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## Temporal Variation in Diet Composition and Use of Pulsed Resource Subsidies by Juvenile Sablefish

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### Abstract

Pulsed resources create an influx of energy that can provide individual and population level benefits to their consumers. As consumers, Sablefish *Anoplopoma fimbria* experience strong seasonal pulses in prey resources during their critical period of juvenile growth in the nearshore marine environment. This study described temporal patterns in diet composition of Sablefish ( $N = 1,081$ ) ranging in size from 226 to 455 mm FL during July and September in St. John Baptist Bay, Alaska. Juvenile Sablefish exploited a large variety of prey taxa characteristic of a generalist predator and experienced significant diet shifts among sampling periods revealing seasonal and interannual variation in resource use. Diets appeared more diverse in 2012 when more invertebrate taxa were consumed compared with 2013 when diets were dominated by herring and salmonid offal. In September of both years, spawning Pink Salmon *Oncorhynchus gorbuscha* were observed within the study area and juvenile Sablefish capitalized on this high energy subsidy, and salmon carcasses were among the top contributors to their diets by weight. However, Sablefish also exploited in situ prey of lower energy, such as benthic invertebrates, suggesting that Sablefish are not entirely reliant on seasonally pulsed, high-energy prey. This study further emphasizes the significance of salmon as a vector of energy across ecosystems and is one of the first to document a marine teleost species scavenging on adult salmon carcasses in coastal marine waters.

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Access to high quality prey resources is essential for survival and growth of a consumer; however, these resources can be temporally dynamic (Hipfner 2008; Yang et al. 2008; Bentley et al. 2012). Many consumers exploit pulsed resources that create short-term influxes of energy within ecosystems (Yang et al. 2008, 2010; Bentley et al. 2012). Pulsed resource subsidies are low in frequency, diverse across systems, and variable within a system (Yang et al. 2010; Bentley et al. 2012). On the individual level, pulsed resources can increase the growth of the consumer (e.g., Wright et al. 2013) and potentially sustain the consumer during periods of low

resource availability (Denton et al. 2009; Eberle and Stanford 2010; Yang et al. 2010). For example, Bentley et al. (2012) documented the profound impact that the influx of Sockeye Salmon *Oncorhynchus nerka* had on ration size and growth rate of Rainbow Trout *O. mykiss* and Arctic Grayling *Thymallus arcticus* in two freshwater streams. Individual benefits from pulsed subsidies can also translate into population-level effects for consumers. Large seed-masting events by beech trees *Nothofagus* spp. in New Zealand (occurring on 4–8 year cycles) have led to peak populations of house mice *Mus musculus* feeding on these seeds, and increased survivability in

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stoats *Mustela erminea*, a predator of the mice (King 1983). The population of consumer species often increases and can act as a lagged second subsidy pulse to other consumers in the system (Ostfeld and Keesing 2000). The magnitude and timing of pulsed subsidies may vary interannually, which has implications for predators that rely on them (Gende et al. 2002; Abraham and Sydeman 2004; Yang et al. 2008). For example, in years of high salmon run size, bears *Ursus* spp. in Alaska selectively consumed the parts of salmon with the highest energetic value, while in years of low salmon returns, bears ate more whole fish (Gende et al. 2002).

At the population level, seasonal resource pulses can influence recruitment in marine fishes, though the extent of this influence is not well understood (Yang et al. 2008). The North Pacific Ocean has variable productivity, which typically peaks in summer (Wong et al. 1995). Seasonal cycles of productivity can strongly influence forage fish and groundfish abundance within this region, and fish yields show strong linkages to primary productivity and zooplankton abundances (Ware and Thomson 2005). For example, successful Walleye Pollock *Gadus chalcogrammus* recruitment is thought to be partially reliant on the pulse of copepods *Calanus* spp. that occurs during late summer and early fall in the Bering Sea (Coyle et al. 2011). In the nearshore marine environment, anadromous fishes such as Pacific salmon *Oncorhynchus* spp. and Eulachon *Thaleichthys pacificus* provide a seasonal energy source for many predators (Sigler et al. 2004). In spring, Steller sea lions *Eumetopias jubatus* aggregate and forage on the energy-rich prespawning Eulachon pulse in Berners Bay, Southeast Alaska (Sigler et al. 2004). Understanding the importance of periodic (e.g., seasonal) high energy prey to consumers can provide insight into ecological drivers of population variability.

Our study focuses on Sablefish *Anoplopoma fimbria* as consumers in the nearshore marine environment of Southeast Alaska where there is strong seasonality and pulses in productivity. Sablefish is a demersal fish species in the northern Pacific Ocean and has a highly variable year-class strength (Sigler et al. 2001). All causes of this fluctuation are unknown; however, recruitment has been related to factors such as copepod abundance, northerly drift in winter currents, warm temperature anomalies, and sea level (McFarlane and Beamish 1992; Sigler et al. 2001; Schirripa and Colbert 2006). Juvenile Sablefish (ages 0–2) inhabit shallow waters on the continental shelf where they are active consumers (Cailliet et al. 1988; Rutecki and Varosi 1997; Sigler et al. 2001). In coastal environments, juveniles experience a critical period of rapid growth (ages 0–2, 0.75 mm/d; Rutecki and Varosi 1997) before migrating to slope waters when they are between ages 3 and 5 (Rutecki and Varosi 1997; Gao et al. 2004). Sablefish feed on zooplankton as larvae (Grover and Olla 1990), and in waters extending from California to British Columbia juveniles consume pelagic prey such as forage fish and euphausiids (McFarlane and Beamish 1983; Cailliet et al. 1988; Laidig

et al. 1997). A study in Monterey Bay, California, showed that Sablefish between 20 and 30 cm fed largely on Northern Anchovy *Engraulis mordax* while larger juvenile Sablefish between 30 and 45 cm fed on euphausiids, other crustaceans, and fish, though these size-classes of Sablefish also inhabited different depths (Cailliet et al. 1988). Adults exploit more benthic prey and feed primarily on fishes, cephalopods, crustaceans, and fishery offal (Buckley et al. 1999; Yang and Nelson 2000). Sablefish are opportunistic predators and their diet changes geographically and temporally based on local prey availability (Tanasichuk 1997; Buckley et al. 1999); therefore, a comprehensive understanding of Sablefish feeding ecology requires diet information across the geographic range of the species. This study fills a gap in the knowledge of juvenile Sablefish feeding ecology in Alaskan waters, including ontogenetic and temporal variation in their diets.

