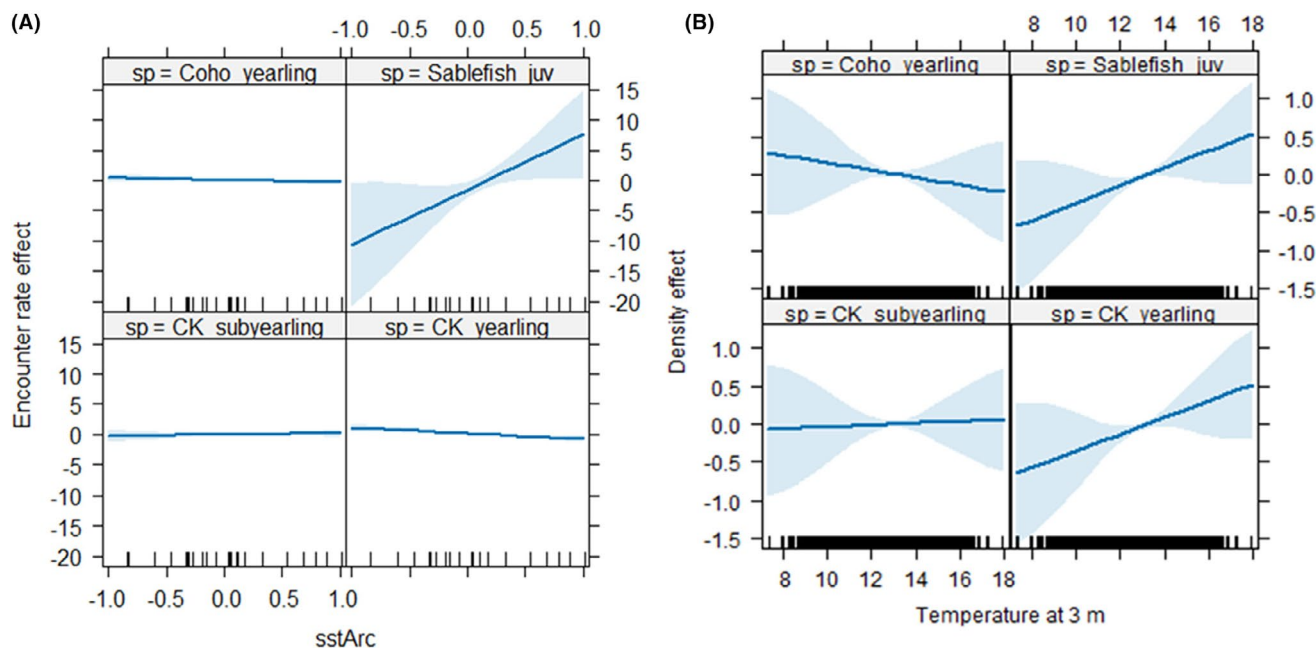


FIGURE 4 (A) Relative effect of an integrated measure of sea surface temperature across an arc in the northeast Pacific Ocean during the previous month (May) of each year (SSTarc) for encounter rates and (B) the relative effect of water temperature at 3 m in June on densities for the four species groups. The SSTarc was based on the anomaly of the average sea surface temperature in the arc of the northeast Pacific Ocean as described in Johnstone and Mantua 2014.

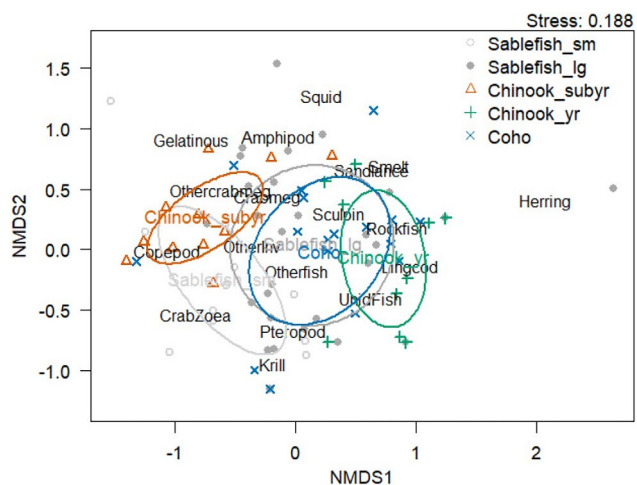


FIGURE 5 Nonmetric multidimensional scaling ordination of the diet composition of small juvenile Sablefish (<120 mm FL; gray circle), large juvenile Sablefish (≥ 120 mm FL; filled gray circle), subyearling Chinook Salmon (orange triangle), yearling Chinook Salmon (green plus), and Coho Salmon (blue x). Ellipses encompass the major and minor axes of each species and are the color of the predator as listed above and the location of prey species (black text) that are most associated with each axis.

