

ARTICLE

# Temporal and Age-Based Variation in Juvenile Sablefish Diet Composition and Quality: Inferences from Stomach Contents and Stable Isotopes

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## Abstract

Prey communities in the North Pacific Ocean have been disrupted by marine heatwaves, and reductions in forage fishes have had notable impacts on upper-trophic-level consumers. Little is known about the potential effects of a changing prey base for some commercially valuable fishes, such as Sablefish *Anoplopoma fimbria*. The objectives of this study were to evaluate temporal and age-based shifts in diets of juvenile Sablefish, with a focus on understanding their reliance on high-quality forage fishes. We collected Sablefish from a bay in Southeast Alaska over 2 years (2017–2019) during their first autumn (September–October; age 0), in late winter (March; age 1), and during their second summer (July; age 1). Pacific Herring *Clupea pallasii* constituted the majority of the Sablefish diet by weight (82.1%) and by frequency of occurrence (40.7%), with variation among months, years, and age-classes. Stable isotopes corroborated our interpretation of diet composition from stomach contents and indicated that age-0 Sablefish sampled in October 2017 relied on more depleted carbon sources than other groups, potentially explained by consumption of adult salmon carcasses. Significant relationships between stable isotope ratios and Sablefish length indicated that size-based diet composition differences were most prevalent during March and July. Sablefish exploited

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prey taxa of variable quality (0.02–5.3 kJ/g), but mean energy density of consumed prey differed little among years or months (3.62–4.48 kJ/g). Overall, 21% of stomachs sampled were empty, with the percentage of empty stomachs peaking in late winter (46%). Stomach content weights expressed as a percentage of body weight were highest in autumn 2018, when Pacific Herring comprised over 80% of the diets by weight. Consumption of high-energy prey, such as Pacific Herring, may contribute to rapid growth of Sablefish during the critical prewinter period. If strong Sablefish year-classes become more frequent with a warming ocean, they will require substantial prey resources to support their growth to adulthood.

The North Pacific Ocean ecosystem is undergoing dramatic ecological changes as warmwater anomalies, known as marine heatwaves, become more frequent (Cavole et al. 2016; Frölicher et al. 2018; Oliver et al. 2018). Shifts in lower-trophic-level production resulting from the marine heatwave of 2014–2016 (Bond et al. 2015) have had cascading effects on higher-trophic-level species. Plankton productivity was low during recent heatwave events (Whitney 2015), and zooplankton communities shifted toward fewer large, energy-rich copepods (McKinstry and Campbell 2018). Abundance of forage fishes, which rely on zooplankton prey, subsequently declined (Suryan et al. 2020); for example, Pacific Herring *Clupea pallasii* (hereafter, "herring"), Pacific Sand Lance *Ammodytes hexapterus*, and Capelin *Mallotus villosus* experienced dramatic reductions in abundance, growth, and body condition during the 2014–2016 marine heatwave in the Gulf of Alaska (Zador and Yasumiishi 2017; Sewall et al. 2019; Thompson et al. 2019; von Biela et al. 2019). These declines in energy-rich forage fishes coincided with nutritional stress and mortality events in higher-trophic-level consumers, including Pacific Cod *Gadus macrocephalus* (Barbeaux et al. 2020), seabirds (Cavole et al. 2016; Piatt et al. 2020), and baleen whales (Savage 2017). Warm waters proved beneficial to some marine species; for instance, gelatinous zooplankton increased in abundance (Brodeur et al. 2018), southerly copepods were more prevalent in Alaskan waters (Batten et al. 2018), and squid were abundant north of their historic range (Cavole et al. 2016).

In the Gulf of Alaska, one commercially valuable marine fish species that apparently thrived during recent marine heatwave events is the Sablefish *Anoplopoma fimbria*. Record-high Sablefish year-classes were reported in the Gulf of Alaska in 2014 and 2016 after a 13-year period of low recruitment (Hanselman et al. 2018). Juvenile Sablefish may be particularly suited to warming oceans. Growth is maximized at relatively warm temperatures of 20°C for age-0 Sablefish (Sogard and Olla 2001) and 16°C for age-1 Sablefish (Krieger et al. 2019), and growth rates of young-of-the-year Sablefish are among the highest known in any teleost (Sogard and Olla 2001). This prodigious growth is fueled by high prey consumption requirements. Using a bioenergetics model, Krieger et al. (2020) estimated that juvenile Sablefish would have needed to feed on energy-rich prey at 55% of their maximum

consumption rates or higher to achieve growth observed in the wild during 2017. Food availability is critical for pelagic juvenile Sablefish, and growth drops dramatically under low-ration conditions (Sogard and Spencer 2004). Thus, while Sablefish appear to physiologically benefit from warm temperatures, surviving their first winter may depend substantially on access to high-quality prey prior to—and perhaps during—the winter period.

Juvenile Sablefish are known to consume high-energy prey that are patchy in space and time, including herring (McFarlane and Beamish 1983; Coutré et al. 2015), juvenile salmon *Oncorhynchus* spp. (Sturdevant et al. 2009), and scavenged adult salmon carcasses (Coutré et al. 2015). However, research on the trophic ecology of postsettlement juvenile Sablefish is limited to only a handful of studies that focused primarily on age-1 individuals during their second summer and autumn (e.g., Sturdevant et al. 2009; Coutré et al. 2015). Seasonal foraging habits of postsettlement juvenile (age-0 and age-1) Sablefish are understudied, despite the potential link between prewinter energy acquisition and survival, as observed in other Alaskan groundfishes (e.g., Heintz et al. 2013). Little is known about temporal shifts in diets of postsettlement Sablefish during their first 2 years, including the composition and energetic quality of prey consumed across multiple seasons. Diets may also shift with size, as larger consumers may be capable of consuming a wider variety of prey types and sizes (Scharf et al. 2000). Ontogenetic diet shifts during the first year of life can account for improved growth, energy storage, and overwinter survival in other fish species (Sutton and Ney 2001; Sewall et al. 2019).

The goal of this study was to fill gaps in knowledge of Sablefish feeding ecology during their postsettlement juvenile life stage (ages 0 and 1). Our objectives were to assess temporal, age-based, and size-based shifts in (1) the taxonomic composition of juvenile Sablefish diets and (2) the quality of prey consumed (i.e., diet quality). Our work builds on past studies by using multiple metrics to evaluate diet composition—stomach contents and stable isotope ratios of carbon and nitrogen—over multiple months, years, and age-classes. We also assessed temporal and age-specific shifts in diet quality to determine when Sablefish may experience higher levels of nutritional stress. We described the nutritional quality of Sablefish diets based on energy densities of stomach contents, relative stomach

content weight (% of body weight), and the percentages of empty stomachs.

**METHODS**

*Field sampling.*—Larval and early juvenile Sablefish reside in the neuston during their first summer and settle into nearshore bays and estuaries as late juveniles in their first autumn (Rutecki and Varosi 1997), spending the next year in these habitats before migrating to deep adult habitat of 200–800 m (Figure 1). We focused on postsettlement stages (age 0 and age 1); therefore, sampling occurred during autumn (September–October), late winter/early spring (March–May), and summer (July) for 2 years (Table 1). Each sampling period was 4–6 d in duration (Table 1). Sablefish were obtained from Saint John Baptist Bay (SJBB), a small bay (3 km in length) on the coast of Baranof Island, Alaska (57.2868°, 135.5659°; Figure 2). Saint John Baptist Bay is 70 m deep at the mouth, but most Sablefish were caught near the head at depths around 25 m. An anadromous stream flows into the bay, and a logging transfer station once existed on the northern shore. Surveys conducted by the National Marine Fisheries Service during the 1980s and 1990s identified SJBB as the only nursery area in Southeast Alaska where juvenile Sablefish are consistently present in high densities (Rutecki and Varosi 1997).

Sablefish were caught by hook and line following the methods of Coutré et al. (2015) and Callahan et al. (2021). We used squid mantles cut into uniform rectangular strips for bait, which allowed us to distinguish bait from any naturally consumed squid prey. Sablefish stomach contents were obtained using gastric lavage according to the methods of Coutré et al. (2015). In brief, we anesthetized, measured, weighed, and conducted gastric lavage on Sablefish. Stomach contents were initially stored frozen so that intact prey items could be used for energy density analysis (see below). The first 20–30 fish caught were euthanized and retained for stable isotope analysis, while

additional Sablefish, sampled for stomach contents only, underwent a short recovery period in clean seawater and were released at their site of capture. We also retained additional fish if necessary to ensure that the subsample was representative of the length distribution of the catch. An opportunistic sample of age-0 Sablefish was donated by commercial salmon fishermen who observed unusually high numbers of pelagic juvenile Sablefish in their purse seines in Deep and Crawfish inlets, about 60 km south of SJBB, during September 2018. These fish were frozen after capture, delivered to the authors, and processed in the same manner as retained Sablefish from SJBB.