Across terrestrial and aquatic systems, the temporal scale at which a consumer population is studied impacts which food resources are identified as important (Ostfeld and Keesing 2000). Therefore, this study aims to identify important prey for juvenile Sablefish in nearshore habitats on multiple temporal scales. Our first objective was to characterize the taxonomic diversity and body sizes of prey that juvenile Sablefish consume. We hypothesized that juvenile Sablefish diets would contain a variety of invertebrate and vertebrate prey, such as euphausiids, cephalopods, and fish, characteristic of a generalist predator based on previous studies (Cailliet et al. 1988; Yang and Nelson 2000). We expected that forage fish could be an important, seasonally abundant prey resource, because juvenile Sablefish in lower latitudes have been found to prey heavily on Pacific Herring *Clupea pallasii* and Northern Anchovy (McFarlane and Beamish 1983; Cailliet et al. 1988). Our second objective was to quantify temporal variation in Sablefish diet and describe their use of seasonal resource pulses. We hypothesized that diets would vary between months and years. In other systems, juvenile fish have exhibited seasonal shifts in diet based on prey availability; for example, Largemouth Bass *Micropterus salmoides* in Lake Opinicon, Ontario, shifted from a diet of zooplankton, insects, and small fish in July to predominantly zooplankton in September within the same year (Keast and Eadie 1985). Sablefish may exploit seasonal pulses of productivity in the coastal marine environment, including anadromous fish that vary in timing and abundance across years. For example, juvenile Sablefish in Southeast Alaska have been recorded feeding on juvenile salmon in pelagic nearshore waters (Sturdevant et al. 2009). Our third objective was to identify ontogenetic shifts in diet. Increased gape size with fish growth often contributes to an increase in the range of prey sizes consumed as predator size increases (Scharf et al. 2000). Therefore, we hypothesized that maximum prey size would increase with Sablefish size and minimum prey size would remain fairly constant, as seen for other generalist consumers (Scharf et al. 2000). Furthermore, juvenile fishes often shift from predominantly

consuming invertebrate prey to eating fish as they grow to adulthood (Mittelbach and Persson 1998).

## METHODS

**Study site.**—This study was conducted in St. John Baptist Bay (SJBB), a shallow bay (depth, 20–73 m) on Baranof Island, Alaska (57°17'0"–57°17'50"N, 135°33'0"–135°35'0"W). The mouth of the bay opens to Salisbury Sound and SJBB has a freshwater input sourced from the head of the bay. We selected SJBB as a site with potentially high densities of juvenile Sablefish based on previous research by the National Marine Fisheries Service (NMFS) (Rutecki and Varosi 1997). Nearshore surveys were conducted by NMFS from 1985 to 1991 throughout Southeast Alaska to determine reliable monitoring sites for juvenile Sablefish (Rutecki and Varosi 1997). Out of 74 sampling sites and 7 years, SJBB was the only location juvenile Sablefish were found consistently, and the bay continues to be sampled annually during the NMFS juvenile Sablefish tagging survey.

**Field sampling.**—All components of this study were conducted in compliance with the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks. To assess temporal variation in diets, stomach contents were collected from Sablefish of ages 0–2 within SJBB over five sampling periods: July 12–16, 2012 ( $N = 302$ ), September 20–23, 2012 ( $N = 271$ ), May 13–17, 2013 ( $N = 4$ ), July 8–12, 2013 ( $N = 391$ ), and September 14–17, 2013 ( $N = 117$ ). Juvenile Sablefish were collected from small research vessels by angling at depths of 18–90 m using squid-baited hooks (size 1/0 J-hooks) during day trips. Captured fish were anesthetized in seawater with MS-222 (tricaine methanesulfonate) at a concentration of 50–80 mg/L for approximately 5 min. Gastric lavage, established as an effective, nonlethal technique to retrieve stomach contents, was used on anesthetized Sablefish, and stomachs were visually inspected to ensure all contents were collected (Kamler and Pope 2001). To assess the relationship between diet composition and juvenile Sablefish size,

FL (mm) and weight (g) were measured. After gastric lavage and measurements, external, plastic-coated, wire spaghetti tags (Floy T-bar anchor) were inserted into the dorsal musculature of each fish. Fish were placed into a recovery tank containing fresh seawater for approximately 15 min to facilitate recovery before returning them to their original capture location. Due to field logistics, stomach contents in July 2012 and July 2013 were frozen and those in September 2012 and September 2013 were preserved in a solution of 80% ethanol. Prey mass was not statistically compared across sampling periods because of the differing preservation methods.

In the laboratory, a blotted wet weight (to the nearest 0.01 g) was obtained for total mass of prey in each stomach and for individual prey items. Prey items were counted, identified to the lowest possible taxonomic level, and measured (SL [mm], if possible). The lowest taxonomic level was determined using identification guides specific to the North Pacific Ocean (e.g., Butler 1980; Kozloff and Price 1996; Smith and Johnson 1996; Shanks 2001; Mecklenburg et al. 2002) and a prey reference collection from intact specimens.

**Analytical methods.**—To quantify the presence of prey in stomachs, the proportion of sampled fish that contained stomach contents was calculated for each sampling period. For all further quantitative analyses, the sampling period May 2013 was excluded due to low sample size ( $N = 4$ ). To address the first objective of describing the taxonomic diversity in diet, cumulative prey curves were plotted for each sampling period (July 2012, July 2013, September 2012, and September 2013) (Ferry and Cailliet 1996). Each curve shows the cumulative number of unique prey taxa identified against the number of stomachs sampled. To reduce bias in the order in which samples were processed, the sample order was randomized 100 times and the mean number of unique prey taxa for each number of stomachs sampled was used to create the mean curve, which was plotted for each sampling period (Ferry and Cailliet 1996). To define the diet composition of juvenile Sablefish for each sampling period, prey taxa were quantified by (1) the frequency of occurrence (FO) of each prey taxon,

TABLE 1. Summary of total fish sampled, mean FL of fish sampled, proportion of fish containing prey, mean growth rate of recaptured fish, mean relative prey weight, and calculated energy density of all prey by sampling period. May 2013 calculations were not included because only one out of four fish contained stomach contents. Mean mass-specific growth rate was calculated using fish that were tagged in July and recaptured in September (2012,  $N = 13$ ; 2013,  $N = 8$ ).

Sampling period	Number of fish sampled	Mean $\pm$ SD FL of fish sampled (mm)	Fish with stomach contents (%)	Mean $\pm$ SD mass-specific growth rate ( $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ )	Mean $\pm$ SD relative prey weight (% body weight)	Energy density of diet (kJ/g)
Jul 2012	302	325 $\pm$ 23	58	0.0046 $\pm$ 0.001	0.2 $\pm$ 0.65	4
Sep 2012	271	366 $\pm$ 21	95		0.2 $\pm$ 0.50	5
May 2013	4	299 $\pm$ 23	25			
Jul 2013	391	334 $\pm$ 19	80	0.0063 $\pm$ 0.001	0.7 $\pm$ 0.94	5
Sep 2013	117	370 $\pm$ 29	97		0.6 $\pm$ 0.79	7

TABLE 2. Diet composition of juvenile Sablefish in SJBB for sampling periods July 2012 ( $N = 175$ ), September 2012 ( $N = 257$ ), July 2013 ( $N = 313$ ), and September 2013 ( $N = 113$ ). Diet composition was quantified by percent frequency of occurrence (%FO), weight (%W), and number (%N). The taxonomic level in which prey items were identified varied and the first column ("Prey taxa") represent the lowest taxon that could be identified. The energy density values from the literature (rounded to nearest kJ/g wet weight) used to estimate the energetic quality of the diet are shown for each prey taxa. Unidentified teleosts and invertebrates were assigned the average energy density of all identified teleost taxa and invertebrate taxa. For salmonid ofal energy contribution, densities of roe and spawned and ripe salmon were averaged.