fullness $\geq 10\%$ of their body weight; the fullest Sablefish weighed 35.9 g and consumed 5.4 g of food or 17.7% of its body weight. None of the Pacific salmon had a stomach fullness greater than 7.2%. Stomach fullness of subyearling Chinook and Coho salmon was significantly lower

at stations where juvenile Sablefish occurred (Figure 7). Subyearling Chinook Salmon had an average stomach fullness \pm SD of $0.38 \pm 0.35\%$ when they were caught together with juvenile Sablefish, which was significantly lower than their stomach fullness at stations where there were no juvenile Sablefish present ($0.97 \pm 0.86\%$; Kolmogorov–Smirnov test: $p < 0.001$; Figure 7). Coho Salmon stomach fullness was also significantly lower ($1.62 \pm 1.87\%$) when they were in spatial overlap with the Sablefish versus $2.02 \pm 1.76\%$ when there was no spatial overlap (Kolmogorov–Smirnov test: $p = 0.04$). Yearling Chinook Salmon had lower stomach fullness when Sablefish were present, but there was not a significant difference (Figure 7).

Juvenile Sablefish were able to consume significantly larger fish prey for their size than either of the yearling juvenile Pacific salmon. Juvenile Sablefish had an average prey-to-predator ratio of 0.32 ± 0.05 , which was a significantly higher fish prey-to-predator ratio than for yearling Chinook Salmon at 0.23 ± 0.06 or for yearling Coho Salmon at 0.24 ± 0.05 (Kruskal–Wallis: $p < 0.001$; Figure 8). Juvenile Sablefish consumed juvenile rockfish of the same size range as those consumed by the juvenile Pacific salmon, even though the Sablefish were approximately 40 mm smaller in fork length (Figure 8). The Sablefish prey length/predator length relative to their length is described by linear regression with the following equation: $\text{PreyFL} = -47.9494 + 0.5835 \times \text{SablefishFL}$ ($p < 0.001$; $r^2 = 0.93$; Figure 8). There were too few freshly consumed fish prey to calculate a prey-to-predator ratio on subyearling Chinook Salmon.

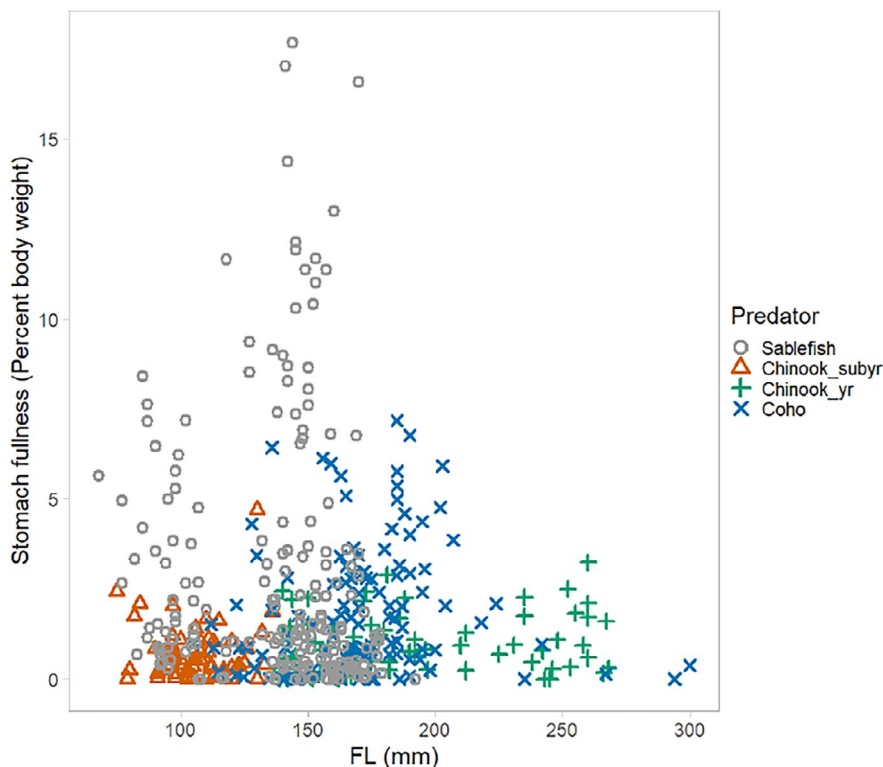


FIGURE 6 Standardized stomach fullness by fork length for juvenile Sablefish (gray circle), subyearling Chinook Salmon (orange triangle), yearling Chinook Salmon (green plus), and Coho Salmon (blue x) in June 2020.

