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ARTICLE

Diets and Trophic Linkages of Epipelagic Fish Predators in Coastal Southeast Alaska during a Period of Warm and Cold Climate Years, 1997–2011

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Abstract

This study identifies important trophic links for epipelagic marine fish predators in Southeast Alaska to improve understanding of marine ecosystem dynamics in response to climate change. Fish predators can be viewed as autonomous samplers whose diets should integrate the available prey taxa commensurate with environmental conditions. We examined fish predators from annual (1997–2011) surveys conducted in May to September by the Southeast Coastal Monitoring (SECM) project of Auke Bay Laboratories in the marine waters of Southeast Alaska. This project has emphasized long-term monitoring of strait and coastal marine habitats used by juvenile Pacific salmon *Oncorhynchus* spp. and associated epipelagic fishes to understand how environmental variation affects the sustainability of salmon resources. From 1,295 surface trawl hauls, trophic links were identified for 2,473 fish representing 19 predator species, principally adult and immature salmon, immature walleye pollock *Theragra chalcogramma*, and spiny dogfish *Squalus acanthias*. The most common fish prey consumed were fish larvae, juvenile salmon, Pacific herring *Clupea pallasii*, capelin *Mallotus villosus*, walleye pollock, lanternfishes (Myctophidae), and Pacific sand lance *Ammodytes hexapterus*, whereas the most common invertebrate prey consumed were euphausiids, decapod larvae, pteropods, and amphipods. This study describes the degree of piscivory, incidence of juvenile salmon prey, and frequency and weight composition of prey in the diets of epipelagic fish predators, but it did not clearly detect an effect of warm-versus-cold climate years on the diets of key planktivorous or piscivorous predators over the 15-year time series. Identifying the persistence of trophic links in epipelagic waters over time is important because climate-related changes in the upper water column have the potential to impact Southeast Alaska marine ecosystem dynamics and the productivity of important regional fisheries by altering key prey resources and trophic interactions.

An understanding of trophic links in marine food webs is important for identifying the prey resources used by predators; important prey that might affect survival; resource partitioning; and potential sources of competition among seabirds, marine mammals, and fish predators (Livingston 1993; Orlov 2004). From a predator perspective, community diet studies provide information about trophic overlap and the prey types and prey quality needed to support harvestable populations of commercially important species. They also permit comparisons between regions that could explain differences in condition of common fish species (Payne et al. 1999; Brodeur et al. 2007; Vollenweider et al. 2011). From a prey perspective, long-term diet monitoring studies can also identify the importance of taxa to predators and reflect changes over time. Many Alaskan studies of marine food habits have focused on (1) commercially important fish species (Clausen 1981; Livingston 1993; Roseneau and Bird 1997; Wing 1985), (2) single forage fish species (Clausen 1983; Naumenko 1987; Foy and Norcross 1999; Thedinga et al. 2006), (3) co-occurring forage fish species (Willette et al. 1997; Purcell and Sturdevant 2001; Sturdevant et al. 1999, 2004), or (4) apex predators such as seabirds and marine mammals (Hatch and Sanger 1992; Zamon 2001; Witteveen et al. 2006;

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Womble and Sigler 2006). The littoral, epipelagic, and larval fish communities encountered in Southeast Alaska have also been described (Orsi and Landingham 1985; Haldorson et al. 1993; Orsi et al. 2007; Csepp et al. 2011). However, regional information on trophic links in Southeast Alaska marine fish communities is lacking, and would improve understanding of ecosystem dynamics and climate-driven mechanisms that affect local fish populations, help to explain year-class strength, and provide information that management can use to foster sustainability of regional fisheries (Rose et al. 2008).

The Southeast Coastal Monitoring (SECM) project of the National Oceanic and Atmospheric Administration's Auke Bay Laboratories, Alaska Fisheries Science Center, has collected fish diet data during fisheries oceanography surveys annually since 1997 (Orsi et al. 2007, 2011). The research has emphasized long-term monitoring of strait and coastal marine habitats used by juvenile Pacific salmon *Oncorhynchus* spp. and associated epipelagic fishes in Southeast Alaska in order to understand how environmental variation affects salmon resources. The primary research goals are to increase understanding of salmon early marine ecology, relationships with co-occurring fishes, and how climate change may affect recruitment and survival, and to produce an annual forecast of adult pink salmon *O. gorbuscha* returns using juvenile salmon abundance and environmental data (Orsi et al. 2011; Wertheimer et al. 2011). Biophysical variables have been monitored routinely using oceanographic instruments, plankton nets, and surface trawls in epipelagic and neritic waters, and data have been summarized in a series of annual reports (e.g., Orsi et al. 2011). Additional SECM publications have described zooplankton trends and consumption (Orsi et al. 2004; Park et al. 2004; Sturdevant et al. 2011), fish communities (Orsi et al. 2007), juvenile salmon diet (Sturdevant et al. 2004, 2012; Weitkamp and Sturdevant 2008), episodic predation impact on juvenile salmon (Sturdevant et al. 2009), the biophysical environment (Orsi et al. 2009), and ecosystem links to salmon harvest (Wertheimer et al. 2011; Orsi et al. 2012). However, a comprehensive report of the predator diets and community trophic links has not been completed to date, and no diet studies have addressed shifts during climate change. Monitoring interannual and climate-related changes in diet and trophic links is important because climate change threatens to alter community composition (Anderson and Piatt 1999; Litzow and Ciannelli 2007) and zooplankton prey production and timing (Mackas et al. 2007), which could influence the degree of predator–prey mismatch and other trophic interactions (Sydeman and Bograd 2009; Walther 2010), leading to trophic cascades (Casini et al. 2009; O'Gorman et al. 2009).