Prey taxa	July 2012			September 2012			July 2013			September 2013			Energy Density (kJ/g)
	%FO	%W	%N	%FO	%W	%N	%FO	%W	%N	%FO	%W	%N	
<b>Fishes</b>													
Pacific Sand Lance <i>Ammodytes hexapterus</i>				0.47	0.35	0.01							6 <sup>a</sup>
Pacific Herring	8.5	28.22	4.21	43.4	37.76	1.09	73.63	81.88	68.46	50	33.29	38.1	5 <sup>a</sup>
Cottidae	0.65	0.34	0.28										4 <sup>a</sup>
Pacific Staghorn Sculpin													4 <sup>a</sup>
<i>Leptocottus armatus</i>				0.47	4.02	0.01							
Gadidae	2.61	2.57	1.4	2.83	1.17	0.04	0.68	1.38	0.4	4.46	0.78	1.83	3 <sup>a</sup>
Pacific Tomcod <i>Microgadus proximus</i>	1.96	18.39	0.84	0.47	0.46	0.01	0.34	1.54	0.2	2.68	1.58	1.1	3 <sup>a</sup>
Walleye Pollock										0.89	1.84	0.37	3 <sup>a</sup>
Hexagrammidae	0.65	1.77	0.28				0.34	0.36	0.2				4 <sup>a</sup>
Osmeridae	0.65	2.76	0.28	8.96	6.04	0.15	7.19	4.42	5.19	1.79	1.11	0.73	6 <sup>a</sup>
Capelin <i>Mallotus villosus</i>	0.65	4.91	0.28	0.47	0.31	0.01	1.37	3.42	1				5 <sup>a</sup>
Eulachon	0.65	8.6	0.28	0.47	1.08	0.01							7 <sup>a</sup>
Pleuronectidae				0.47	0.17	0.01							4 <sup>a</sup>
Teleostei, unidentified	30.07	13.87	12.92	51.42	12.56	0.79	25.34	3.84	16.37	26.79	4.14	12.09	5
<b>Invertebrates</b>													
Crustaceans													
Crustacea	6.54	0.21	2.81	0.94	0.05	0.01				0.89	0.41	0.37	4 <sup>b</sup>
Amphipoda	0.65	0	0.28	3.77	0.02	0.07	0.34	0	0.2				3 <sup>b</sup>
Gammaridea	2.61	0.05	2.25	1.42	0	0.05	0.34	0	0.2				3 <sup>b</sup>
Hyperiidia	7.19	0.14	3.37	2.83	0.02	0.09	2.74	0.02	5.39	0.89	0	0.37	3 <sup>b</sup>
Copepoda	1.31	0.29	20.51	5.66	0.01	0.09							2 <sup>b</sup>
Decapoda	0.65	0.05	3.65	0.94	0	0.01							4 <sup>b</sup>
Caridea	0.65	0.02	0.28	1.89	0.03	0.03							5 <sup>b</sup>
Dendrobranchiata	0.65	0.03	0.56										5 <sup>b</sup>
Oplophoridae	0.65	0.03	0.56										5 <sup>b</sup>
Penaeidea	1.31	0.04	0.56										5 <sup>b</sup>
Larval crustaceans													
Brachyura (Zoea)	3.92	0.11	7.87										3 <sup>c</sup>
Anomura	0.65	0	0.28	0.47	0	0.01							3 <sup>c</sup>
Canceridae	3.27	0.26	1.4										3 <sup>c</sup>
Grooved mussel crab <i>Fabia subquadrata</i>	0.65	0	0.28										3 <sup>c</sup>
Pinnotheridae	7.19	0.14	9.55										3 <sup>c</sup>
Portunidae	0.65	0	0.28										3 <sup>c</sup>
Euphausiacea							0.34	0.01	0.2				5 <sup>b</sup>
<i>Euphausia pacifica</i>				48.58	17.78	96.55							5 <sup>b</sup>
Other invertebrates													
Bivalvia				2.83	0.01	0.04							2 <sup>b</sup>
Limidae	0.65	0.02	0.56										2 <sup>b</sup>
Cephalopoda							0.34	0.15	0.2	0.89	0.12	0.37	4 <sup>b</sup>
Ctenophora	9.8	1.24	5.62	1.89	0.73	0.02	1.03	0.13	0.6				0 <sup>b</sup>

TABLE 2. Continued.

Prey taxa	July 2012			September 2012			July 2013			September 2013			Energy Density (kJ/g)
	%FO	%W	%N	%FO	%W	%N	%FO	%W	%N	%FO	%W	%N	
Gastropoda				1.89	0.02	0.04							2 <sup>b</sup>
Holothuroidea	1.31	0.7	0.56										1 <sup>b</sup>
Nematoda	0.65	0	0.28										0 <sup>b</sup>
Polychaeta	0.65	0.32	0.28							0.89	0.21	0.37	3 <sup>b</sup>
Nereididae	1.96	7.79	0.84							0.89	0.56	0.37	3 <sup>b</sup>
Echiuridae				0.94	1.52	0.01							3 <sup>b</sup>
Pycnogonida	0.65	0	0.28										4 <sup>c</sup>
Salpidae	1.31	0.14	0.56										0 <sup>b</sup>
Sipunculidae	1.31	2.83	0.56	0.47	0.4	0.01							2 <sup>b</sup>
Invertebrate, unidentified	1.96	0.11	0.84	6.13	0.64	0.08	0.34	0	0.2				3
				<b>Offal</b>									
Salmonidae				16.51	14.03	0.21				65.18	54.7	31.14	9 <sup>d</sup>
Teleostei							1.37	2.83	0.8				5 <sup>a</sup>
Cirripedia (molted exoskeleton)	11.11	0.12	5.9	0.94	0	0.01							0 <sup>b</sup>
				<b>Other material</b>									
Algae and terrestrial leaf litter	19.61	3.9	8.43	41.04	0.81	0.54	0.68	0.03	0.4	31.25	1.27	12.82	0 <sup>e</sup>

<sup>a</sup>Anthony et al. (2000).<sup>b</sup>Caffoupe and Heymans (2005).<sup>c</sup>Foy and Norcross (1999).<sup>d</sup>Hilderbrand et al. (2004).<sup>e</sup>Not included in energetic quality of the diet.

calculated as the number of samples containing prey taxon  $i$  divided by the total number of sampled Sablefish that contained food, (2) the proportion of prey taxon by weight ( $pW$ ), calculated as the total weight of prey taxon  $i$  divided by the total weight of all taxa, and (3) the proportion of prey taxon by number ( $pN$ ), calculated as the count of prey taxon  $i$  divided by the count of all prey taxa (Chipps and Garvey 2007). These three metrics emphasize different aspects of diet and together describe important prey contributing to diet (Chipps and Garvey 2007).