Juvenile Sablefish size, ontogenetic and interannual diet patterns, and energy density

The average size \pm SD of juvenile Sablefish (all years combined) was 87.0 ± 24.0 mm FL in May, 141.9 ± 31.8 mm FL in June, and 250.4 ± 26.5 mm FL in September (Figure 9). Length-frequency plots of juvenile Sablefish in June showed that juvenile Sablefish were large in 2004 when very few fish were <150 mm FL, and in 2016 and 2020 the size-frequency plots had a bimodal size distribution (Figure 10). Sablefish in 2004 and 2016 were significantly larger than all the other years, and fish caught in 2023, 2018, 2021, and 2020 were significantly larger than all the rest of the years (Kruskal–Wallis; $p < 0.001$). Juvenile Sablefish were longer on average during June surveys, when the ocean surface temperatures were warmer, with the exception of 2017 (Figure 10). The length–weight relationship for the retained 2020 juvenile Sablefish was $\log_{10}(\text{weight in g}) = -5.396 + 3.19015 \times \log_{10}(\text{fork length in mm})$ ($p \leq 0.0001$; $r^2 = 0.98$; $n = 193$).

Juvenile Sablefish exhibited significant ontogenetic shifts in diet composition, with fish between 60 and 119 mm consuming significantly different prey than fish 120–179 mm FL (Figure 11; SIMPROF; $p < 0.05$). The prey responsible for the significant size-based diet differences between the smaller and larger Sablefish were that smaller Sablefish ate more copepods (SIMPER; 14.4%),

whereas larger juvenile Sablefish ate more crab megalopae (SIMPER; 10.8%) and juvenile rockfish (9.5%; SIMPER; Figure 11). Sablefish were piscivorous within every size-bin (Figure 11), and the Sablefish that were 60–119 mm had a diet composition that was on average 24.5% fish prey, and larger Sablefish had on average 42.2% fish prey. Diets did not significantly vary interannually for either small or large Sablefish (ANOSIM; $p > 0.05$).

Lastly, the energy density of smaller juvenile Sablefish was significantly lower than that of larger Sablefish (ANOVA: $p < 0.001$). Small Sablefish (<120 mm; $n = 27$) had an average caloric value \pm SD of 4.5 ± 0.3 kJ/g wet weight (21.3 ± 0.75 kJ/g dry weight). Larger Sablefish (>120 mm; $n = 29$) had an average energy density \pm SD of 4.8 ± 0.3 kJ/g wet weight (21.8 ± 0.64 kJ/g dry weight).

DISCUSSION

Juvenile Sablefish have expanded their distribution into nearshore waters over the past 26 years, coinciding with climate-driven increases in ocean temperatures. This nearshore expansion has resulted in increased spatial overlap between juvenile Sablefish and recently out-migrated juvenile Pacific salmon during the critical early marine phase of their life cycle. During warmer ocean conditions, juvenile Sablefish consumed similar types of