We summarize the summer food habits of the 19 predator species captured in the Southeast Alaska epipelagic marine fish community during the SECM 15-year time series (Table 1). The purposes of the study were to identify trophic links between these predators and their fish and invertebrate prey, to identify

TABLE 1. Number of predators examined by species and month from 1,295 surface trawl hauls in the marine waters of Southeast Alaska over the 15-year period from 1997 to 2011. Blanks indicate no samples.

Predator species		May	Jun	Jul	Aug	Sep	Total
Pink salmon[a]	*Oncorhynchus gorbuscha*		105	384	92		581
Chum salmon[a,b]	*O. keta*		58	41	23		122
Sockeye salmon[a,b]	*O. nerka*		9	14	3	0	26
Coho salmon[a]	*O. kisutch*		17	24	78	9	128
Chinook salmon[a,b]	*O. tshawytscha*	54	233	139	55	9	490
Dolly Varden	*Salvelinus malma*	1	3				4
Sablefish[c]	*Anoplopoma fimbria*		1	57	17	10	95
Walleye pollock[b]	*Theragra chalcogramma*	106	222	143	105	25	601
Pacific cod[a]	*Gadus macrocephalus*		10	1			11
Pacific hake[a]	*Merluccius productus*		1	2	2		5
Salmon shark[a]	*Lamna ditropis*					1	1
Spiny dogfish[a]	*Squalus acanthias*		62	208	37	3	310
Black rockfish[a]	*Sebastes melanops*		4	2	2		8
Dusky rockfish[a]	*Sebastes ciliatus*		2				2
Pacific herring[c]	*Clupea pallasii*	3	14	1			18
Pacific sandfish[a,b]	*Trichodon trichodon*	8	5	6	2	14	35
Jack mackerel[a]	*Trachurus symmetricus*				1		1
Pomfret[a]	*Brama japonica*			14			14
Starry flounder[a]	*Platichthys stellatus*	5	11	2	1	2	21
Grand total		177	767	1038	418	73	2,473

[a]Adult.
[b]Immature.
[c]Age 0 or age ≥1 or juvenile.

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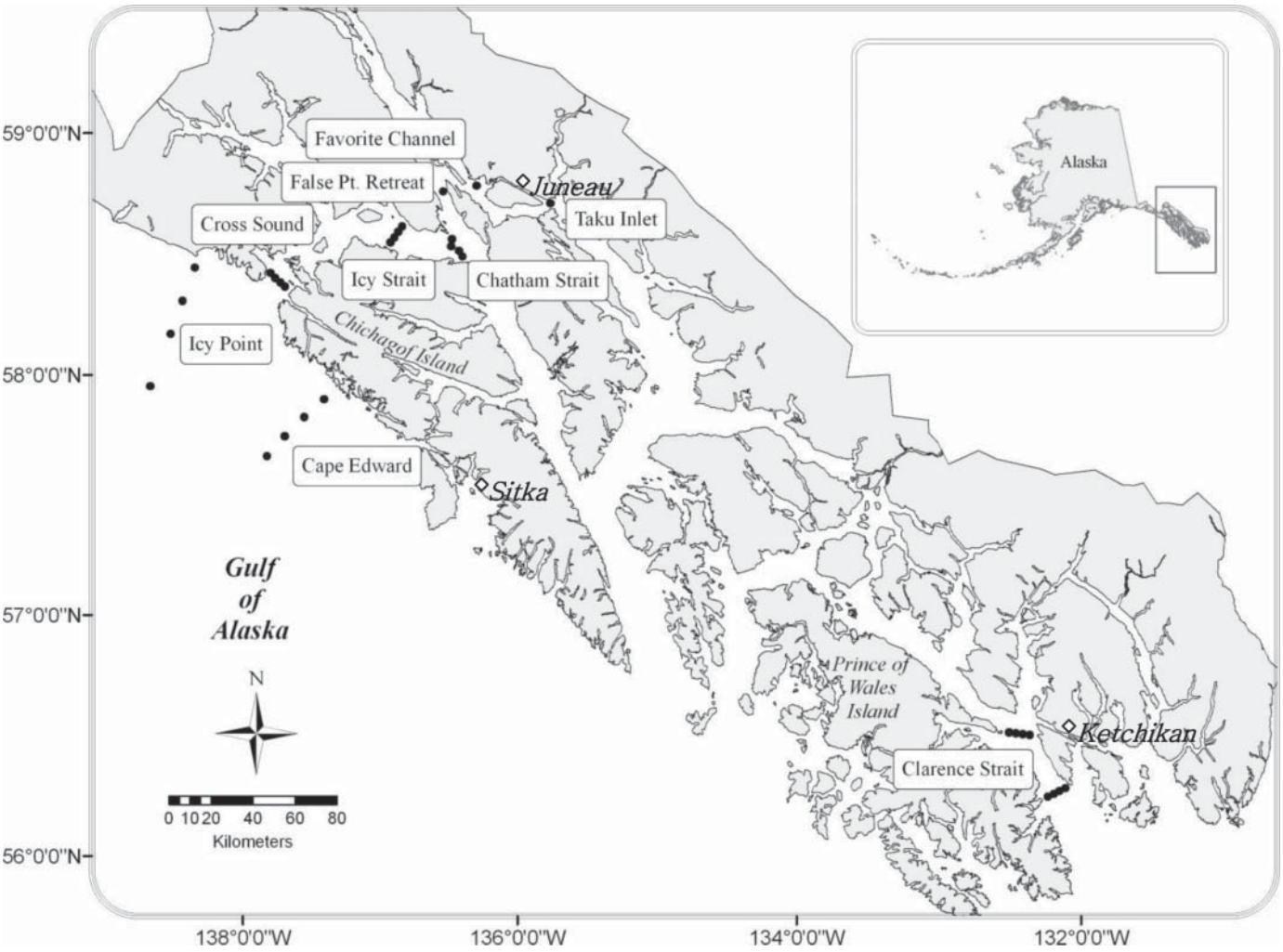