The second objective of this study addressed the temporal variation in prey resource use by juvenile Sablefish and their use of seasonally pulsed prey. Quantifying prey taxa by frequency of occurrence, weight, and number provided initial insight into observed differences in important prey among periods. Multivariate analyses using PRIMER version 6 were then applied to test for statistical differences in diet composition among seasons and years and identify prey taxa that account for differences in diets (Clarke and Gorley 2006). For multivariate analyses, taxonomic groupings of family level or higher were used to reduce bias due to differences in the taxonomic resolution with which prey were identified. Unidentified teleost and invertebrate prey were not included and Sablefish with empty stomachs were not included in multivariate analyses. Sampling periods used in analyses were: July 2012, July 2013, September 2012, and September 2013. Analysis of

similarity (ANOSIM) was used to test for significant temporal differences in diet composition (Clarke and Gorley 2006) by comparing within-group and between-group similarities to test for differences among groups (Clarke and Warwick 2001). The ANOSIM tests were performed on a pairwise resemblance matrix calculated using the Jaccard distance measure and prey presence or absence data (Clarke and Gorley 2006). Prey mass was not compared across sampling periods due to different sample preservation methods used (frozen versus ethanol fixation). The ANOSIM tests were performed to determine whether there were significant differences between sampling period (July 2012, July 2013, September 2012, and September 2013), month (July 2012 and 2013 combined, September 2012 and 2013 combined), and year (2012 and 2013). To determine potential variation in important prey taxa, similarity percentages (SIMPER) were used to determine which prey taxa contributed most to dissimilarities among sampling periods based on prey presence or absence (Clarke 1993).

To compare the energetic quality of the resources being exploited among sampling periods, the energy density of an average Sablefish diet was estimated as

$$\sum_{i=1}^n P_i \times E_i,$$

where  $n$  is the total number of prey taxa in the diet,  $P_i$  is the proportion by weight of prey taxon  $i$ , and  $E_i$  is the energy density of prey taxon  $i$  (kJ/g wet weight). Invertebrate and teleost prey energy densities were obtained for North Pacific and Gulf of Alaska species published by Foy and Norcross (1999), Anthony et al. (2000), and Cauffopé and Heymans (2005). If energy densities were provided for multiple size-classes within a species, we used the energy density for the size most comparable with the prey consumed by Sablefish. Energy densities vary widely within species and this calculation does not account for the amount of the resource that is assimilated, but serves as a general comparison of energy obtained among sampling periods (Anthony et al. 2000).

To evaluate the relative prey sizes exploited, invertebrate and teleost prey lengths (SL) were measured, and the ratio of prey length to predator length was calculated. To test for ontogenetic shifts in teleost prey size, quantile regression was used to define the relationship between teleost prey length and juvenile Sablefish length (Scharf et al. 2000). Determining whether the range of prey sizes consumed widens with increased predator size can provide insight into gape limitation and trophic niche breadth (Scharf et al. 2000). This analysis included only teleost prey items for which a length measurement was possible.

## RESULTS

A total of 1,081 Sablefish (226 mm–455 mm FL) were sampled between July 2012 and September 2013. In both 2012 and 2013, Sablefish FL in September (2012:  $366 \pm 21$  mm [mean  $\pm$  SD],  $N = 271$ ; 2013:  $370 \pm 29$  mm,  $N = 117$ ) was higher than in July (2012:  $325 \pm 23$  mm,  $N = 302$ ; 2013:  $334 \pm 19$  mm,  $N = 391$ ) (Table 1). This size range corresponds to age-0–2 fish, although 93% of fish sampled fell within the size range of age-1 fish (Rutecki and Varosi 1997). In September 2012, 16 fish were recaptured that had been tagged in July 2012, and in September 2013, eight fish were recaptured that had been tagged in July 2013. Mass-specific growth rates over the 2-month period between recaptures were  $0.0046 \pm 0.001$  g·g<sup>-1</sup>·d<sup>-1</sup> (mean  $\pm$  SD) in 2012 and  $0.0063 \pm 0.001$  g·g<sup>-1</sup>·d<sup>-1</sup> in 2013 (Isely and Grabowski 2007). Mean growth rates in FL were  $0.53 \pm 0.16$  mm/d in 2012 and  $0.60 \pm 0.14$  mm/d in 2013. No recaptures occurred between years (Table 1).

To describe the composition of juvenile Sablefish diets, a total of 2,662 prey items grouped into 48 invertebrate and vertebrate prey taxa were identified (45% to species level, 9% to family level; Table 2). During all sampling periods fish occasionally regurgitated prey at the surface; when possible this was captured with a net and included in the analyses. The majority of regurgitated prey was Pacific Herring. Across all sampling periods, Pacific Herring was the dominant prey type by weight (55%), followed by salmonid offal (16%) and smelt (osmerids combined, 7%). Salmonid offal included skin,

bones, organs, and eggs from moribund salmon and salmon carcasses washed into SJBB from the inlet creek subsequent to spawning. Euphausiidae was the only invertebrate prey group that contributed >1% of the diet by weight (5%). Most of the dominant prey items by weight also had a high frequency of occurrence in the Sablefish sampled, with the most frequently occurring taxa being Pacific Herring (49%), salmonid offal (14%), and euphausiids (13%). Euphausiids were the most numerically abundant prey (90%); however, large numbers of euphausiids were consumed in only one sampling period (September 2012). In all sampling periods, algae and terrestrial leaf litter accompanied prey items in stomachs.

To describe temporal variation in resource use by Sablefish, diets were compared across sampling periods. The number of fish sampled and the percentage of fish that contained stomach contents varied among sampling periods (Table 1). In both years, September sampling trips yielded a higher proportion of fish with stomachs containing prey items than in July, and the lowest proportion of stomachs containing prey occurred in July 2012 (excluding May 2012; Table 1). The cumulative prey curve for each sampling period increased at a different rate without reaching a clear asymptote even when almost 300 fish were examined (Figure 1), confirming the opportunistic feeding behavior of juvenile Sablefish. The average number of unique prey taxa in 100 stomachs sampled ranged from 10 in July 2013 to 25 in July 2012, suggesting that across periods there may be differences in taxonomic diversity of diets. The number of unique taxonomic groups in July and September 2012 were notably higher than in 2013 (Figure 1). Across sampling periods there was variation in the dominant prey taxa based on number, frequency of occurrence, and weight (Table 2).