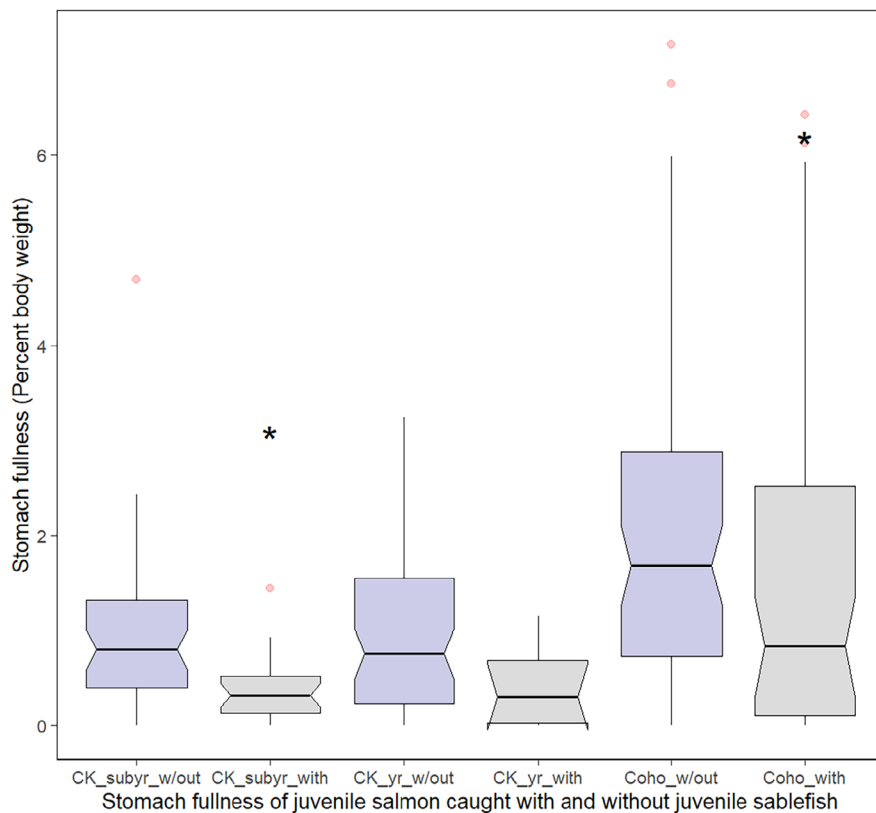


FIGURE 7 Standardized stomach fullness of juvenile Pacific salmon at sampling stations with and without juvenile Sablefish in June 2020. Significant differences ($p < 0.05$) between Pacific salmon stomach fullness with and without Sablefish are denoted by an asterisk. Box plot displays median and interquartile range, with the notch displaying the confidence interval around the median, and circles are outliers.

prey as the Pacific salmon in nearshore waters, which could have negative consequences for Pacific salmon populations that are already in severe decline (Crozier et al. 2021; Beamish 2022). In 2020, juvenile Sablefish exhibited several competitive advantages relative to juvenile Pacific salmon in the NCC, including consuming more food per meal relative to predator size and having the ability to forage on larger fish prey sizes for a given predator size. Juvenile Sablefish, with their feeding advantages, could access more food, potentially placing Pacific salmon at a disadvantage, especially when food resources are limited. Moreover, these competitive advantages increase if Sablefish become more numerically dominant compared with Pacific salmon and forage for the same prey resources.

Comparing the distribution and year-to-year variability of juvenile Sablefish and Pacific salmon densities showed distinct differences between the populations and their response to ocean temperature. Juvenile Sablefish had a larger interannual change in density, relative to the Pacific salmon, and higher coefficient of variation across the survey domain, with catch and encounter rates positively related to warmer basin- and local-scale temperatures. Even when the models account for temperature-driven effects, however, encounter rates

and densities of Sablefish have increased within the sampling domain in June. Catch data from the Northwest Fisheries Science Center's (NWFSC) bottom-trawl survey (2003–2015) indicated that newly settled juvenile Sablefish were collected in highest numbers around 44–45°N (Tolimieri et al. 2018). In contrast, the spatial-temporal model of surface-caught juvenile Sablefish did not show increased catches in the southern end of the survey area (44–45°N) during the study period, and the catches were many times higher than those caught in the bottom-trawl survey, which used a net designed to catch larger fish (Tolimieri et al. 2018). Pacific salmon, on the other hand, had lower spatial variability, and the overall model average showed that Pacific salmon were concentrated around the Columbia River mouth and northward, with small numbers of Coho Salmon also in the south. The low spatial variability of Pacific salmon in June is understandable because Pacific salmon enter the ocean in spring and summer from the Columbia River, or rivers along Oregon and Washington coasts, and begin to migrate northward (Weitkamp 2010; Weitkamp et al. 2012; Teel et al. 2015). Overall, while juvenile Sablefish exhibited significant interannual changes in density and high variability in distribution associated with temperatures, Pacific salmon displayed lower spatial variability and a