FIGURE 1. Localities (dark dots) sampled with a Nordic surface trawl by the Southeast Coastal Monitoring project in inshore, strait, and coastal habitats in the marine waters of the northern and southern regions of Southeast Alaska from 1997 to 2011. See Table 2 for annual sample sizes and number of hauls by month and habitat.

the principal prey categories targeted and the seasonality of prey utilization, to determine the incidence of juvenile salmon in diets, and to examine for a relationship between diet variation and climate change.

METHODS

Field sampling.—Annual oceanographic sampling and surface trawling for juvenile salmon and associated epipelagic ichthyofauna were conducted from May to September 1997–2011 with the NOAA ship *John N. Cobb* and other vessels. Over the 15-year time series, inshore, strait, and coastal habitats were sampled in the northern and southern regions of Southeast Alaska (Figure 1; Table 2). Trawling focused on strait habitat and targeted juvenile salmon en route to the Gulf of Alaska through these migration corridors in summer months. Predators were captured opportunistically and shipboard sampling was designed to examine for potential predation on juvenile salmon. Eight core stations were sampled in Icy Strait in the northern region (June–August) each year; eight additional stations were sampled in Clarence Strait in the southern region (June–July) in 2005–2007 and 2009 (Figure 1; Table 2). During the first 5 years of the study, trawling was also conducted in May and September in Icy Strait to document juvenile salmon prearrival and departure (Table 2). Inshore habitat was sampled at five stations during five of the early study years to monitor fish residency after they entered the marine environment. Coastal habitat in the Gulf of Alaska was sampled at four stations off of Icy Point (weather-permitting) during 11 years, with eight additional stations sampled at Cross Sound and Cape Edward in a few years.

The Nordic 264 rope trawl used was 184 m long and fished the surface water directly astern of the vessel (Orsi et al. 2007, 2011). Samples were typically collected during daylight hours

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TABLE 2. Number of epipelagic fish predators (total $n = 2{,}473$) examined from surface trawl hauls (total $n = 1{,}295$) in inshore, strait, and coastal habitats by the Southeast Coastal Monitoring (SECM) project in marine waters of the northern and southern regions of Southeast Alaska (SEAK) from 1997 to 2011 by sampling locality, month, and year. Blanks indicate no sampling. The number of trawl hauls is in parentheses.