Sablefish diets differed significantly among sampling periods (ANOSIM: Global  $R = 0.278$ ,  $P < 0.001$ ) (Table 3). Pairwise tests revealed that all sampling periods were significantly different from each other (ANOSIM Table 3). Diet composition was significantly different between years and between months (ANOSIM year:  $R = 0.165$ ,  $P < 0.001$ ; ANOSIM month:  $R = 0.094$ ,  $P < 0.001$ ) (Table 3). Based on SIMPER, the largest differences among sampling periods were due to variation in occurrence of herring, salmonid offal, and euphausiids (Table 4). Diet quality, in terms of energetic content and weight, was the highest in September 2013 (7 kJ/g), intermediate in September 2012 and July 2013 (5 kJ/g), and lowest in July 2012 (4 kJ/g) (Table 1). The higher ration size and high energetic content of salmonid offal (Hilderbrand et al. 2004) suggests Sablefish had a greater energy intake in September 2013.

The specific differences among sampling periods were evident when important prey groups were compared (Table 2). In July 2012, the majority of stomachs contained invertebrate prey, of which the most frequently occurring groups were larval brachyuran crabs (16%), molted barnacle exoskeletons (Cirrepedia, 11%), and gammarid and hyperiid

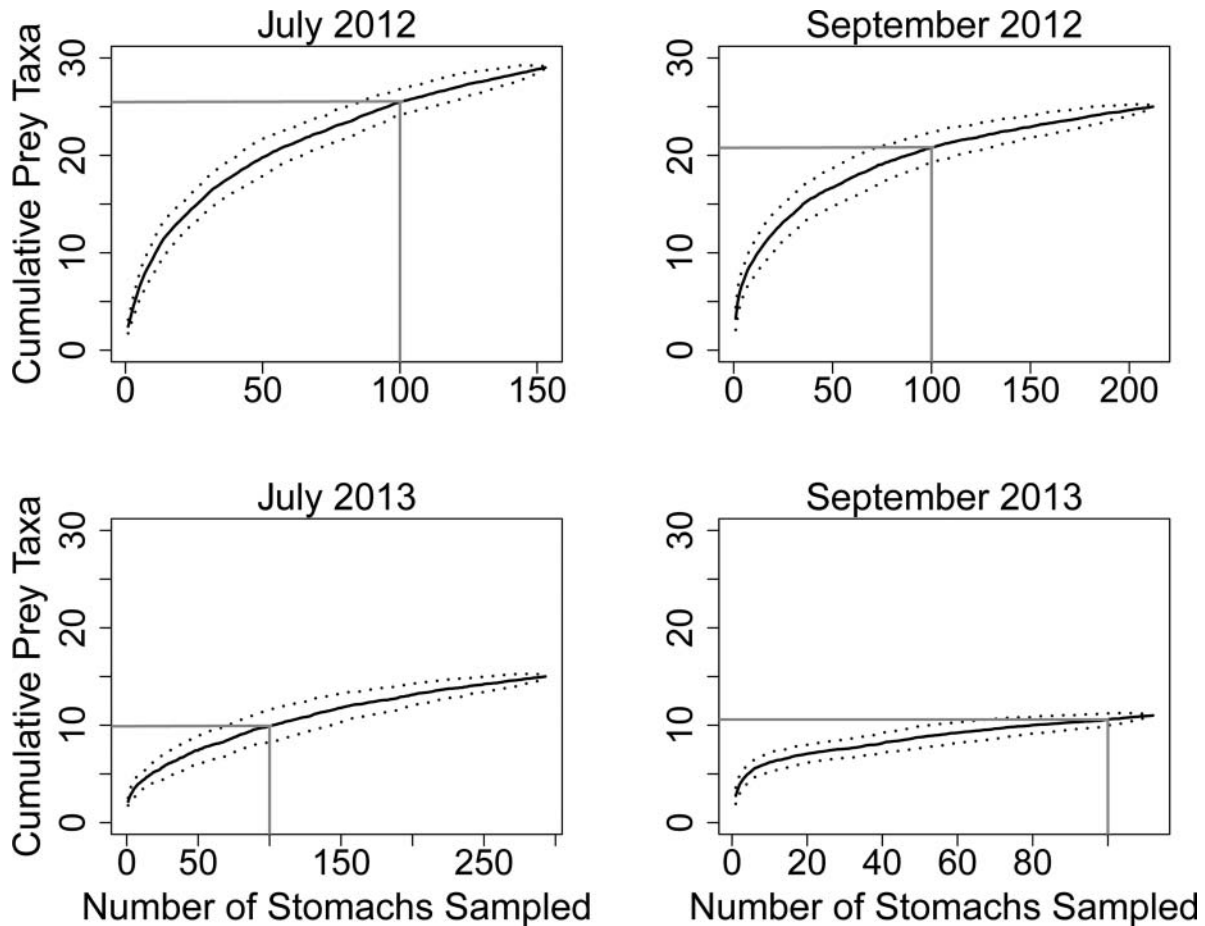


FIGURE 1. Cumulative prey curves for Sablefish sampled in July 2012 ( $N = 165$ ), September 2012 ( $N = 219$ ), July 2013 ( $N = 299$ ) and September 2013 ( $N = 113$ ). The solid line represents the mean cumulative number of unique prey taxa based on randomizing the order in which stomachs were sampled 100 times. The dotted lines represent the SD. To compare sampling periods, gray vertical and horizontal lines signify the mean number of cumulative prey taxa at 100 stomachs sampled (July 2012 = 25, September 2012 = 21, July 2013 = 10, September 2013 = 11).

amphipods (10%). By frequency of occurrence, the most common fish prey was Pacific Herring (9%). By number, 71% of the diet was composed of invertebrates, of which larval brachyuran crabs made up 20% of the diet. Although invertebrates were more abundant and occurred more frequently in samples from Sablefish stomachs in July 2012, the diet by weight was dominated by fishes (80%), particularly Pacific Herring (28%) and gadids (21%). Worms, including polychaetes and sipunculids, comprised 11% of the total diet by weight. In September 2012, the diets contained fewer unique prey taxa and were dominated by Pacific Herring, euphausiids, and salmonid offal. Herring occurred in 43% of fish sampled in this period and made up 38% of the diets by weight. This was the only sampling period in which euphausiids were found in substantial quantities (FO, 49%;  $pN$ , 97%;  $pW$ , 18%). Salmonid offal was found in 17% of the stomachs and made up 14% of the diet by weight. In addition to finding salmonid offal in the

stomachs, we observed numerous Pink Salmon *O. gorbuscha* returning to spawn at the time of sampling within SJBB.

The majority of the diet by all three metrics was made up of herring in July 2013 (FO, 74%;  $pN$ , 68%;  $pW$ , 82%). Smelt occurred in 9% of the samples and contributed 8% to the diet by weight and 6% by number. In contrast to July 2012, Sablefish stomachs sampled in July 2013 had fewer unique prey taxa, and invertebrate prey taxa only occurred in 5% of the sampled stomachs. Samples from September 2013 had the lowest number of unique taxonomic groups. In September 2013, salmonid offal was the most important prey item by frequency of occurrence and weight, 65% and 55%, respectively. Herring were the most numerically abundant (38%), occurred in 50% of the samples, and comprised 33% of the diet by weight.