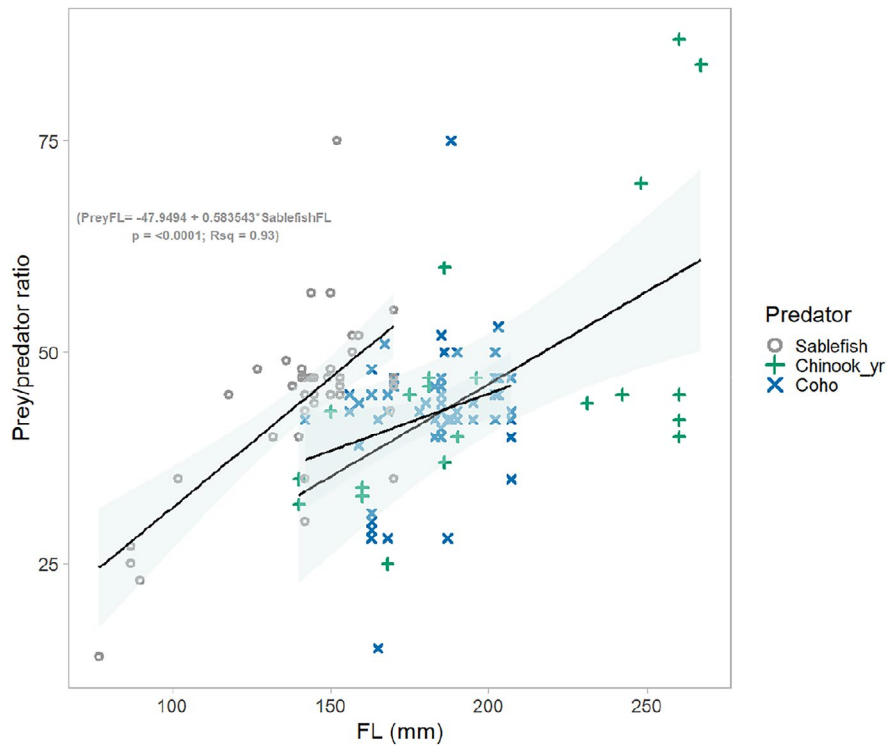


FIGURE 8 Fish prey–predator ratio by fork length for juvenile Sablefish (gray circle), yearling Chinook Salmon (green plus), and Coho Salmon (blue x) in June 2020. The significant relationship between prey length and predator length for juvenile Sablefish is in gray text. Too few fresh fish were consumed by subyearling Chinook Salmon to display.

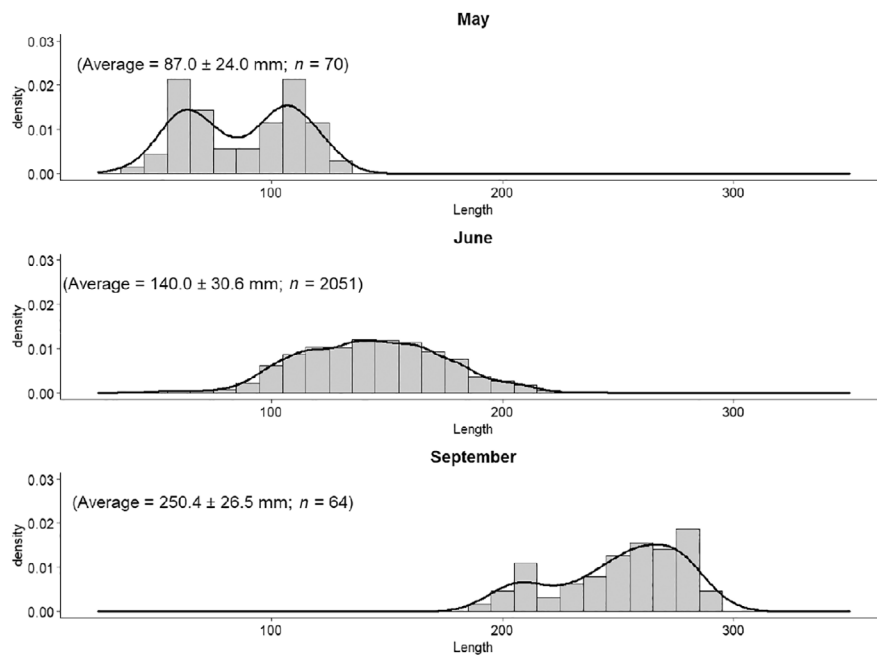


FIGURE 9 Fork length (mm) density distribution plots of juvenile Sablefish during their first marine summer: May, June, and September. All years are combined, and the average ± SD fork length and sample size are in small text.

concentration around the Columbia River, consistent with their recent freshwater life history.

Understanding how climate-driven changes in species distribution and abundance affect trophic interactions in populations is important for successful

management of fisheries (Venegas et al. 2023, Gleiber et al. 2024a, Gomes et al. 2024a). Most climate research has focused on changes in distribution and not how trophic interactions are altered (Green et al. 2022). Recent temperature-driven changes in nekton abundance and