	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	Total
Strait habitat, northern SEAK: Icy and Chatham Straits																
May	45 (8)	49 (8)	38 (4)		13 (4)					0 (4)						145 (28)
Jun	9 (8)	11 (8)	38 (8)	51 (13)	34 (21)	71 (17)	106 (33)	49 (26)	10 (20)	17 (20)	8 (20)	3 (8)		20 (20)	112 (28)	539 (250)
Jul	0 (9)	27 (12)	72 (8)	31 (10)	88 (24)	26 (21)	46 (17)	74 (25)	24 (23)	20 (20)	38 (28)	10 (28)	61 (30)	18 (20)	134 (28)	669 (303)
Aug	11 (9)	3 (12)	37 (12)	15 (12)	47 (24)	23 (20)	69 (21)	10 (22)	5 (8)	9 (8)	16 (12)	8 (20)	22 (17)	15 (20)	38 (28)	328 (245)
Sep	0 (4)	1 (4)	6 (8)	10 (16)	14 (27)											31 (59)
Total	65 (38)	91 (44)	191 (40)	107 (51)	196 (100)	120 (58)	221 (71)	133 (73)	39 (51)	46 (52)	62 (60)	21 (56)	83 (47)	53 (60)	284 (84)	1,712 (885)
Strait habitat, southern SEAK: Clarence Strait																
Jun									6 (20)	16 (20)	7 (20)					29 (60)
Jul									18 (21)	28 (20)	25 (17)		25 (16)			96 (74)
Total									24 (41)	44 (40)	32 (37)		25 (16)			125 (134)
Inshore habitat, northern SEAK: Taku Inlet, Favorite Channel, and False Point Retreat																
May	12 (3)	7 (2)						2 (3)								21 (8)
Jun	12 (3)	6 (3)	7 (3)	6 (3)				20 (3)								51 (15)
Jul	0 (3)	3 (3)	31 (3)	9 (3)												43 (12)
Aug	0 (3)	2 (4)	3 (3)	4 (3)												9 (14)
Sep	1 (2)	2 (3)	20 (3)	2 (3)												25 (11)
Total	25 (14)	20 (15)	61 (12)	21 (12)				22 (6)								149 (60)
Coastal habitat, northern SEAK: Cross Sound, Icy Point, and Cape Edward																
May	6 (8)									5 (2)						11 (10)
Jun	20 (8)	24 (12)	28 (11)	6 (8)	12 (4)	3 (4)	4 (2)	7 (4)							44 (4)	148 (57)
Jul	3 (8)	75 (16)	13 (11)	69 (6)	27 (4)	8 (8)	23 (4)	2 (4)						6 (4)	5 (4)	231 (69)
Aug	9 (8)	9 (8)	8 (8)	7 (8)		4 (7)		37 (6)						0 (4)	7 (4)	81 (53)
Sep	10 (8)	1 (7)	3 (8)	3 (4)												17 (27)
Total	48 (40)	109 (43)	52 (38)	85 (26)	39 (8)	15 (19)	27 (6)	46 (14)		5 (2)				6 (8)	56 (12)	488 (216)
Grand total	138 (92)	220 (102)	304 (90)	213 (89)	235 (108)	135 (77)	248 (77)	201 (93)	63 (92)	95 (94)	94 (97)	21 (56)	108 (63)	59 (68)	340 (96)	2,473 (1,295)

over several days at the end of each month; predators from 13 night (2100–0600 hours) trawls were sampled (mainly in 2001 and 2004 in strait habitat). Net-mouth dimensions were 18 m wide by 24 m deep. The trawl headrope wing tips were buoyed so the top end of the net fished directly under the surface. Net meshes decreased from 162.6 cm at the jib lines aft to 10.1 cm at the cod end; a 6.1-m long, 0.8-cm knotless liner mesh was sewn into the cod end. The trawl was fished across each station one to four times per month for 20 min at approximately 1.5 m/s (3 knots) to cover 1.9 km (1.0 nautical mile).

Shipboard sample processing.—Large, potential fish predators of juvenile salmon were euthanized, sorted, identified, counted, measured (mm; fork length [FL]), wet weighed with a spring scale (g or kg), and stomach-sampled. Typically, all stomachs were examined per haul (up to 20 stomachs per species in unusual cases of abundance). Large individuals of smaller species such as Pacific herring were also examined in early years to confirm lack of predation on juvenile salmon because herring predation had been locally documented in inshore habitat (Thorsteinson 1962). The percentage gut fullness volume ($FV_{\%}$) of each fish was visually classified (0, 10, 25, 50, 75, 100%, and distended), and total content weight (W; 0.1 g via spring scale) was estimated by subtracting the empty stomach weight from the full stomach weight. Fish and invertebrate prey were identified without aid of a microscope and categorized into broad taxa (generally to family or order). In addition to "unidentifiable" categories of fish and invertebrate remains, we specified a category for white granular matter (indicating jellyfish or oikopleuran remains). The percent composition by volume ($V_{\%}$) was visually estimated for each category, then converted to percent weight ($W_{\%} = W \times V_{\%}$). Prey life stage was noted when possible, and individual or group prey lengths (total or fork) were recorded for intact specimens, especially in later years.

Data analysis.—Size (mean FL and wet weight), feeding intensity, and food habits were summarized by species over the entire time series. Feeding intensity included percent frequency of empty guts ($EMTY_{\%}$) and its inverse, percent feeding ($FDG_{\%} = 100 - EMTY_{\%}$), mean content percent body weight ($BW_{\%}$), and $FV_{\%}$ for the subset of fish with food in their guts. To describe food habits for the community as a whole, prey categories were classified as invertebrate or fish (salmon, nonsalmon, or unidentifiable digested remains), and their $W_{\%}$ was graphically summarized over the entire time series. This analysis permitted us to determine the degree of piscivory among the species and their potential roles as predators of juvenile salmon. To identify which prey were utilized, we tabulated the incidence or percent frequency of occurrence ($FO_{\%}$) of the fish and invertebrate categories by predator species across the entire time series. We estimated diet overlap between predator species pairs using the PRIMER-E multivariate statistical package (Plymouth Routines in Multivariate Ecological Research, version 6; Clarke and Warwick 2001). A matrix of Bray–Curtis similarity indices was computed from the square root-transformed $FO_{\%}$ and the $W_{\%}$ multivariate prey composition data sets. Diet overlap was considered significant for values ≥ 50. To examine when prey were utilized, we graphically summarized the monthly

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$FO_{\%}$s across the entire predator community. To examine the temporal importance of these prey, we graphically summarized the monthly $W_{\%}$s (excluding adult salmon prey in three spiny dogfish) to indicate bioenergetic (nutritional) contribution to the predator community. We also tabulated the monthly size range (FL; mm) of prey fish categories used by the epipelagic fish community. These data are based on the subset of measured prey samples and were considered to be semiquantitative.