*Laboratory processing.*—In the laboratory, frozen stomach contents were transferred to ethanol prior to processing, except for prey items that were removed for energy content and isotope analysis (below). Total stomach content mass was weighed (blotted wet weight, nearest 0.01 g); individual prey items were then identified to the lowest feasible taxonomic level following the methods of Coutré et al. (2015) and were weighed to the nearest 0.01 g. Energy density (kJ/g wet mass), a measure of prey quality, was measured from representative prey that were sampled from Sablefish stomachs when intact specimens with minimal digestive damage were found. Other prey items were collected opportunistically in the field in conjunction with Sablefish sampling. Herring were assigned ages (age 0 or age 1) based on lengths (Paul and Paul 1998). We measured energy densities using calorimetry according to the methods of Siddon et al. (2013). In brief, prey items were dried at 135°C to a constant weight by using a LECO thermogravimetric analyzer (LECO, St. Joseph, Michigan) or at 60°C by using a drying oven. Prey weighing 5 g or less were dried whole, and prey over 5 g were homogenized and a tissue aliquot was dried. We composited invertebrate prey types (Hyperiididae, Mysidae, and some Polychaeta) with insufficient mass to analyze individually. Dried samples were crushed into a powder, pressed into a pellet, and combusted with a Parr 6725 bomb calorimeter (Parr Instrument

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Timing of early life history events	Age-0	Spawning (300-500 m deep) <sup>1</sup>			Eggs/nektonic larvae <sup>1</sup>		Epipelagic juveniles <sup>2</sup>			Young-of-the-year (200-320 mm FL) <sup>3,4</sup> settle into nearshore habitats			
	Age-1	Juveniles (230-450 mm FL) <sup>3,4</sup> maintain nearshore residence; Some begin migration to adult habitat											
	Age-2	Some age-2s nearshore <sup>3</sup> ; Migration to deep water						Caught in commercial fishery and survey <sup>5</sup>					

FIGURE 1. Timing of Alaskan Sablefish early life history stages. Orange shading represents fish in deep adult habitats, gold represents eggs/larval fish, blue represents fish in the nekton, and green represents fish in shallow nearshore waters. Life stage transitions may vary individually and geographically. (<sup>1</sup>Mason et al. 1983; <sup>2</sup>Sigler et al. 2001; <sup>3</sup>Rutecki And Varosi 1997; <sup>4</sup>length ranges adjusted using data from this study; <sup>5</sup>Hanselman et al. 2018.).

TABLE 1. Summary of catch and diet metrics for Sablefish collected in Saint John Baptist Bay, Deep Inlet, and Crawfish Inlet, Alaska ( $N$  = number of fish caught). Means are presented with SDs in parentheses. Water temperature (Temp) is the average across the sampling period, measured at a depth of 25 m (Callahan et al. 2021).

Year-class	Sampling					$N$	FL (mm)		Diet energy density (kJ/g)	Non-empty stomachs (%)	Relative stomach content weight (% of body weight)
	Age	Year	Month	Dates	Temp ( $^{\circ}$ C)		Mean (SD)	Range			
2016	1	2017	Oct	16–20	9.6	245	368 (27)	280–460	4.10 (0.97)	92	0.80 (0.95)
2017	0	2017	Oct	16–20	9.6	54	277 (17)	234–310	3.62 (0.80)	83	0.66 (0.72)
	1	2018	Jul	16–20	8.6	69	343 (19)	265–380	4.37 (0.61)	96	1.29 (1.45)
2018	0	2018	Sep	20–21		45	203 (10)	180–225	4.36 (0.54)	89	4.69 (3.62)
	0	2018	Oct	18–23	9.9	292	247 (13)	205–280	4.37 (0.37)	68	2.98 (2.34)
	1	2019	Mar	14–18	6.2	39	286 (20)	236–320	4.47 (0.16)	54	1.02 (2.08)
	1	2019	Jul	15–19	8.6	318	316 (26)	255–384	4.48 (0.37)	75	1.64 (2.28)

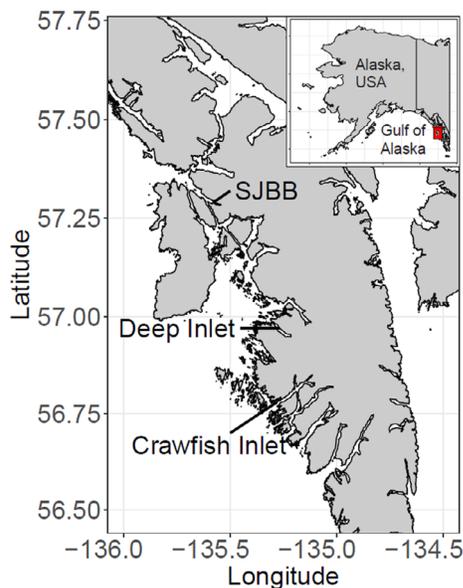


FIGURE 2. Map of Baranof Island, Alaska. All samples were taken in Saint John Baptist Bay, except for September 2018 age-0 fish, which were caught in Deep and Crawfish inlets.

Company, Moline, Illinois) to determine energy density. We used benzoic acid standards and replicate tissue samples to verify calorimeter precision and accuracy. Benzoic acid was added to dried gelatinous zooplankton prey tissue to facilitate combustion, and the energy from benzoic acid was removed from the final prey values.

We determined the relative abundance of stable isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ), reported as per mille values (‰), from retained Sablefish and from prey that were processed for energy density. Values of  $\delta^{13}\text{C}$  are only slightly enriched from resource to consumer and are indicative of nutrient source. For example,  $\delta^{13}\text{C}$  is more depleted in marine and pelagic nutrient sources and

more enriched in nearshore and benthic sources (Davenport and Bax 2002; Miller et al. 2008). In contrast,  $\delta^{15}\text{N}$  enriches from resource to consumer as it is incorporated into consumer tissue and is therefore used to infer relative trophic level. One milligram of freeze-dried dorsal muscle for Sablefish and a subsample of dried, homogenized tissue for prey were weighed into tin capsules with a Sartorius ME5 microbalance (Sartorius, Göttingen, Germany) prior to analysis. Samples were analyzed using a Thermo FlashSmart elemental analyzer in line with a Thermo Finnigan DeltaPlus XP continuous-flow isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany). Measured  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were scale calibrated based on contemporaneously analyzed isotopic reference materials from the International Atomic Energy Agency (IAEA-N-1, IAEA-CH-7, and IAEA-CH-3) and the U.S. Geological Survey (USGS25, USGS40, and USGS41). Internal laboratory standards were also included with all samples as quality controls (purified methionine, homogenized Chinook Salmon *O. tshawytscha* muscle). Long-term records of internal standards yielded an analytical precision (SD) of 0.10‰ for  $\delta^{13}\text{C}$  and 0.15‰ for  $\delta^{15}\text{N}$ .

**Data preparation.**—We compared diet metrics among the following distinct combinations of month, year, and age when captured (hereafter referred to as "groups"): October 2017 age 1, October 2017 age 0, July 2018 age 1, September 2018 age 0, October 2018 age 0, March 2019 age 1, and July 2019 age 1 (Table 1; Figure S1 available in the Supplementary Material separately online). We verified the ages of retained fish by counting their otolith annuli (Callahan et al. 2021). For released fish, we fitted a mixture model to the bimodal length distribution using the mixtools package in R (Benaglia et al. 2009) and used the resulting 306-mm cutoff to assign ages (Figure S2).