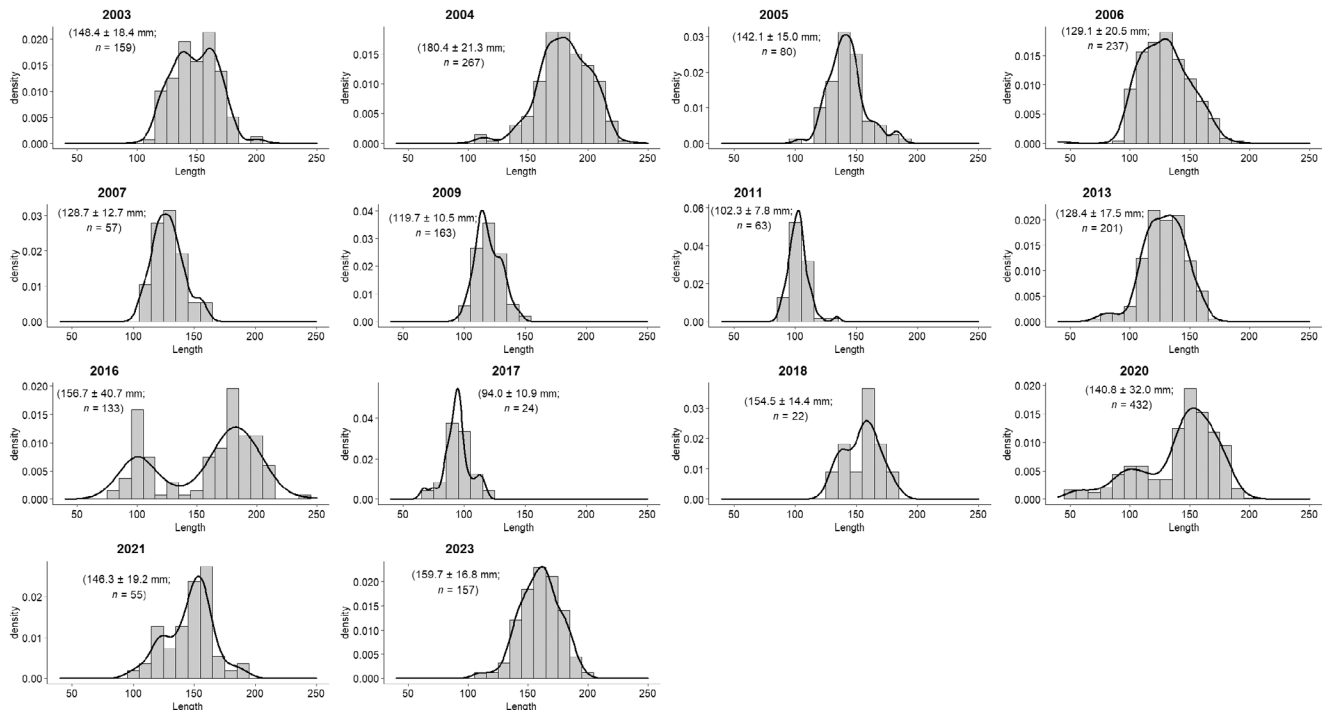


FIGURE 10 Fork length (mm) density distribution plots of juvenile Sablefish sampled in June by year, with average \pm SD length and sample size in small text.

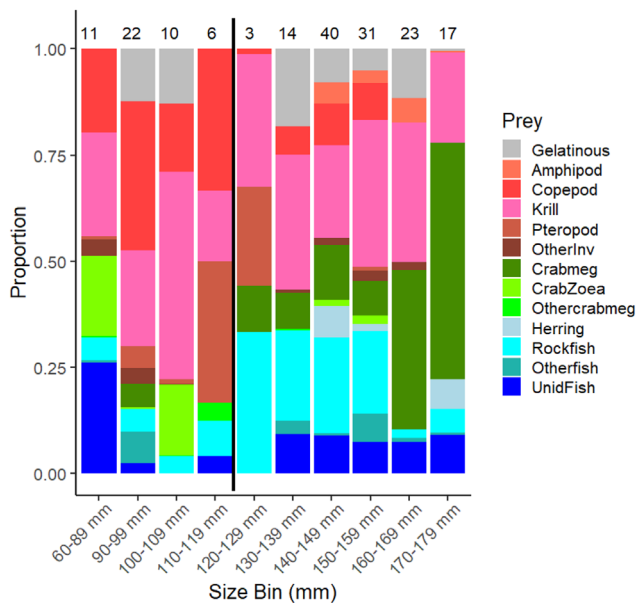


FIGURE 11 Diet composition of juvenile Sablefish by size-bins based on proportion of prey consumed (wet weight), with sample size at the top of the bar plots. The vertical line denotes the size where diets were significantly different between the size-bins based on similarity profile analysis. See Table 1 for explanation of prey items.

distribution are well documented in the NCC (Santora et al. 2017; Auth et al. 2018; Brodeur et al. 2019; Morgan et al. 2019; Thompson et al. 2019; Barbeaux et al. 2020).

For example, the distribution and abundance of market squid *Doryteuthis opalescens* (Chasco et al. 2022) have changed in relation to warmer sea surface temperatures, in that their distribution has radiated northward over the past 20 years. Because this movement has increased spatial overlap with Endangered Species Act-listed Columbia River juvenile Pacific salmon, it is important to understand the recent trophic habits of market squid to estimate the impact they may have on Pacific salmon. Earlier studies of market squid showed that they consumed prey types such as crab megalopae, krill, and juvenile fish and fed at relatively similar trophic position to both juvenile Pacific salmon and Sablefish (Miller and Brodeur 2007; Miller et al. 2010; present study), all of which reside together in the upper water column. Building a traits-based framework of the micronekton that Pacific salmon and other predators feed upon in the NCC can help us better predict how prey–predator interactions could change due to warming ocean conditions (Gleiber et al. 2024b). Additionally, a recent update of a NCC end-to-end ecosystem model, which included data from the recent increases in market squid, allows modeling of how climate and changes in predator–prey relationships affect the marine food web (Gomes et al. 2024b).