Prey size was also quantified and compared with predator size to describe ontogenetic shifts in diet (Figure 2). Prey

TABLE 3. Results of two-way crossed analysis of similarity (ANOSIM) testing for differences in diet composition between months and years. One-way ANOSIM pairwise comparisons were made to determine significant differences among sampling periods. All tests were based on presence-absence diet data, with 9,999 permutations and significance set at 0.01. Unidentified teleost prey, unidentified invertebrate prey, and Sablefish with empty stomachs were not included in the multivariate analyses.

Test	Global $R^a$	$P$
Two-way ANOSIM test		
Year	0.305	<0.001
Month	0.267	<0.001
ANOSIM sampling period pairwise tests		
Jul 2012 vs. Sep 2012	0.217	<0.001
Jul 2012 vs. Jul 2013	0.382	<0.001
Jul 2012 vs. Sep 2013	0.179	<0.001
Sep 2012 vs. Jul 2013	0.268	<0.001
Sep 2012 vs. Sep 2013	0.167	<0.001
Jul 2013 vs. Sep 2013	0.305	<0.001

<sup>a</sup> $R$  in the case of the sampling period pairwise tests.

lengths ranged from 0.1 to 204.7 mm and sampled Sablefish consumed prey up to 60% of their body length (FL). The upper and lower bounds of the length-based quantile regression

showed no significant increasing or decreasing trend in teleost prey size with predator ontogeny ( $N = 727$ ; 5th quantile:  $\beta = -0.085$ ,  $P = 0.118$ ) ( $N = 727$ ; 95th quantile:  $\beta = -0.014$ ,  $P = 0.948$ ). The majority of herring consumed by juvenile Sablefish fell within the size range observed for age-0 fish (Norcross et al. 2001); however, the herring consumed in September sampling periods were generally smaller than those consumed in July (Figure 3).

## DISCUSSION

Overall, juvenile Sablefish exploited a large variety of prey taxa, which is characteristic of a generalist predator, and significant diet shifts occurred between sampling periods revealing temporal variation in resource use. Diets appeared more taxonomically diverse, and more invertebrate taxa were found in 2012 than in 2013 when herring and salmonid offal dominated diets. The energetic quality of the diet, prey mass, and Sablefish growth rate were all lower in 2012 than in 2013, suggesting that the nutritional condition of Sablefish varies across years. Based on the quantity of salmonid offal in the diets, juvenile Sablefish are capable of taking advantage of seasonally available, high energy prey within SJBB. The July 2012 sampling period was particularly distinct. During this period a higher proportion of empty stomachs

TABLE 4. Results of similarity percentages (SIMPER) analyses determining the overall mean dissimilarity between sampling periods (%) and identifying the primary prey groups contributing to those differences. Contributing prey groups listed make up 90% of the dissimilarity for each pair of sampling periods.

Prey group	Sampling period					
	July 2012, September 2012	July 2012, July 2013	September 2012, September 2013	July 2013, September 2013	September 2012, July 2013	July 2012, September 2013
Mean dissimilarity	97	94	80	72	76	97
<b>Contribution to difference (%)</b>						
Clupeidae	22	48	27	40	40	25
Salmonid offal	8		32	43	9	35
Euphausiidae	21		20		25	
Brachyura	6	7				6
Ctenophora	5	6				5
Cirripedia	5	6				5
Osmeridae	5	6	5	5	9	2
Hyperiidea	3	5			3	3
Gadidae	3	3	4	5	2	5
Crustacea	3	4				3
Arthropoda	3		3		3	
Copepoda	2					
Bivalvia	2					
Cancridae	1	2				
Gammaridea		2				
Polychaeta	1	2				2



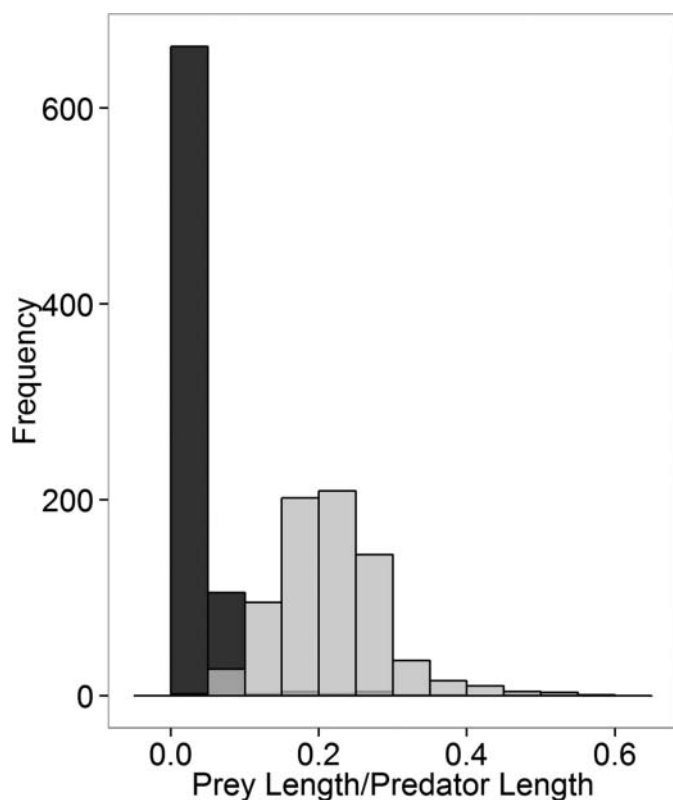


FIGURE 2. Frequency distribution of the prey length : predator length ratios for juvenile Sablefish grouped by invertebrate prey (black bars) and teleost prey (gray bars), in increments of 0.05 (sampling periods combined,  $N = 1,532$ ).

were observed and there was a higher occurrence of relatively low-weight and low-energy invertebrate species; high-energy prey may have been sparse during this sampling period. Also, *Euphausia pacifica* was an important prey item in Sablefish diets only in September 2012. This krill species is typically found near the continental shelf break in the North Pacific Ocean; however, it occurs in inner shelf habitats in late summer and early fall (Pinchuk et al. 2008). If Sablefish consumed euphausiids relative to their availability, the occurrence of euphausiids in diets during September 2012, but not September 2013, suggests that euphausiids were not present in SJBB during the fall 2013 sampling period. Alternatively, Sablefish may have avoided euphausiids in favor of alternative prey in September 2013. Prey availability may influence the differences in diet composition and proportion of empty stomachs between seasons, but we are unable to evaluate the functional response of Sablefish to their prey due to limited information about in situ prey resource abundance. The fish and invertebrate community composition has not been characterized for SJBB and the bay is relatively understudied despite its importance as rearing habitat for commercially valuable species, such as Sablefish, Pacific Herring, and Pink Salmon (Rutecki and Varosi 1997; Piston and Heintz 2011).