**Calculation of diet composition indices.**—We summarized diet composition in each group using two diet

indices: percent weight (% $W$ ) and frequency of occurrence (Chipps and Garvey 2007). To calculate % $W$  for each prey taxon  $i$ , we first summed the weight of prey  $i$  across all Sablefish  $j$ , then divided the total weight of prey  $i$  by the sum of weights of all prey types  $P$  consumed by all sampled predators  $S$ :

$$\%W_i = \frac{\sum_{j=1}^S w_{ij}}{\sum_{i=1}^P \left( \sum_{j=1}^S w_{ij} \right)} \times 100. \quad (1)$$

Weights of the frozen prey used in energy density analysis were converted to ethanol equivalent weights using taxon-specific regressions (Supplementary Material available separately online), as preservation in ethanol reduces weight through desiccation. Frequency of occurrence was calculated for each group by dividing the number of stomachs containing prey type  $i$  by the total number of non-empty stomachs analyzed in that group. Parasites (Nematoda and Caligidae) and plant material found in stomachs were excluded from diet indices and subsequent analysis, as they contributed negligible energy to the consumer. Gelatinous prey (Ctenophora, *Aurelia*, *Aequorea*, and *Cyanea*) were included in frequency of occurrence but excluded from % $W$  due to degradation when preserved.

*Diet composition comparisons among groups.*— We used multivariate measures to statistically compare the source of Sablefish energy intake among groups. We calculated relative energy intake (kJ/g predator) for individual Sablefish by multiplying the weight of each prey taxon in a stomach by that prey taxon's energy density (Table 2) and then dividing by the weight of the predator. Some stomachs contained prey with weights that were too low for the resolution of our scale (0.01 g); their weights were set to 0.001 g. We also aggregated some taxa for this analysis: greenlings were assigned to genus *Hexagrammos*, righteye flatfishes were assigned to family Pleuronectidae, hyperiid amphipods were assigned to family Hyperiididae, crab larvae were grouped (crab larvae), shrimp were grouped (decapod shrimp), and polychaete worms were grouped into Polychaeta. We excluded the following from multivariate analysis: unidentified fish, unidentified invertebrates, amphipods that were too digested to identify to the family level, and other crustaceans that could not be identified to a lower taxonomic level than those listed above (together, 8% of total consumed mass). The March 2019 age-1 Sablefish group was also excluded due to low sample size.

We used nonmetric multidimensional scaling (NMDS) with pairwise Bray–Curtis distances to visualize differences in energy intake between groups, and NMDS axis loadings (correlation coefficients) were calculated to identify prey taxa that were driving the observed variation. We fourth-root transformed the energy intake values prior to calculating the distance matrix to reduce the influence of a few

large values. Since distances in the ordination plot are fitted to dissimilarities among samples, completely distinct samples dominate the fitted distances and distort all other distances. We therefore excluded stomachs ( $n = 6$ ) containing a single prey taxon that was never found together with other prey taxa (Sablefish, Pacific Sand Lance, or Lingcod) from NMDS analysis, as they were completely dissimilar from other stomach samples. We tested for homogeneous dispersion among groups, an assumption of subsequent analyses, by using a one-way ANOVA to test for differences in mean distances from the group centroids. To statistically test for differences in prey energy sources among groups, we used permutation-based ANOVA (PERMANOVA), followed by similarity percentages (SIMPER) analysis to identify the prey species that were driving the differences. Permutation-based ANOVA calculates a pseudo- $F$ -statistic from the distance matrix and generates a  $P$ -value based on permutation; a  $P$ -value less than 0.05 indicates that the centroids of the groups being compared are different (Anderson and Walsh 2013). Partial  $R^2$  values are a measure of effect size, indicating the proportion of sum of squares from the total explained by each group (Oksanen et al. 2019). Multivariate analyses were conducted in R version 3.5.2 (R Core Team 2020) using the package vegan version 2.5-6 (Oksanen et al. 2019).

We also evaluated temporal and size-based shifts in diet composition using stable isotope analysis. We tested for differences in mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between groups by using a one-way ANOVA to identify monthly or annual diet changes. We investigated size-based diet shifts within groups by fitting linear regressions of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  on Sablefish length by group. To assess how well stomach contents represented long-term foraging, we compared Sablefish trophic position and carbon sources with prey isotopic ratios to qualitatively evaluate the reliance of Sablefish on the taxa analyzed.

*Diet quality comparisons among groups.*— We used multiple metrics to compare quality of Sablefish diets among groups, including energy densities of individual prey taxa and the aggregate stomach contents, frequency of empty stomachs, and relative stomach content weight (% of body weight). We used energy density based on wet weight for Sablefish prey throughout this study because wet weight is more ecologically relevant than dry mass, as Sablefish consume live prey. However, measurements of wet mass-based energy density can be imprecise due to variable estimates of fish moisture content (Montevicchi and Piatt 1987; Van Pelt et al. 1997; von Biela et al. 2019). To reduce this measurement variability, we used the mean moisture content of a given taxon rather than individual moisture contents to calculate energy density on a wet mass basis. Specifically, we divided the measured dry mass of prey type  $i$  in a given stomach sample by  $1 - f_i$ , where  $f_i$  is the mean moisture content of prey type  $i$ , to estimate

TABLE 2. Mean energy density (kJ/g, wet mass basis) of prey consumed by Sablefish. Sample sizes are shown in parentheses for values derived from this study. For cases in which energy density values were borrowed from related taxa, the source species is listed. Prey energy densities from September 2018 were not measured; we used October 2018 values for September 2018 age-0 prey.

Taxon	Oct 2017	Jul 2018	Oct 2018	Mar 2019	Jul 2019	Source
<b>Fish</b>						
Pacific Sand Lance					5.2	AFSC–ABL 2020
Sablefish					3.6	Callahan et al. 2021
Pacific Herring (age 0 and age 1)	4.6 (9)	4.8 (1)	4.5 (8)	4.5 <sup>a</sup>	4.5 (19)	This study
Shiner Perch <i>Cymatogaster aggregata</i>	5.3 (1)			4.8 (1)		This study
Gadid	4.2 <sup>a</sup>		4.2 (6)			This study: Pacific Tomcod <i>Microgadus proximus</i>
Greenling					3.4 (1)	This study: Kelp Greenling <i>Hexagrammos decagrammus</i>
Lingcod <i>Ophiodon elongatus</i>		3.9 <sup>a</sup>	3.9 (1)			This study
Snake Prickleback <i>Lumpenus sagitta</i>	4.6					AFSC–ABL 2020: Slender Eelblenny <i>Lumpenus fabricii</i>
Flatfish					3.1 (2)	This study: Dover Sole <i>Microstomus pacificus</i>
Rockfish	4.4					AFSC–ABL 2020: <i>Sebastes</i> spp.
Larval fish			3.8		3.8	AFSC–ABL 2020: Capelin larvae
Salmon spp.	5.3		5.3			Gende et al. 2004
<b>Invertebrates</b>						
Hyperiid amphipod	2.7 (7)		3.2 (2)		3 <sup>b</sup>	This study
Gammarid amphipod	3 <sup>b</sup>		3 <sup>b</sup>		3 <sup>b</sup>	This study: hyperiid amphipod
Shrimp	3.9	3.9	3.9		3.9	AFSC–ABL 2020: Crangonidae
Euphausiid	3.7		3.7		3.7	AFSC–ABL 2020: Arctic krill <i>Thysanoessa raschii</i>
Mysid	4 (4)		4 <sup>c</sup>			This study
Isopod			3.3			AFSC–ABL 2020: <i>Saduria</i> spp.
Crab	3.3	3.3	3.3		3.3	LaRoche and colleagues, unpublished data: Dungeness crab <i>Metacarcinus magister</i>
Crab larva		3.3	3.3		3.3	Foy and Paul 1999: decapod zoea
Copepod spp.					4.2	AFSC–ABL 2020: <i>Calanus</i> spp.
Insect			3			AFSC–ABL 2020: Insecta
Bivalve		2.6	2.6			AFSC–ABL 2020: butter clam <i>Saxidomus giganteus</i>
Gastropod	2.8		2.8			AFSC–ABL 2020: <i>Limacina helicina</i>
Squid	4.3 <sup>d</sup>	4.3 <sup>d</sup>		4.3 (1)		This study: market squid <i>Doryteuthis opalescens</i>
Polychaete worm	5.2 <sup>a</sup>	4.8 <sup>c</sup>	5.2 (3)		4.8 (15)	This study
Spoon worm	2.6 <sup>f</sup>	2.6 <sup>f</sup>				Karnovsky 1969: <i>Urechis caupo</i>
Peanut worm	2.0 <sup>g</sup>					Karnovsky 1969: <i>Phascolosoma agassizii</i>
Asteroidea			2.9			AFSC–ABL 2020: northern basket star <i>Gorgonocephalus arcticus</i>
Moon jelly <i>Aurelia aurita</i>	0.02 <sup>h</sup> (2)					This study

TABLE 2. Continued.