Long-term trends in diets were examined by season, climate, and year using prey $W_{\%}$ data for the most common predator species. First, we compared overall seasonal diets of the four adult and immature salmon species, walleye pollock and spiny dogfish by month across years for strait and coastal habitats. Next, we examined for climate effects on diets of three key species in strait habitat in warm versus cold years, including pink salmon, Chinook salmon, and walleye pollock. Last, we graphically summarized interannual diet variation by month and year in strait habitat for these key predators.

The climate analysis was composed of two parts. The first part entailed testing to confirm that local temperature in Icy Strait for the 15-year time series was correlated with an ocean-basin scale index that signals climate change. For this, we compared the monthly SECM summer (May–August) mean temperature of the 20-m integrated water column (the stratum where predators were captured) from 1997 to 2011 to a common climate metric, the El Niño/La Niña Southern Oscillation (ENSO) Multivariate ENSO Index (MEI; Wolter 2012). The SECM summer mean temperature was computed from monthly CTD data at 1-m increments per station, for a total of at least 160 observations per month each year (Orsi et al. 2011; Wertheimer et al. 2011). The MEI data used was the average of the 12 months beginning in September of the year prior to our sampling year, to capture the lag effect of propagating ocean–atmospheric teleconnections from the equatorial Pacific Ocean. We tested for correlation of the SECM summer temperatures with the MEI using Minitab 16 (Minitab 2010). The linear relationship was characterized by the Pearson's product-moment correlation coefficients, r ($-1 \leq r \leq 1$) and associated P-value.

For the second part of the climate analysis, diet years were categorized as warm or cold based on whether the SECM summer temperature was above or below the long-term mean. We aggregated diets for each of the three key predator species by warm versus cold years across June, July, and August for graphical presentation. We then tested for species (3), month (3), and climate effects (2; warm versus cold) on the square-root-transformed multivariate diet composition using two procedures in PRIMER-E (Clarke and Warwick 2001). The nonmetric multidimensional scaling procedure was used to assess the strength of the grouping relationships by a distance measure, the stress value. The analysis of similarity (ANOSIM) procedure was used to test for a global effect of warm versus cold climate and for differences between species and month pairs. The ANOSIM R-statistic ($0 \leq R \leq 1$) indicates separation between groups, with an associated P-value.

RESULTS

Spatial and Temporal Predator Catch Patterns

A total of 2,473 epipelagic fish predators representing 19 species were examined from 1,295 surface trawls in inshore, strait, and coastal habitats of Southeast Alaska during May, June, July, August, and September 1997–2011 (Tables 1, 2). Trawling effort occurred primarily in strait habitat (1,019 hauls) and less in coastal (216 hauls) and inshore (149 hauls) habitats (Table 2). Consequently, this spatial pattern was reflected in predator samples: 74% from strait, 20% from coastal, and 6% from inshore habitats. Temporally, predators were captured in May (7%), June (31%), July (42%), August (17%), and September (3%; Table 1). The most common species were adult pink salmon, immature Chinook salmon, walleye pollock, and spiny dogfish (Table 3). The less common predator species were captured in specific habitats or in rare years. For example, pomfret and jack mackerel were captured only in 1997, 2000, and 2001 in coastal habitat; Pacific hake were captured only in 2003, 2006 and 2007 in strait habitat; juvenile sablefish were captured only in 1997–1998 in coastal habitat and in 1999 in strait habitat; and Pacific cod were captured in 1999 in coastal habitat and in 2003 in strait habitat. The limited collections from May (1997–1999, 2001, and 2006) included substantial numbers only of immature Chinook salmon and walleye pollock (Table 1).

Size and Feeding Intensity

The largest common predators examined included adult Pacific salmon and spiny dogfish (mean FL = 507–649 mm), excluding salmon shark (Table 3). Intermediate-sized predators (about 300–400 mm FL) included immature Chinook salmon, Dolly Varden, juvenile sablefish, immature walleye pollock, Pacific cod, and starry flounder. The smallest predators (>175 mm) included Pacific herring and Pacific sandfish. Overall, at least 50% of each predator species examined had been feeding; the few exceptions included sockeye salmon (42% feeding), starry flounder (48%), and the one jack mackerel with an empty gut. Higher feeding percentages (74–89%) were observed for most salmon species, the Gadiformes (walleye pollock, Pacific cod, and Pacific hake), and sablefish, Pacific herring, and Pacific sandfish. Gut $FV_{\%}$ averaged between 30% and 69% overall, and was lower for species with lower $FDG_{\%}$. Gut $BW_{\%}$ was highest for coho salmon and Chinook salmon, sablefish, and Pacific sandfish (about 1–6%). Gut $BW_{\%}$ averaged <1% for the Pacific herring, walleye pollock, starry flounder, and spiny dogfish.