Exploitative competition for food resources occurs when one competitor attempts to access a shared resource and consumes more of it first. Overall temperature can affect feeding behavior and intake amount but also how

food is digested and absorbed and how much energy is allocated towards activity and growth, which varies by species (Volkoff and Rønnestad 2020). The average stomach fullness of juvenile Sablefish was many times higher than both subyearling and yearling Chinook Salmon and approximately 30% higher than Coho Salmon in 2020. The extremely high stomach fullness of Sablefish observed during this study, which documented that 7% of the Sablefish consumed >10% of their body weight in food, was also observed in Sablefish in southeastern Alaska (Sturdevant et al. 2009). With over 16,000 juvenile Pacific salmon stomachs analyzed, just 0.03% had stomach fullness >10% (Bizzarro et al. 2023). In terms of amount of food eaten per meal, juvenile salmonids are clearly inferior competitors relative to Sablefish that have the physical ability to consume more per meal than juvenile Pacific salmon.

The age-0 recruitment for Sablefish in 2020 was one of the highest observed (Johnson et al. 2023). Juvenile Pacific salmon returned as adults from out-migration year 2020 in average numbers (Chinook Salmon) and above average numbers (Coho Salmon), suggesting sufficient food resources for both Pacific salmon and Sablefish in 2020 (https://www.fpc.org/web/apps/adultsalmon/Q_adult_counts_annualtotalsquery.php; last accessed March 2024). Even though Pacific salmon had lower stomach fullness when they were co-located with juvenile Sablefish, the negative impacts to Pacific salmon survival appeared to be minimal in 2020. Pacific salmon feeding at reduced rates in the presence of Sablefish could have occurred for several reasons, such as uneven prey distribution, differential feeding rates, and/or possibly feeding suppression of Pacific salmon in the presence of juvenile Sablefish. Stomach fullness of subyearling Chinook Salmon has also been shown to be significantly less in the presence of high biomasses of the Pacific sea nettle jellyfish *Chyrsora fuscescens* (Ruzicka et al. 2016). Additionally, the overall stomach fullness of Pacific salmon in 2020 was little different from other years (Brodeur et al. 2007; Dale et al. 2017; Daly et al. 2017). In the end, when there are plenty of food resources, both Pacific salmon and Sablefish can grow well together.

It is unknown if the *nearshore* juvenile Sablefish sampled survived and successfully recruited to the adult population. In general, earlier fish hatch dates and higher growth rates during the larval and juvenile stages have been observed during warmer ocean conditions (Atkinson 1994). Results are mixed on whether or not earlier and shorter egg, larvae, and/or juvenile duration of fish in warmer ocean conditions were followed by positive changes in recruitment success and population growth (Fennie et al. 2023; Szuwalski et al. 2023; Almeida et al. 2024). A positive correlation between

temperature and growth has been identified for larval and early juvenile stages of Sablefish (Sogard 2011; Tolimieri et al. 2018), and in 2020, the age-0 Sablefish recruitment was estimated to be greater than any other recruitment year in the >100-year time series (Johnson et al. 2023). If the numbers of juvenile Sablefish continue to increase relative to Pacific salmon, competition pressure could also escalate, especially if food resources decline. The adverse effects of competition on Pacific salmon may arise regardless of whether or not juvenile Sablefish that expanded into nearshore waters successfully recruit to the adult population. Future work could include sampling the population further from shore and conducting stable isotope analysis of adult Sablefish that have successfully recruited into the population in order to reconstruct ontogenetic feeding habitats and any changes in feeding location (Gao et al. 2004). What is known is that Sablefish have recently had unprecedented recruitment successes during warm conditions, and managers responded by increasing annual catch limits (<https://www.regulations.gov/document/NOAA-NMFS-2023-0108-0001>; last accessed March 2024). Rapid responses of increased catch limits after large recruitment events may aid in reducing the possibility of large-scale density-dependent mortality.