Taxon	Oct 2017	Jul 2018	Oct 2018	Mar 2019	Jul 2019	Source
Ctenophore	0.03 <sup>h</sup> (6)					This study

<sup>a</sup>Value borrowed from the October 2018 measurement.

<sup>b</sup>Averaged from the October 2017 and October 2018 hyperiid measurements.

<sup>c</sup>Value borrowed from the October 2017 measurement.

<sup>d</sup>Borrowed from the March 2019 measurement.

<sup>e</sup>Borrowed from the July 2019 measurement.

<sup>f</sup>Calculated from percent dry lipid and protein values (Karnovsky 1969; body wall), moisture values from polychaetes (this study), and conversion factors from lipid and protein to energy density (36.43 and 20.10 kJ/g, respectively; Brett 1995).

<sup>g</sup>Calculated from Karnovsky (1969) as for spoon worms except that lipid and protein values were measured from the entire worm.

<sup>h</sup>Energy density was measured but not used in analysis.

its wet mass. In addition to measuring energy density for individual taxa, we calculated energy densities of the aggregate stomach contents for each Sablefish group. For each stomach, we calculated the total energy contributed by each prey taxon (i.e., prey weight  $\times$  prey energy density), divided by the total stomach content weight. When energy density was not measured for a prey taxon in the month during which it was consumed, we borrowed values from other months or used literature values (Table 2). We also report average ( $\pm$ SD) stomach content energy densities across individuals within a given Sablefish group.

We assessed variation in meal size by examining the percentage of empty stomachs and the stomach content weight expressed as a percentage of body weight (hereafter, "relative stomach content weight") for each group. Relative stomach content weight was calculated by dividing the total weight of stomach contents by the weight of the Sablefish and multiplying by 100. For this analysis, we used total frozen stomach content weights (Supplementary Material). Stomach content weights are not directly equivalent to daily consumption estimates, as prey may linger in stomachs for longer than 1 d. For example, Sturdevant et al. (2009) estimated that at 12°C, Chum Salmon *O. keta* that were consumed by Sablefish would be 50% digested after 14 h. Additionally, stomach content weights are less than actual prey weight consumed due to the effects of digestion. Given these caveats, we used stomach content weight (% of body weight) as a relative rather than absolute indicator of consumption that can reflect shifts in feeding rates. We  $\log_e$  transformed the relative stomach content weight to achieve a normal distribution and then compared the mean among groups by using a one-way ANOVA.

## RESULTS

### Temporal, Age-Based, and Size-Based Shifts in Diet Composition

Stomach contents from 1,064 juvenile Sablefish were analyzed in the study (Table 1; Figure S1). Sablefish were

captured on all sampling trips except for late-winter/early spring sampling (April 30–May 5) in 2018, when no fish were caught despite a level of sampling effort that was comparable to effort in other periods. Of the subset of fish that were retained for stable isotope analysis ( $n = 241$ ), only 4.5% had trace contents remaining in their stomachs after gastric lavage. Herring was the dominant prey type in the diet for all but one Sablefish group (March 2019 age 1), contributing between 18.8% and 85.0% of the diet by weight depending on the group (i.e., combination of month, year, and age-class; Table 3). October 2017 age-1 and March 2019 age-1 Sablefish were the only groups in which another taxon besides herring exceeded 10% of the diet by weight: Shiner Perch (19.9%) and scavenged salmon remains (11.6%) were important for October 2017 age-1 fish, and Shiner Perch (15.0%) and squid (50.9%) were important for March 2019 age-1 fish. Herring were also the most frequently occurring prey taxon in stomachs, as they were present in 9–64% of Sablefish, depending on the group (Table 3). Age-0 and age-1 Sablefish in October 2017 had high frequencies of occurrence ( $>20\%$ ) of hyperiid amphipods, mysids, and scavenged remains of adult spawning salmon (Table 3). Gelatinous organisms consisted primarily of ctenophores but also *Aequorea* and *Aurelia* spp. and occurred frequently in diets of July 2018 age-1 (34%) and July 2019 age-1 (29%) Sablefish. Polychaete worms were also common in diets of July age-1 fish, occurring in 8% of stomachs in 2018 and 19% of stomachs in 2019. Frequency of occurrence of unidentified fish was high, ranging from 28% to 60% of stomachs in each sampling group (Table 3).

The energy sources in diets differed statistically among groups, and herring drove these differences. For the NMDS analysis of dietary energy source, two dimensions adequately described the observed variation (stress = 0.17). Herring energy intake was strongly correlated with the first NMDS axis (loading = 0.87; Figure 3). Multivariate dispersion of energy intake differed between Sablefish groups (ANOVA:  $F = 33.3$ ,  $P < 0.001$ ), with the lowest dispersion observed in October 2018 age-0 fish; thus,

PERMANOVA results should be interpreted with caution. Dietary energy sources differed significantly among groups (Table S2 available in the Supplementary Material separately online), and all groups were significantly different from one another except for July 2018 age-1 and September 2018 age-0 fish ( $P=0.13$ ). Pairwise PERMANOVA comparisons indicated that the largest differences were between October 2017 Sablefish and other groups (except October 2018 age-1 fish), with  $R^2$  values ranging from 0.16 to 0.32 (Table S2). The October 2018 age-0 versus October 2017 age-1 comparison ( $R^2=0.23$ ) was the only other pairwise comparison with a PERMANOVA  $R^2$  exceeding 0.10. Herring contributed most to dissimilarity percentages (SIMPER) in pairwise comparisons of energy source between groups, explaining 21–66% of dissimilarities. Hyperiididae, Mysididae, salmon, crab larvae, and polychaetes were the other top contributors to energy source dissimilarities.

Variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  indicated annual, monthly, and age-based diet shifts. In both sampling years, members of the same cohort showed enrichment of  $\delta^{13}\text{C}$  between October and July. Fish from the 2018 year-class had more enriched  $\delta^{13}\text{C}$  compared to those of the 2017 year-class (Figure 4). Similarly,  $\delta^{15}\text{N}$  was enriched in July 2019 age-1 fish compared to October 2018 age-0 fish, which were members of the same cohort (Figure 4). In contrast,  $\delta^{15}\text{N}$  showed little difference between October 2017 age-0 and July 2018 age-1 fish (Figure 4). Size-based stable isotope patterns within groups also differed. Values of  $\delta^{13}\text{C}$  decreased significantly with FL in October fish of all year-classes, while  $\delta^{13}\text{C}$  increased significantly with FL in March 2019 age-1 individuals (Figure 5). All groups except for October 2017 age-1 fish showed an increase in  $\delta^{15}\text{N}$  with length (Figure 6).

Sablefish occupied a higher trophic position than their herring prey (Figure 7). Differences in mean  $\delta^{15}\text{N}$  between Sablefish and age-0 herring ranged from 0.9‰ in October 2018 to 2.1‰ in July 2019. Sablefish  $\delta^{13}\text{C}$  was enriched 0.1–1.4‰ relative to age-0 herring except for October 2017 age-0  $\delta^{13}\text{C}$ , which was depleted by 0.7‰ compared to October 2017 herring. July 2019 age-1 Sablefish had a 0.9‰ greater mean  $\delta^{15}\text{N}$  and a 0.3‰ lower  $\delta^{13}\text{C}$  than their age-1 and older herring prey. Of the other prey we analyzed, Dover Sole in July 2019 had the most depleted  $\delta^{13}\text{C}$  at  $-21.1$ ‰ and polychaete worms (Nereidae) in October 2018 had the most depleted  $\delta^{15}\text{N}$  at 7.9‰.

### Temporal and Age-Based Variation in Diet Quality

Prey energy density varied among taxa, with fish tending to have higher energy densities than invertebrates (Table 2). The mean energy density ( $\pm$ SD) of herring was similar between October 2017 ( $4.5 \pm 0.21$  kJ/g) and October 2018 ( $4.6 \pm 0.18$  kJ/g; Table 2). In July 2019, the energy density of age-1 and older herring ( $4.7 \pm 0.33$  kJ/g)

was higher than that of age-0 herring ( $4.3 \pm 0.06$  kJ/g;  $t$ -test:  $t=4.09$ ,  $P=0.003$ ). Other fish ranged in energy density from 3.4 to 5.3 kJ/g. Polychaete worms had the highest energy density among invertebrate taxa, with a mean ( $\pm$ SD) of  $4.8 \pm 0.24$  kJ/g in July 2019, when they were most prevalent in diets. Small crustaceans were generally low in energy density, with hyperiid amphipods at  $2.7 \pm 0.09$  kJ/g and mysids at  $4.0 \pm 0.06$  kJ/g in October 2017. The prey with the lowest energy density were ctenophores at  $0.029 \pm 0.017$  kJ/g and *Aurelia* at  $0.016 \pm 0.003$  kJ/g. Mean diet energy density did not vary widely among groups (3.6–4.5 kJ/g); qualitatively, October 2017 fish had lower mean diet energy densities and higher SDs compared to the other groups (Table 1).