Planktivores and Piscivores

Piscivores, planktivores, and omnivores were clearly distinguished when predators were ordered by declining contribution of fish to the diets (Figure 2). Piscivorous species ($W_{\%} > 80\%$ fish prey) included black rockfish, coho and Chinook salmon, juvenile sablefish, Pacific hake, and Pacific sandfish. The utilization of juvenile salmon prey was greatest for juvenile sablefish ($W_{\%} = 76\%$) and was noted in six additional predator species. All other predators except the four Dolly Varden (omnivorous)

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TABLE 3. Predator size and feeding intensity as the percent of individuals feeding ($FDG_{\%}$), the percent fullness volume ($FV_{\%}$), and prey percent body weight ($BW_{\%}$) for 19 fish species and 2,473 individuals captured in summer in 1,295 surface trawl hauls in the marine waters of Southeast Alaska over the 15-year period from 1997 to 2011. Blanks indicate no data.

		Mean size (SE)		Feeding intensity (SE)		
Predator species	*N*	Fork length (mm)	Wet weight (g)	$FDG_{\%}$	$FV_{\%}$	$BW_{\%}$
Pink salmon[a]	581	507 (2)	1,620 (20)	74	36 (2)	0.3 (0.0)
Chum salmon[a,b]	122	649 (6)	3,377 (109)	84	32 (3)	0.4 (0.0)
Sockeye salmon[a,b]	26	595 (19)	2,671 (190)	42	15 (6)	0.1 (0.0)
Coho salmon[a]	128	630 (7)	3,328 (114)	84	57 (4)	1.2 (0.1)
Chinook salmon[a,b]	490	396 (5)	1,000 (70)	84	56 (2)	1.2 (0.1)
Dolly Varden	4	305 (27)	320 (74)	100	26 (16)	0.8 (0.3)
Sablefish[c]	95	319 (6)	386 (17)	83	58 (5)	2.6 (0.3)
Walleye pollock[b]	601	407 (4)	527 (12)	89	42 (1)	0.6 (0.1)
Pacific cod[a]	11	338 (30)	417 (189)	82	30 (7)	0.3 (0.1)
Pacific hake[a]	5	527 (29)	890 (90)	80	66 (20)	1.4 (0.8)
Salmon shark[a]	1	1830		100	100 (0)	
Spiny dogfish[a]	310	641 (7)	1,597 (59)	51	12 (1)	0.9 (0.1)
Black rockfish[a]	8	521 (17)	2,613 (253)	63	48 (18)	1.6 (0.7)
Dusky rockfish[a]	2	300 (20)	510 (160)	50	40 (40)	0.2 (0.2)
Pacific herring[c]	18	192 (6)	74 (8)	89	58 (6)	0.6 (0.1)
Pacific sandfish[a,b]	35	173 (6)	87 (12)	83	68 (8)	6.3 (1.1)
Jack mackerel[a]	1	574		0	0	
Pomfret[a]	14	352 (6)	1,058 (42)	100	51 (10)	0.4 (0.1)
Starry flounder	21	347 (14)	563 (102)	48	28 (9)	0.5 (0.3)

[a]Adult.
[b]Immature.
[c]Age-0 or age ≥1 or juvenile.

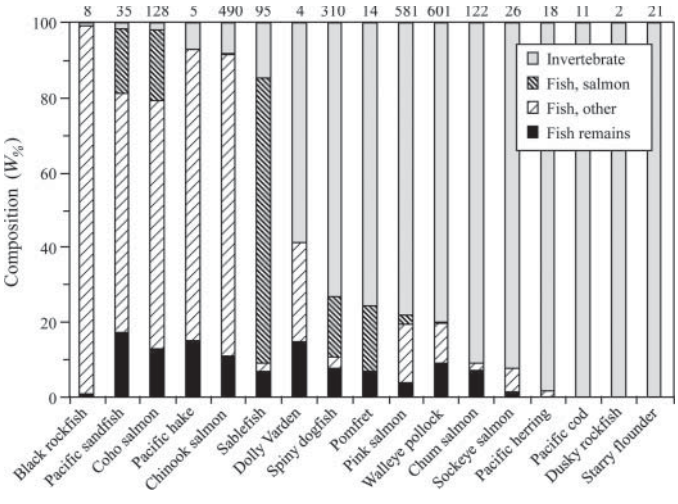


FIGURE 2. Degree of piscivory and overall food habits by weight composition ($W_{\%}$) among 18 epipelagic fish species captured in marine waters of Southeast Alaska from May to September 1997–2011. Fish are ordered by increasing $W_{\%}$ of invertebrate prey. The number of fish examined is indicated above the bars. A single jack mackerel with an empty stomach and a salmon shark that contained adult salmon flesh were omitted (see Table 1).

were planktivorous ($W_{\%} > 75\%$ invertebrate prey), including spiny dogfish; pomfret; adult pink, chum, and sockeye salmon; walleye pollock; starry flounder; Pacific herring; Pacific cod; and dusky rockfish.