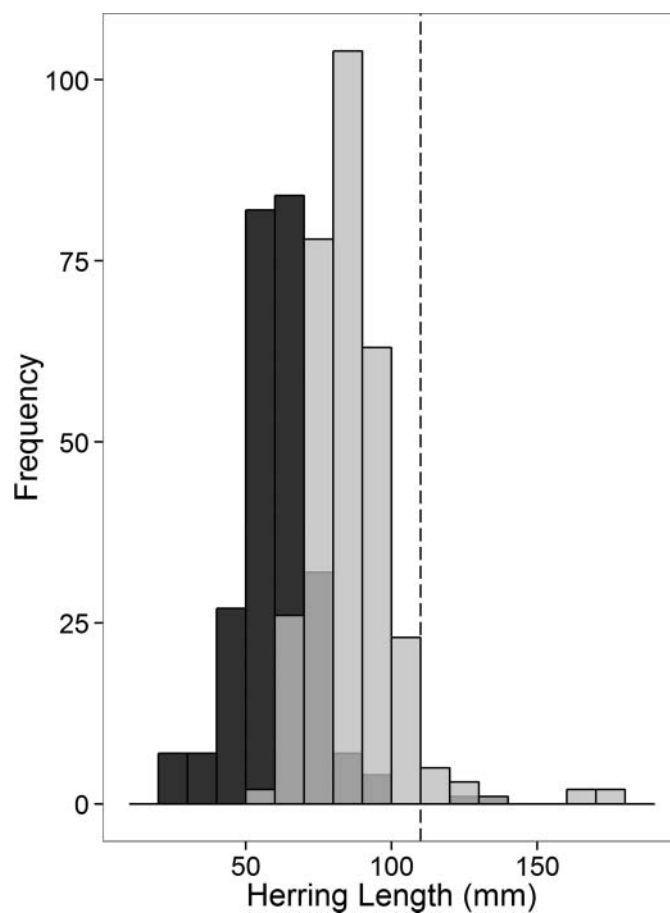


FIGURE 3. Frequency distribution of Pacific Herring prey lengths (mm SL) by month (combined sampling periods;  $N = 568$ ), in 10-mm increments. Black bars represent September herring prey lengths, light gray bars represent July herring prey lengths, and dark gray bars indicate overlap between September and July length distributions. The vertical dashed line is the mean size for age-1 herring in August (110 mm; Norcross et al. 2001).

In Alaskan waters, previous studies have characterized diets for larval and early age-0 Sablefish (90–200 mm) and Sablefish >400 mm (Grover and Olla 1990; Yang and Nelson 2000; Sigler et al. 2001). Sigler et al. (2001) found that age-0 Sablefish diets were dominated by euphausiids (%W) and other zooplankton, while only larval-stage teleosts were consumed. The current study fills a gap in the knowledge of Sablefish feeding ecology in coastal Southeast Alaska by providing diet information for Sablefish ranging from 226 to 455 mm in length. In the current study, a high proportion of the diet for all sampling periods by weight for Sablefish was pelagic fish, primarily Pacific Herring, which was also the most important prey for juveniles (ages 0–3) studied in British Columbia (McFarlane and Beamish 1983). Unlike previous juvenile Sablefish studies in lower latitudes, the current study documents juveniles scavenging on salmon carcasses (McFarlane and Beamish 1983; Cailliet et al. 1988). However, throughout their range Sablefish have exhibited opportunistic feeding on fishing vessel discards (Buckley et al. 1999; Yang and Nelson

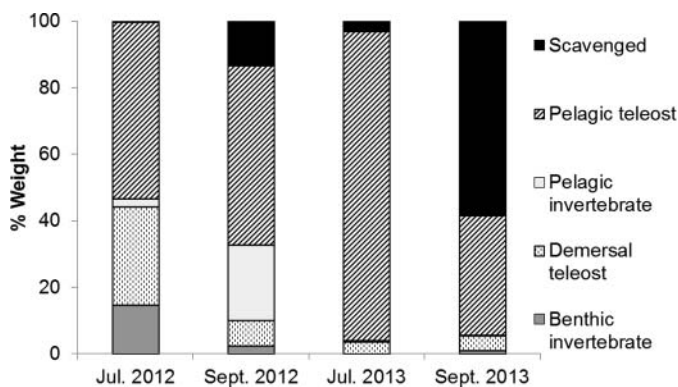


FIGURE 4. Diet composition by prey weight across sampling periods (July 2012,  $N = 356$ ; September 2012,  $N = 841$ ; July 2013,  $N = 415$ ; September 2013,  $N = 204$ ). Unidentified teleost and invertebrate prey were excluded from the plotted prey categories by weight as they did not fit within one specific group.

2000). In the 1990s fishery offal contributed notably to Sablefish diet, and in the Gulf of Alaska in 1996, 32% of their diet by weight was scavenged fishery discards (Buckley et al. 1999; Yang and Nelson 2000). Clear ontogenetic shifts in diet were not observed over the range of Sablefish sizes sampled in the current study; however, comparing our results with previous studies suggests that juvenile Sablefish switch to a diet dominated by teleost prey between ages 0 and 1 and are opportunistic, and the prey species exploited by Sablefish varies with location and timing.

Although diet composition varied between the months and years sampled, forage fish, such as herring and smelt, were a consistent component of the diet. As for many marine predators, Pacific Herring were the most important prey in juvenile Sablefish diet by weight and frequency of occurrence. Although Sablefish were larger in September, they were consuming smaller herring than in July, suggesting that environmental factors accounted for variation in prey fish size instead of ontogeny within the predator size range sampled. This is corroborated by the lack of a significant trend between prey size and predator size. In September sampling periods there may have been more age-0 Pacific Herring available for juvenile Sablefish to exploit than in July due to herring early life history. For example, Pacific Herring in Prince William Sound, Alaska, spawn in April and age-0 herring appear in nearshore nursery grounds by August (Stokesbury et al. 1999; Norcross et al. 2001). Herring were found in stomachs during all sampling periods; however, in July 2012 there was a markedly low frequency of herring occurrence in the diet compared with other periods. Herring stock biomass was not considered low in 2012 within this region of Southeast Alaska (Hebert 2013), and the sparse occurrence in the diets in July may be due to the timing of sampling. Although Pacific Herring remain associated with the nearshore during their first few years of life, aerial surveys conducted in Prince William Sound have revealed that the age composition and spatial

distribution of herring schools in coastal inlets varies among months (Norcross et al. 2001). In Southeast Alaska, Carlson (1980) found that Pacific Herring schools rarely remained in one concentrated location throughout the summer when they are actively searching for food. The mobility of herring schools suggests that the availability of this resource to Sablefish within SJBB pulses on a weekly to monthly scale throughout the summer and fall.