Across all sampled fish, 79% of stomachs contained prey. July 2018 age-1 Sablefish had the lowest incidence of empty stomachs (4%), while March 2019 age-1 fish had the highest incidence (46% empty; Table 1). Across all fish, relative stomach content weight averaged 1.8% of body weight, and mean  $\log_e$  transformed relative stomach content weight varied by group (ANOVA:  $F=50.0$ ,  $P<0.001$ ; Table 1; Figure 8). The highest relative stomach content weight in an individual fish (13.9% of body weight) was observed in September 2018. Overall, the mean relative stomach content weight was highest in September 2018 age-0 fish at 4.69%, followed by October 2018 age-0 fish at 2.74%. The lowest mean relative stomach content weight occurred in October 2017 age-0 fish (0.66%).

### DISCUSSION

This study improves our understanding of the feeding ecology of postsettlement juvenile Sablefish, particularly their reliance on high-energy forage fishes. Our results confirm that Sablefish consume taxonomically diverse prey of varying energy densities, similar to findings by Sturdevant et al. (2009) and Coutré et al. (2015), but herring represented the major constituent of Sablefish diets across months, years, and ages. Significant relationships between stable isotope ratios and Sablefish length indicated that size-based diet composition differences were most prevalent during March and July but occurred to some extent in other months. Diets of October 2017 age-0 and October 2017 age-1 Sablefish differed most from those of other groups, in part due to higher consumption of hyperiid amphipods. We also observed variation in the prey quantity consumed, with the highest proportion of empty stomachs observed in March 2019 age-1 Sablefish, the highest values of relative stomach content weight (% of body weight) occurring in October 2018, and exceptionally large meals consumed by some individuals in most groups. Voracious consumption in juvenile Sablefish has been well documented (Sogard and Olla 2001; Krieger et al. 2019),

TABLE 3. Summary of diet composition by Sablefish group ( $N$  = number of fish with non-empty stomachs), reported as percentage of prey by weight (first value in each cell) and percent frequency of occurrence of prey in stomachs (second value in each cell). Identifiable taxa comprising over 10% of prey by weight or occurrence are indicated in bold type. Fishes are arranged alphabetically by common name.

Taxon	Oct 2017 age 1 ( $n = 229$ )	Oct 2017 age 0 ( $n = 45$ )	Jul 2018 age 1 ( $n = 66$ )	Sep 2018 age 0 ( $n = 40$ )	Oct 2018 age 0 ( $n = 201$ )	Mar 2019 age 1 ( $n = 21$ )	Jul 2019 age 1 ( $n = 238$ )
<b>Fish</b>							
Gadidae (cod)	3.4, 1.3			0.6, 5	1.3, 1		
Dover Sole							1.0, 1.3
Flatfish, right-eyed (Pleuronectidae)							1.2, 1.8
Greenling <i>Hexagrammos</i> sp.							0.5, 0.4
Kelp Greenling							5.3, 0.4
Lingcod			0.8, 1.5		3.8, 1.5		
<b>Pacific Herring</b>	<b>46.6, 26.3</b>	<b>57.1, 9.3</b>	<b>79.9, 29.2</b>	<b>82.8, 52.5</b>	<b>85.0, 63.8</b>	<b>18.8, 25</b>	<b>81.4, 43</b>
Pacific Sand Lance							0.1, 0.4
Rockfish <i>Sebastes</i> spp.	2.3, 0.9						
Sablefish							1.2, 0.4
<b>Salmon remains (<i>Oncorhynchus</i> sp.)</b>	<b>11.6, 23.2</b>	<b>2.3, 7</b>		<b>1.7, 17.5</b>			
<b>Shiner Perch</b>	<b>19.9, 9.4</b>					<b>15, 5</b>	
Snake Prickleback	0.3, 0.4						
Unidentified larval fish			0.5, 1.5		0.5, 2.5		<0.05, 0.4
Unidentified teleost	5.8, 36.6	30.4, 41.9	5.7, 47.7	6.2, 40	8.6, 50.3	15.1, 60	4.5, 27.6
<b>Invertebrates</b>							
Crustacea, unidentified	<0.05, 4.5	0.4, 9.3	<0.05, 1.5	2.2, 15	<0.05, 1.5	<0.05, 5	0.2, 2.6
Amphipoda, unidentified	0.1, 9.4	<0.05, 25.6	0.1, 26.2	<0.05, 10	<0.05, 5		
<b>Hyperiidæ</b>	<b>4.9, 49.6</b>	<b>2.0, 48.8</b>		<b>&lt;0.05, 2.5</b>	<b>&lt;0.05, 0.5</b>		<b>&lt;0.05, 0.9</b>
Gammaridae	<0.05, 1.3	<0.05, 2.3		0.1, 2.5	<0.05, 0.5		<0.05, 0.4
Decapoda, unidentified shrimp			0.2, 1.5				
<i>Crangon</i> sp.	<0.05, 0.9	<0.05, 2.3			<0.05, 0.5		<0.05, 0.4
Euphausiidae	<0.05, 1.3	<0.05, 2.3			<0.05, 0.5		<0.05, 0.4
<b>Mysidae</b>	<b>0.8, 33</b>	<b>3.1, 37.2</b>			<b>&lt;0.05, 3</b>		
Isopoda				<0.05, 2.5			
Decapoda, unidentified crab	1.2, 2.7		2.1, 7.7		<0.05, 0.5		3.0, 0.9
<b>Decapoda, crab larva</b>			<b>0.5, 3.1</b>	<b>4.5, 12.5</b>			<b>&lt;0.05, 2.2</b>
Calanoid copepod							<0.05, 0.4
Harpacticoid copepod							<0.05, 0.4
Insect				<0.05, 2.5	<0.05, 0.5		
Bivalve	0.1, 0.4		0.4, 1.5		0.1, 1.5		<0.05, 0.4
Gastropoda	<0.05, 2.2				<0.05, 0.5		
Cephalopoda	<0.05, 0.9						
<b>Teuthida</b>	<b>&lt;0.05, 0.9</b>		<b>&lt;0.05, 1.5</b>			<b>50.9, 15</b>	
<b>Polychaeta</b>	<b>&lt;0.05, 1.7</b>	<b>0.3, 4.7</b>	<b>4.6, 7.7</b>				<b>0.8, 14</b>
Nereidae	<0.05, 0.4			0.3, 10			0.3, 12
Echiura	0.6, 0.4		0.3, 1.5				
Sipunculidae	0.1, 0.4						
Asteroidea					0.8, 3		
<b>Cnidaria/Ctenophora</b>	<b>NA, 8.9</b>	<b>NA, 14</b>	<b>NA, 33.8</b>		<b>NA, 3</b>		<b>NA, 28.1</b>
Unidentified invertebrate	0.2, 1.3	0.2, 4.7	0.1, 1.5		<0.05, 1.5		<0.05, 0.9
Unidentified tissue	1.7, 16.1	4.0, 25.6	4.6, 32.3	1.7, 7.5	<0.05, 1	0.2, 10	0.4, 14