Sablefish can consume large prey for their size and have been documented preying on juvenile Pacific salmon that were one-third to half of their body length (Sturdevant et al. 2009). This study estimated that a 200-mm-FL Sablefish could consume a 68.7-mm fish, approximately the size of the smallest subyearling Chinook Salmon caught during sampling, but no predation on salmonids was identified. Only during the warm ocean conditions of 2004 and 2016 had some juvenile Sablefish grown to larger than 200 mm by late June, which limited the possibility of age-0 Sablefish consuming small Pacific salmon early in the summer. The size of juvenile Sablefish sampled in surface waters has been shown to increase throughout the summer, with the largest juvenile Sablefish being approximately 300 mm FL (McFarlane and Beamish 1983; Brodeur and Pearcy 1986; present study). By fall, age-0 Sablefish begin to reside deeper in the water column. These fish, along with Sablefish age 1 to age 2, will sometimes migrate to shallow waters to feed (Kendall and Matarese 1987; Coutré et al. 2017; Ehresmann et al. 2018) and modify their movements according to food availability (Sogard and Olla 1998 [laboratory study]). As such, the greater predation risk to Pacific salmon by young Sablefish appears to come from 1- to 2-year-old Sablefish that migrate to shallow waters for feeding, especially in spring and summer, when the juvenile Pacific salmon are small (Ehresmann et al. 2018). Diet analysis of groundfish sampled during NMFS's 2019 bottom-trawl survey revealed that an age-2 Sablefish consumed at least one hatchery

spring yearling Chinook Salmon in the upper Columbia River basin shortly after the Chinook Salmon entered the ocean weeks earlier, based on tagged information (D. L. Draper, unpublished data). While juvenile Sablefish have the potential to prey on juvenile Pacific salmon, this study found no evidence of such predation in 2020, suggesting that the risk is minimal during the early ocean entry period for Pacific salmon but may increase as Sablefish grow and their movements change.

Early onset of piscivory can be critical to the growth and survival in marine fishes (Keeley and Grant 2001; Reglero et al. 2014; Callahan et al. 2021b), and approximately 25% of the smallest juvenile Sablefish in this study consumed fish prey, while Sigler et al. (2001) observed that similarly sized Sablefish rarely ate fish prey. Grover and Olla (1987) analyzed the diets of age-0 Sablefish less than 28.5 mm and did not find any fish in the diets. The smallest Sablefish analyzed for diets in this study was 68 mm and 31% of its diet was fish, so the onset of piscivory likely occurs in fish between 28.5 and 68 mm. Approximately 30% of the diets of 68–180-mm Sablefish were fish prey, and by the time juvenile Sablefish (age 0) are benthic and over 200 mm, they are eating closer to 70–80% fish prey (Callahan et al. 2021b). Growth of juvenile Sablefish under laboratory conditions was optimized at temperatures between 12°C and 16.8°C, and using bioenergetics modeling, when juvenile Sablefish consumed high-energy food such as fish prey while feeding at just 55% of their maximum capacity, they can grow to be the size observed in the ocean (Krieger et al. 2020). Both Krieger et al. (2020) and Sogard (2011) suggested that there may be a link between the timing of the onset of piscivory and their recruitment success, and the juvenile Sablefish in 2020 were more piscivorous than previous studies (Grover and Olla 1987). There was also a significant positive energy–size relationship between the smaller and larger juvenile Sablefish, which may reflect increased foraging success as observed in Callahan et al. (2021a). The energy density values from this study were similar to those observed by Callahan et al. (2021a), though higher than those observed by Van Pelt et al. (1997), which were indirectly derived from proximate composition rather than bomb calorimetry.

CONCLUSIONS

Sablefish have seen marked increases in recruitment, from across their entire geographic range of California to the Bering Sea, since the onset of warm ocean condition in 2014–2015 and are predicted to have favorable recruitment under future climate scenarios (Haltuch et al. 2019; Fisheries and Oceans Canada 2020; Goethel et al. 2021; Zolotov 2021). Conversely, some Pacific salmon

populations along the west coast of North America have been declining since the warm ocean conditions of 2014–2015 and are predicted to have rapid declines under future climate scenarios (Katz et al. 2013; Wells et al. 2020; Crozier et al. 2021; Weber et al. 2021; Beamish 2022). Modeling results demonstrated that increased temperature in nearshore waters has opened up more habitat for juvenile Sablefish to feed and grow in direct competition with recently out-migrated juvenile Pacific salmon. With Pacific salmon and Sablefish eating similar prey types and Sablefish having higher feeding intensity, growth rates, and the ability to eat larger prey for their size, juvenile Pacific salmon could experience an increased competitive disadvantage. Some Pacific salmon populations are already predicted to decrease primarily due to ecological responses to increased ocean temperatures. Yet their outlook could be worse than previously thought if novel trophic interactions with a competitor like juvenile Sablefish continue to increase. Understanding these interactions and their potential impacts is important for the effective management and conservation of these species.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

All data available upon request to the corresponding author.

ETHICS STATEMENT

Fish sampling and handling protocols were in compliance with Oregon State University Institutional Animal Care and Use Committee (IACUC 2022–0269) policies, and NMFS does not require an Institutional Animal Care and Use Committee review. Collections were made with scientific research permit #1410-14R with the Endangered Species Act Section 10.

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SUPPORTING INFORMATION

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