Prey Utilization and Diet Overlap

Twenty-four fish and 16 invertebrate prey categories were recorded from predator guts (Table 4). We identified fish and invertebrate prey consumed by each epipelagic predator species and listed prey categories from those shared by most predator species to those shared by fewest predator species; we then ordered the predators by diminishing diversity of fish prey (Table 4). The most common category of fish prey (present in 13 predator species) was unidentifiable (highly digested fish remains) and was among the highest prey incidence ($FO_{\%}$). Field notes indicate that most of these fish remains were probably not salmon, which are identifiable to species for up to 16 h postingestion (Sturdevant et al. 2009) but were probably other common fish prey categories (M. Sturdevant and E. Fergusson, unpublished data). The next four most common categories (unidentified fish larvae, juvenile salmon, Pacific herring, and capelin *Mallotus villosus*) were present in nearly half of the predator species, generally at lower incidence. Juvenile salmon in juvenile sablefish guts was an exception ($FO_{\%} = 34\%$). Walleye pollock, lanternfish (Myctophidae), and Pacific sand lance

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TABLE 4. Frequency of occurrence of 24 fish and 16 invertebrate (plankton) prey categories in the guts of 18 epipelagic fish predator species captured in surface trawl hauls in the marine waters of Southeast Alaska over the 15-year period from 1997 to 2011. Frequencies are calculated only for fish that were feeding (one jack mackerel with an stomach empty was excluded). The fish and invertebrate prey categories are listed from those shared by the most predator species to those shared by the fewest. The predator species are ordered from left to right by diversity of fish prey. Categories that did not occur in a predator's gut contents are blank.

	Chinook salmon	Coho salmon	Pink salmon	Walleye pollock	Sablefish	Spiny dogfish	Chum salmon	Pacific sandfish	Black rockfish	Pacific hake	Sockeye salmon	Dolly Varden	Pomfret	Pacific herring	Salmon shark	Dusky rockfish	Pacific cod	Starry flounder
Number of fish	490	128	581	601	95	310	122	35	8	5	26	4	14	18	1	2	11	21
Empty (%)	15.7	15.6	25.5	11.5	16.8	49.0	15.6	17.1	37.5	20.0	57.7	0.0	0.0	11.1	0.0	50.0	18.2	52.4
Fish prey categories																		
Unidentified remains	25.2	34.3	9.7	8.6	19.0	10.1	8.7	27.6	20.0	50.0	9.1	25.0	14.3					
Unidentified larvae	17.7	4.6	10.6	3.9	2.5	0.6	4.9				9.1			6.3				
Juvenile salmon	0.2	17.6	0.9	0.2	34.2	5.1		10.3					7.1					
Pacific herring	6.1	18.5	1.2	0.2	1.3	3.8	1.9	48.3										
Capelin	20.8	3.7	0.2	1.5	1.3		1.0	3.4		25.0								
Walleye pollock	9.0	6.5	0.9	0.8	1.3	0.6	1.0											
Lanternfishes (Myctophidae)	6.1	2.8	1.4	0.2			1.0			25.0								
Pacific sand lance *Ammodytes hexapterus*	5.6	3.7	1.6	0.6			1.0		20.0									
Greenlings (Hexagrammidae)	0.5	0.9				3.8			20.0									
Sculpins (Cottidae)	1.0		0.5		2.5							50.0						
Flatfish (Pleuronectidae)	2.7		0.9				1.9											
Northern smoothtongue *Leuroglossus schmidti*	0.5		0.2	0.6														
Poachers (Agonidae)	0.7		0.2									25.0						
Wolf-eel *Anarrhichthys ocellatus*	0.5				1.3				20.0									
Smelts (Osmeridae)	1.0		0.5															
Rockfish (Scorpaenidae)			0.5			0.6												
Sablefish		7.4							20.0									
Pacific sandfish	0.2								20.0									
Stichaeids	0.7	0.9																
Adult salmon						1.9									100.00			
Eulachon *Thaleichthys pacificus*				0.4														
Prowfish *Zaprora silenus*		0.9																
Quillfish *Ptilichthys goodei*	0.5																	
Pacific saury *Cololabis saira*		2.8																
Invertebrate (plankton) prey categories																		
Euphausiids	19.9	17.6	39.5	65.0	12.7	28.5	10.7		20.0	25.0	9.1	50.0	50.0	18.8				10.0
Unidentified remains	1.9	1.9	2.5	10.5	3.8	42.4	10.7	10.3	20.0	25.0			21.4	12.5			22.2	20.0
Decapod larvae	10.9	14.8	62.6	20.7	10.1	0.6	9.7	6.9			36.4	50.0	35.7	18.8				50.0
Pteropods	0.2	6.5	18.0	6.8	27.8	0.6	12.6				18.2		7.1	6.3		100.0	33.3	20.0
Amphipods	9.4	10.2	29.8	25.9	6.3	8.2	10.7				36.4		50.0	6.3				10.0
Shrimp	2.4	0.9	2.1	3.4	2.5	1.9				50.0								
Cephalopods	6.5	2.8	1.4	0.8		6.3	1.0						71.4					
Copepods	0.5		1.6	31.6			1.9	6.9						62.5			88.9	
Jellyfish (Ctenophora or Cnidaria)			1.6	0.6	8.9	8.2	23.3											
Polychaetes			0.9	0.8		1.9	1.0				9.1							
Oikopleurans	0.2			10.7			23.3											
Mysids	0.2			0.2														
Salps							2.9											
White granular matter							26.2											
Chaetognaths				0.6														