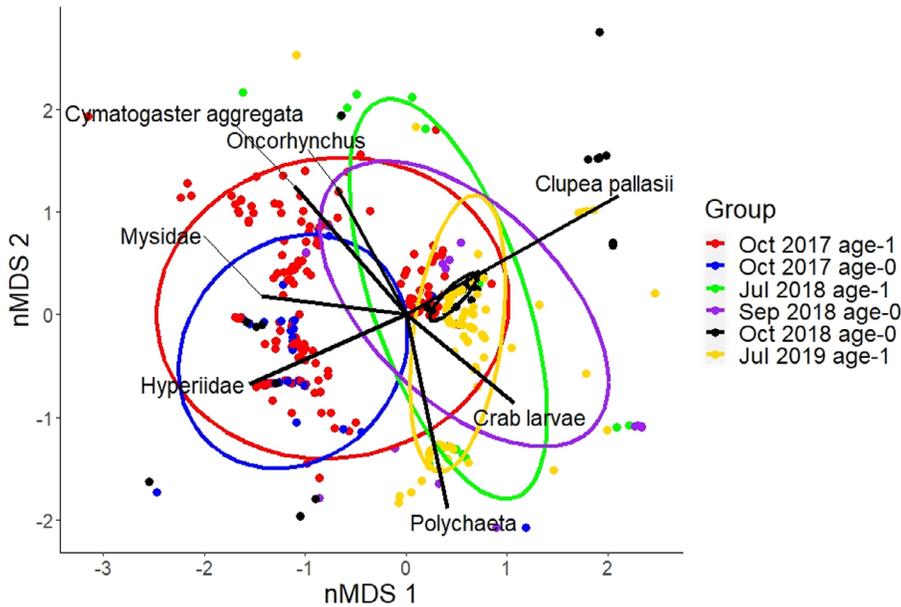


FIGURE 3. Nonmetric multidimensional scaling (NMDS) of Sablefish dietary energy source, with 95% confidence ellipses for the mean position of each group (*Cymatogaster aggregata* = Shiner Perch; *Clupea pallasii* = Pacific Herring). Vectors show prey that were significantly correlated with NMDS axes ( $P < 0.001$ ,  $R^2 > 0.10$ ).

and Sturdevant et al. (2009) observed even higher relative stomach content weights in age-1 Sablefish (up to 19%) than were found in this study. Foraging opportunities in the wild are patchy, and fish generally consume only 43% of their maximum daily ration (Armstrong and Schindler 2011), but Sablefish likely feed at higher rates (Krieger et al. 2019). At maximum rations, prey quality must average 4.65 kJ/g or higher to explain the observed growth of Sablefish between August and October (Krieger et al. 2020), which is similar to the energy density of 4.6 kJ/g that we measured for October 2017 herring.

This study has several sampling and analytical limitations that must be taken into account when interpreting the findings. We obtained stomach contents during 5-d sampling periods, and prey taxa consumed outside of those time windows were not documented; however, the stable isotopes, which reflect diets over a longer period, largely corroborated our stomach content analysis. We did not catch any fish in April–May 2018, and sample sizes were lower in March 2019 than in other months. Temperature in SJBB during these periods was approximately 6°C, and Sablefish in laboratory conditions have been observed to avoid cold temperatures less than 8°C (Sogard and Olla 1998). We hypothesize that our lower catch rates may have resulted from (1) the movement of Sablefish out of our sampling area and into warmer thermal refugia or (2) reduced feeding activity of Sablefish in SJBB due to colder temperatures and/or lower food availability during winter and early spring. An additional sampling limitation is that our field collections occurred in

one geographic location, and prey availability and quality likely vary across the wide geographic range of Sablefish.

An additional caveat is that some prey energy density measurements used in our analysis were taken from the literature, measured in a different month, or measured in a small number of individuals for some taxa. As herring were the dominant prey in the diets and the most adequately sampled for energy density, we believe this source of error to be small overall. Even for herring, however, energy density values for September 2018 and March 2019 were borrowed from October 2018. Based on a study of seasonal cycles in herring energy density (Vollenweider et al. 2011), differences in energy density between September and October of the same year were likely to be small, but March values could have been substantially lower than October values, potentially leading to an overestimate of dietary energy content in March. Our exclusion of gelatinous prey from energy source analysis discounts the possible importance of this frequently underestimated prey type for Sablefish diets (Arai 2005). Polychaete worms, which were either Nereidae or not identifiable to family, had higher energy density measurements than expected for invertebrates. Some of these worms may have been epitokes (i.e., swimming reproductive forms; Hébert Chatelain et al. 2008), which may have increased their susceptibility to predation by Sablefish. Prey items that are too heavily digested to identify is a common issue in fish diet studies, and unidentifiable fish were present in all groups sampled. October 2017 age-0 fish had the highest percentage of unidentified fish in their stomachs at 30.4%; although many of these

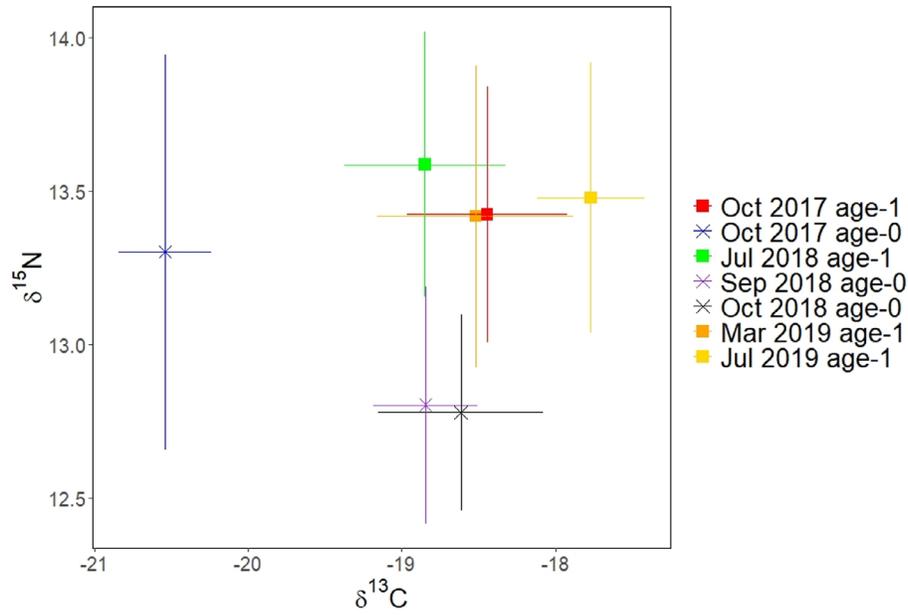


FIGURE 4. Biplot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for each Sablefish group (squares = age 1; x-symbols = age 0). Whiskers represent  $\pm\text{SD}$ .

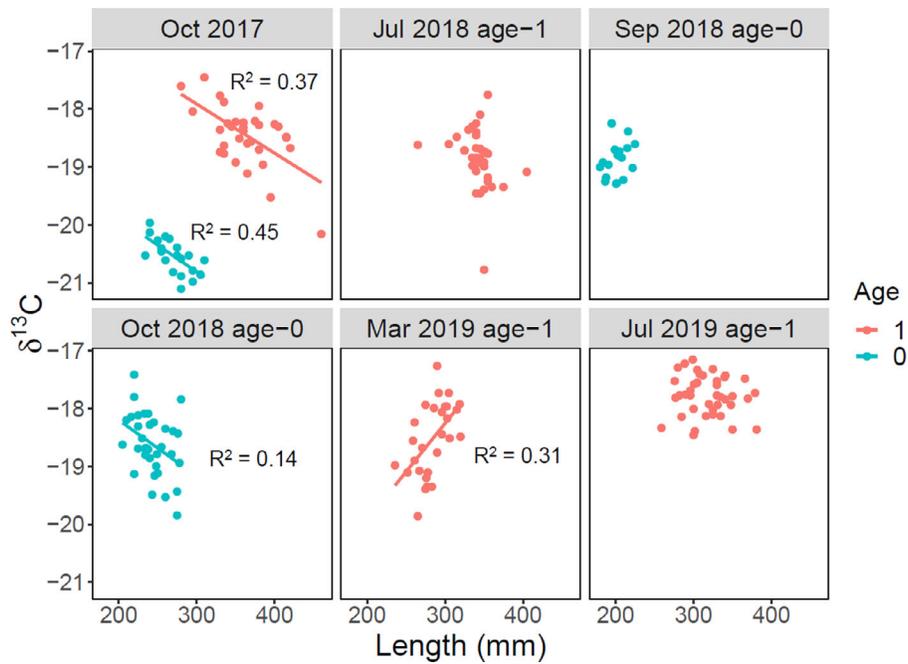


FIGURE 5. Scatterplots with fitted linear regression lines showing the relationship between  $\delta^{13}\text{C}$  and FL for each group of Sablefish (blue = age 0; red = age 1). Only regression lines with significant ( $P \leq 0.05$ ) slopes are shown.

remains were putatively identified as herring, they could not be definitively distinguished from other teleost fish due to the advanced state of degradation. Relatively intact fish prey, which heavily outweighed unidentifiable fish during other sampling periods, were rare in October 2017 age-0 diets. Thus, we have a less complete

understanding of diet composition for that group. Pairing stomach content analysis with DNA-based techniques can improve identification of heavily digested meals (Carreon-Martinez et al. 2011).