The lack of salmonid offal in the diets during July sampling periods, paired with the known seasonal migration patterns of Pacific salmon, suggests that juvenile Sablefish are taking advantage of this pulsed resource when it is available. The only sampling period in which forage fish made up <50% of the diet by weight was September 2013, when the majority of the diet was composed of scavenged salmon. We estimated the highest energy diet for juvenile Sablefish during this period. Pacific salmon pulses have been widely documented to be a beneficial source of marine derived nutrients to terrestrial predators, such as bears, wolves, foxes, and martens; freshwater predators, such as Arctic Grayling, Dolly Varden *Salvelinus malma*, and Rainbow Trout; and avian predators, such as bald eagles *Haliaeetus leucocephalus*, gulls, crows, and common ravens *Corvus corax* (Willson and Halupka 1995; Schindler et al. 2003; Bentley et al. 2012). Documentation of marine predators exploiting adult spawning salmon pulses in the nearshore has primarily focused on mammals including seals, sea lions, and cetaceans (Willson and Halupka 1995; Saulitis et al. 2000; Sinclair and Zeppelin 2002). Although nearshore marine fish species are known to exploit out-migrating juvenile salmon, the current study is one of the first to document a marine teleost species scavenging on adult salmon carcasses in coastal marine waters. In 1999, juvenile Sablefish fed on juvenile salmon migrating from freshwater to the Gulf of Alaska, suggesting that they cue to multiple life stages of salmon as a food resource (Sturdevant et al. 2009). This study

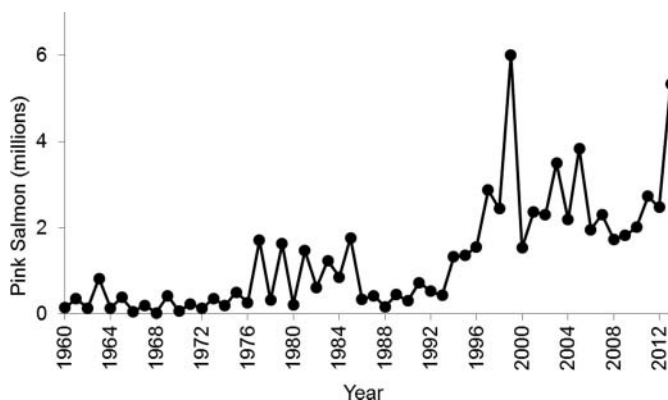


FIGURE 5. Pink Salmon escapement index for the northern outside region of Southeast Alaska, including St. John Baptist Bay. Pink Salmon are regionally cyclic in abundance and had anomalously high harvest and escapement in 2013 (Piston and Heint 2011). Data were provided by A. Piston, Alaska Department of Fish and Game.

further emphasizes the significance of salmon as a vector of energy across ecosystems and indicates a need for continued research to better understand the importance of spawning salmon to marine predators.

While we could not definitively identify consumed salmon to species, we observed many moribund mature Pink Salmon in SJBB during the September sampling periods. Based on field observations and the known timing of Pink Salmon returns to this region from late July to late September (Smoker et al. 1998; Piston and Heintz 2011), it is likely that this species accounts for a high proportion of the salmonid offal observed in Sablefish diets. Pink Salmon stocks in Southeast Alaska have had dominant odd-year run strength since 1999, with poor even-year runs since 2006 that exaggerate this cyclicity (Piston and Heintz 2011). In 2013, Southeast Alaska had the second highest Pink Salmon harvest on record, and a large return was predicted due to previously favorable ocean conditions for these fish as juveniles (Figure 5) (ADFG 2013). The occurrence of a vastly larger Pink Salmon run size in 2013 than in 2012 may explain the higher contribution of salmonid offal to the diet of juvenile Sablefish in 2013.

Energy gained by Sablefish at the juvenile life stage from high quality prey, such as salmon and herring, can translate into growth or lipid storage. Other fishes such as Rainbow Trout and Arctic Grayling experience significantly increased ration size and growth rate as a result of increased salmon densities (Bentley et al. 2012). Average ration size increased by up to 491% for Arctic Grayling and 200% for Rainbow Trout when Sockeye Salmon densities were high in two freshwater streams, and Rainbow Trout switched to a diet of almost entirely salmon (Bentley et al. 2012). In locations where resources may be limited in winter, energy allocation in fishes can switch from growth to lipid storage in the fall (Sogard and Spencer 2004). In May 2013, sampling occurred when water temperature was 3°C, which may be near the lower metabolic threshold for juvenile Sablefish. In laboratory experiments, juvenile Sablefish exposed to temperatures <2°C for longer than 60 s experienced a loss of equilibrium followed by mortality (Sogard and Olla 1998). The four fish caught in May were lethargic, with only one individual containing a sparse amount of prey, suggesting that Sablefish do not feed as actively within SJBB during colder periods. In juveniles, both increased lipid storage and growth are beneficial for overwinter survival, and allocation of energy towards one physiological function may require sacrificing an increase in the other (Post and Parkinson 2001; Sogard and Spencer 2004). Although this tradeoff exists, juvenile Sablefish that were provided high rations and optimal conditions in a laboratory setting did not exhibit a tradeoff between lipid storage and growth; instead storage and growth were positively correlated (Sogard and Spencer 2004). Thus, consumption of high energy prey by Sablefish during July and September may be particularly important

for maintaining good condition as they enter the winter period of low productivity.

Many consumers opportunistically shift their diets to a high proportion of a pulsed resource; for example, the damselfish, *Pomacentrus amboinensis*, specialized on coral propagules during coral spawning events (McCormick 2003). Similarly, Sablefish in SJBB may specialize on salmon during their spawning migrations. While high-energy prey like herring and salmon are important to Sablefish nutrition, these pulsed resources are ephemeral (Figure 4). In contrast, benthic invertebrates such as polychaetes, gammarids, and bivalves are more regularly available in situ but are of lower quality (Figure 4). The ability of Sablefish to exploit a large variety of autochthonous and allochthonous prey suggests that they are not solely dependent on the influx of spawning salmon, but that the pulse may contribute to overwinter survival and rapid juvenile growth. However, evaluating the potential for pulsed resources to confer population-level benefits to Sablefish requires continued investigation into the relationships between energy consumption, growth, and survival of juvenile Sablefish. Moreover, sampling for 4–5 d each month provided a snapshot of Sablefish diet within SJBB that may not be representative of entire months or years. Juvenile Sablefish feeding ecology should be studied in SJBB and other nearshore habitats on a longer temporal scale (i.e., additional seasons and years) to better reveal the dynamic nature of their resource use, for example, through the use of stable isotopes. Thoroughly understanding the consumer–resource relationships of juvenile Sablefish can provide insight into how they will respond to anthropogenic and environmental disruptions to resource abundance in the North Pacific Ocean and coastal marine habitats.

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