Interpretation of diet composition from stable isotopes would be strengthened if Sablefish trophic discrimination

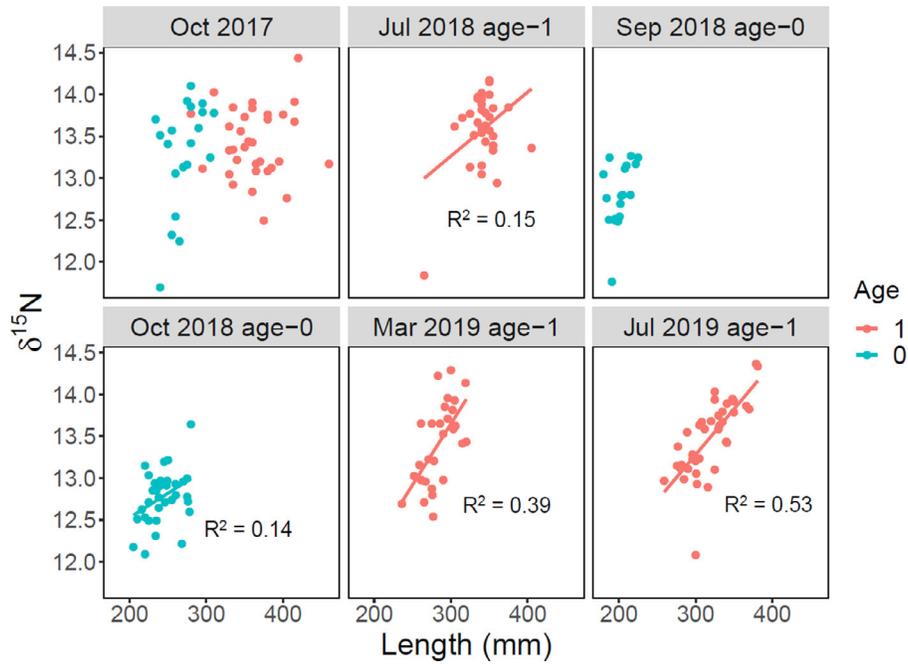


FIGURE 6. Scatterplots with fitted linear regression lines showing the relationship between  $\delta^{15}\text{N}$  and FL for each group of Sablefish (blue = age 0; red = age 1). Only regression lines with significant ( $P \leq 0.05$ ) slopes are shown.

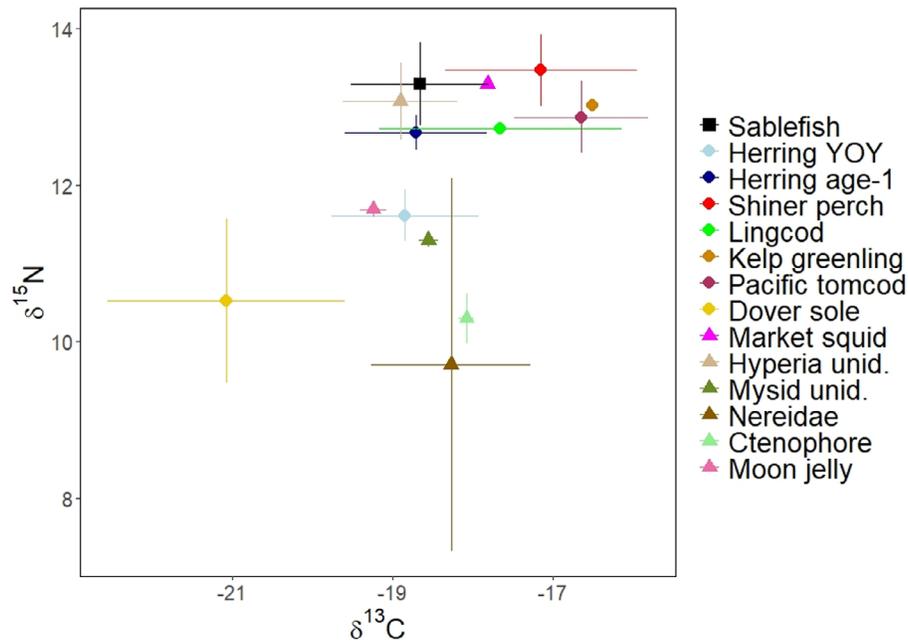


FIGURE 7. Biplot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for Sablefish (square), fish prey (circles), and invertebrate prey (triangles). Whiskers represent  $\pm\text{SD}$  (herring = Pacific Herring; YOY = age 0; unid. = unidentified).

factors were known and if more prey had been sampled for isotopes. The broadly used  $\delta^{15}\text{N}$  trophic discrimination factor of approximately 3.4‰ (DeNiro and Epstein 1981) is likely high for juvenile Sablefish due to their fast

growth. Nitrogen isotope discrimination factors for fast-growing individuals tend to be lower (Trueman et al. 2005; Varela et al. 2012), and prey quality also influences nitrogen stable isotope trophic discrimination factors

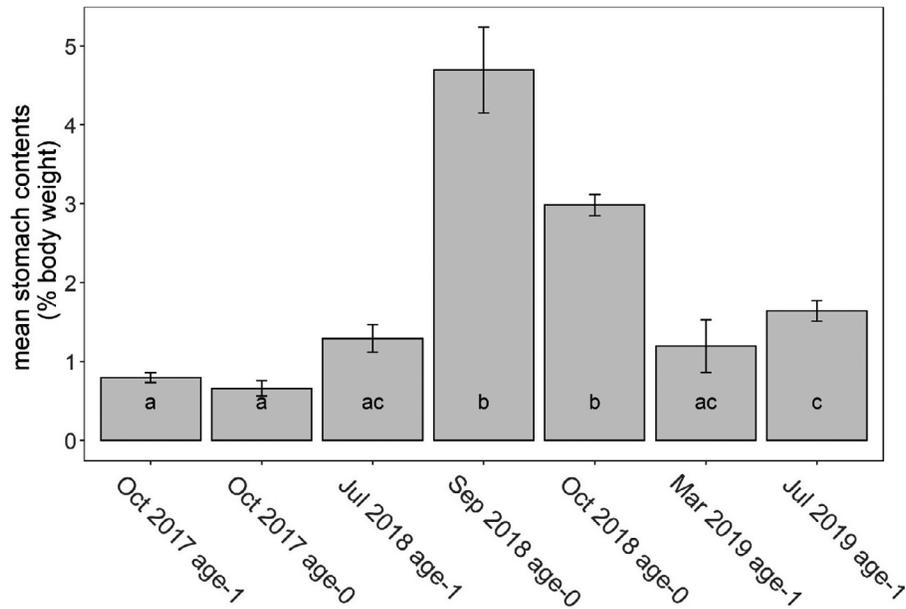


FIGURE 8. Mean ( $\pm$ SE) relative stomach content weight (i.e., stomach content weight expressed as a percentage of body weight) for each group of Sablefish. Letters indicate significant differences between groups from Tukey honestly significant difference pairwise comparisons of  $\log_e$  transformed relative stomach content weight.

(Barton et al. 2019). Given these precautions, we consider the 0.9–2.1‰ differences in mean  $\delta^{15}\text{N}$  between Sablefish and age-0 herring, together with the prevalence of herring in stomachs, as reasonable evidence for high reliance on herring.

### Energetic Contribution of Key Prey Groups

The large contribution of fish prey in Sablefish diets suggests the importance of piscivory for Sablefish growth and survival. Sablefish have been previously reported to rely heavily on fish prey by their second summer (Sturdevant et al. 2009; Coutré et al. 2015); our results corroborate these findings and demonstrate reliance on fish prey during their first autumn (September–October). This early ability to consume high-energy fish prey relative to other species likely allows Sablefish to continue rapid growth during their first autumn (Krieger et al. 2020; Callahan et al. 2021). Pelagic age-0 Sablefish can consume fish prey late in their first summer (Grinols and Gill 1968; Sigler et al. 2001), but the exact timing of their switch to piscivory remains uncertain and is an important knowledge gap.

Herring constituted the majority of fish prey by weight and occurrence for most groups, and differences in the quantity of herring consumed drove diet dissimilarities in the SIMPER analysis. Herring have previously been identified as an important food source for juvenile Sablefish (McFarlane and Beamish 1983; Coutré et al. 2015). Forage fish, such as herring, are critical components of the

North Pacific marine ecosystem, supporting valuable higher-trophic-level, commercially important fishes as well as other top consumers (Ainley et al. 1996; Duffy et al. 2010; Moran et al. 2018). Herring also support subsistence and commercial fisheries in the region and serve as a cultural keystone species for Indigenous peoples of the Pacific Northwest coast (Thornton et al. 2010; Moss 2016). Ensuring that forage fish are available for fisheries and the food web may become an increasingly important goal in ecosystem-based fisheries management as consumption rates of ectotherms increase in a warming ocean.

Pacific salmon constitute another energy-rich prey resource that varies seasonally and annually in availability. In this study, October sampling took place after the peak of the salmon spawning migration, but Coutré et al. (2015) found that scavenged salmon carcasses comprised over half of Sablefish diets by weight in September 2013. We detected scavenged salmon in diets of fish caught in October 2017, a strong Pink Salmon *O. gorbuscha* return year, but there was no evidence of salmon scavenging in October 2018, a year with record-low Pink Salmon returns (Zador and Yasumiishi 2018). Fluctuations in salmon runs likely affect the energy available to juvenile Sablefish, and Sablefish recruitment to age 2 is positively correlated with Pink Salmon returns in the Sablefish's age-0 year (Yasumiishi et al. 2015). Sablefish may benefit twice from strong Pink Salmon returns by feeding on carcasses as age-0 fish in the autumn and on abundant smolts as age-1 fish the following spring. Although our sampling did not coincide

with juvenile salmon (smolt) out-migration, Sablefish also prey heavily upon smolts (Sturdevant et al. 2009) and even aggregate to consume recently released hatchery smolts (Rhea Ehresmann, Alaska Department of Fish and Game, personal communication). Smolt predation by a large Sablefish year-class is substantial enough to potentially reduce salmon returns (Sturdevant et al. 2009).

Sablefish do not exclusively consume high-energy prey. Gelatinous organisms are the lowest quality prey found in Sablefish diets, with energy densities 148 times lower than that of the lowest quality herring. However, gelatinous prey consumption is common in marine organisms (Purcell and Arai 2001; Arai 2005), and previous studies have documented adult and juvenile Sablefish using gelatinous food sources (Brodeur et al. 1987; Yang and Nelson 1993; Sigler et al. 2001). Sablefish stomachs were reportedly full of pyrosomes in 2016 (Linda Behnken, Alaska Longline Fishermen's Association, personal communication), when pyrosomes proliferated in the North Pacific (Brodeur et al. 2018). Gelatinous prey may require reduced handling time and digest quickly, which would allow fish to consume them at much higher rates than fish prey in the same amount of time (Arai et al. 2003). Given the frequency of ctenophores in the diets of July 2019 age-1 Sablefish when herring were also available, either consuming jellies does not prevent Sablefish from continued foraging on higher quality prey or the benefit to consuming gelatinous prey is not confined to energy intake. For example, moon jellies, which were consumed by Sablefish, are also a source of essential fatty acids that support neurological and physiological functioning in fish and other vertebrates (Stenvers et al. 2020). Whether gelatinous organisms are consumed opportunistically or actively selected by foraging Sablefish is unknown.

#### Ontogenetic Diet Shifts: Variation with Age and Month

October 2017 was the only month with multiple Sablefish age-classes, allowing for a direct comparison of age-0 and age-1 diets. Diets of both age-0 and age-1 fish contained prey that were rare in other sampling periods, including mysids, hyperiid amphipods, and adult salmon remains; these prey taxa separated October 2017 Sablefish of both ages from other groups in our multivariate analyses. October 2017 fish also had diets with below-average energy density compared to other groups, due to consumption of low-energy-density crustaceans during this month. The presence of Shiner Perch in the stomachs of age-1 Sablefish but not age-0 Sablefish was a major age-based difference. Shiner Perch are abundant in nearshore ecosystems (Johnson et al. 2015) but may be too large for gape-limited October age-0 Sablefish to capture. October 2017 age-0 Sablefish also had more depleted  $\delta^{13}\text{C}$  than co-occurring age-1 individuals. One potential explanation may be that a larger proportion of age-0 tissue was derived from consumption of adult salmon, which return

to nearshore ecosystems with relatively depleted  $\delta^{13}\text{C}$  compared to age-1 fish. Literature values of  $\delta^{13}\text{C}$  for Pink Salmon (e.g.,  $-20.6\text{‰}$ ; Chaloner et al. 2002) are similar to the mean value we measured in October 2017 age-0 Sablefish ( $-20.5\text{‰}$ ). Although we observed a higher contribution of salmon to age-1 Sablefish stomach contents, our sampling occurred after the peak salmon migration and is likely not representative of diets in preceding weeks. Higher consumption of salmon by the fastest growing individuals may account for the unexpected negative relationship between  $\delta^{13}\text{C}$  and length in October 2017 age-0 and age-1 groups.

The first winter is a period of nutritional deficiency for many North Pacific marine fish species (Foy and Paul 1999; Heintz and Vollenweider 2010). Sablefish grow through their first winter but deplete energy stores during that period (Callahan et al. 2021), and our results provide some evidence that Sablefish experience poorer foraging during winter than in other seasons. March 2019 age-1 Sablefish had the highest proportion of empty stomachs and had lower relative stomach content weights than Sablefish collected in the previous autumn. Herring nutritional content declines during winter (Paul et al. 1998; Vollenweider et al. 2011; Gorman et al. 2018), which would translate to less energy intake per individual herring consumed. We did not obtain sufficiently intact herring for calorimetry in late winter, and we substituted October 2018 herring energy densities for our analysis, which may have inflated the average March 2019 age-1 diet quality. The presence of prey in late-winter stomachs shows that Sablefish feed during winter, which is not surprising given observed Sablefish growth between autumn and spring and bay temperatures suitable for feeding (Krieger et al. 2019; Callahan et al. 2021).

#### Annual Diet Variation and Future Change

We found annual variation in relative amounts of prey consumed, with a low relative stomach content weight (% of body weight) in October 2017 fish (e.g., 450% lower in October 2017 age-0 fish than in October 2018 age-0 fish). October 2017 age-0 and October 2018 age-0 Sablefish also had the most dissimilar diets, with the highest PERMANOVA pairwise  $R^2$  value. October 2017 age-0 diets included a larger quantity and variety of small crustaceans compared to October 2018 age-0 diets, which were dominated by herring. October 2017 age-0 Sablefish had a lower relative stomach content weight, but empty stomachs occurred less often for this group than for October 2018 age-0 fish. These apparent differences in feeding between years may be related to interannual variation in prey availability or ecological interactions between Sablefish cohorts. For example, the more abundant age-1 Sablefish in October 2017 may have outcompeted age-0 individuals for larger fish prey. Stable isotopes, which reflect food consumed and

assimilated into Sablefish tissues in the weeks prior to our sampling, indicate that October 2017 age-0 Sablefish had depleted  $\delta^{13}\text{C}$  and enriched  $\delta^{15}\text{N}$  compared to October 2018 age-0 individuals. This may have resulted from greater consumption of salmon carcasses in autumn 2017 compared to 2018, as adult Pink Salmon exhibit depleted  $\delta^{13}\text{C}$  and enriched  $\delta^{15}\text{N}$  compared to other prey items (Chaloner et al. 2002), and 2018 was a year with record-low Pink Salmon returns (Zador and Yasumiishi 2018). October 2017 age-0 Sablefish were larger and in better condition than October 2018 age-0 individuals (Callahan et al. 2021), adding credence to the hypothesis that Sablefish may have consumed more salmon in 2017 compared to 2018, prior to our stomach content sampling.

Environmental conditions can dramatically alter the nutritional quality and abundance of forage species on an annual basis. Herring and other forage fish in the Gulf of Alaska and California Current were in poorer condition during the 2014–2016 marine heatwave than in preceding years (Brodeur et al. 2019; Sewall et al. 2019; von Biela et al. 2019). Reduced quality of forage fish prey may translate to lower growth, smaller prewinter sizes, and greater depletion of energy reserves during winter for juvenile Sablefish (Krieger et al. 2020; Callahan et al. 2021), potentially increasing their demand for other prey. Evaluating potential mechanistic links between diet quality and Sablefish recruitment dynamics would require longer time series of prey quality and Sablefish nutritional condition during high- and low-recruitment regimes. Warming may increase the availability of other forage species to Sablefish. For instance, arrival of abundant schools of market squid in Sitka waters coincided with the marine heatwave of 2014–2016 (Cavole et al. 2016). Large winter sizes and flexible foraging habits may enable Sablefish to exploit novel prey sources, such as squid, and may help to explain how Sablefish have benefited from the changing prey fields that accompany a warming ocean.

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## SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.