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TABLE 5. Diet overlap between 17 epipelagic fish predator species pairs captured in surface trawls in marine waters of Southeast Alaska from 1997 to 2011. Overlap is computed as Bray–Curtis similarity indices from square-root-transformed percent weight (top rows) and percent frequency (bottom rows, underlined) of prey categories across all months, years, and locations. Overlap of ≥50% is indicated by bold italics.

	Chinook salmon	Coho salmon	Pink salmon	Walleye pollock	Sablefish	Spiny dogfish	Chum salmon	Pacific sandfish	Black rockfish	Pacific hake	Sockeye salmon	Dolly Varden	Pomfret	Pacific herring	Dusky rockfish	Pacific cod
Coho	***55***															
salmon	***69***															
Pink	42	34														
salmon	***59***	***61***														
Walleye	36	24	***56***													
pollock	49	***53***	***71***													
Sablefish	24	37	40	36												
	53	***63***	***62***	***54***												
Spiny	26	25	35	26	45											
dogfish	41	47	***50***	45	***52***											
Chum	20	13	39	48	42	37										
salmon	***51***	***52***	***65***	***64***	***57***	46										
Pacific	35	***59***	29	16	35	36	16									
sandfish	37	***50***	30	37	45	36	35									
Black	19	23	13	12	9	8	8	10								
rockfish	30	37	26	28	30	42	26	25								
Pacific	50	30	21	30	23	17	16	22	5							
hake	49	39	32	37	35	43	28	35	36	49						
Sockeye	22	8	***59***	42	29	17	32	5	4	10						
salmon	38	47	***61***	***58***	***50***	34	49	21	17	16						
Dolly	26	19	45	30	24	21	21	20	5	24	32					
Varden	37	32	43	40	35	22	22	26	24	31	32					
Pomfret	28	32	37	30	49	***68***	29	41	9	19	25	30				
	41	***50***	***61***	***62***	50	49	42	36	30	35	47	46				
Pacific	18	4	43	49	16	21	26	5	5	5	38	34	21			
herring	39	44	***56***	***68***	46	37	48	32	25	26	***57***	29	48			
Dusky	0	0	21	10	13	0	12	0	0	0	45	0	0	6		
rockfish	0	9	16	10	23	0	13	0	0	0	22	0	11	15		
Pacific	0	0	5	15	0	26	10	6	5	0	0	0	6	***51***	0	
cod	5	12	21	35	25	21	25	26	15	17	15	0	23	***58***	41	
Starry	5	5	44	19	18	0	18	0	0	0	37	44	9	32	24	0
flounder	30	39	***51***	***51***	48	38	44	28	24	23	***64***	30	***52***	***68***	28	38

prey were utilized by approximately one-third of the predator species at low $FO_{\%}$, and the 16 remaining fish prey categories were consumed occasionally (Table 4). Low rates of cannibalism were evident for walleye pollock and pink salmon. Only spiny dogfish and the salmon shark ate adult salmon. For invertebrate prey, the top five prey categories with high $FO_{\%}$s by 11–14 predator species included euphausiids, decapod larvae, pteropods, and amphipods. We speculated that the liquefied, unidentified remains category that occurred frequently was typically euphausiids (orange color) or decapod larvae (brown color). The remaining 11 invertebrate prey categories were utilized less commonly, but sometimes occurred frequently in one or two predator species (e.g., copepods in Pacific cod and walleye pollock, white granular matter in chum salmon, cephalopods in pomfret; Table 4). Decapod larvae identifications were confirmed to be principally noncommercial species (e.g., *Cancer* spp., *Oregonia* spp., *Chionocetes* spp., *Fabia* spp., or pagurids; Wing 1985, W. Park, Auke Bay Laboratories and E. Fergusson, unpublished data).

Diet overlap among predator species pairs was more common by prey $FO_{\%}$ and generally showed higher values than overlap by prey $W_{\%}$ (Table 5). Walleye pollock and pink salmon diet overlapped with other species' diets most commonly (6–8 species), based on $FO_{\%}$, reflecting their wide prey spectrum. The highest diet overlap occurred between two planktivores, walleye pollock and pink salmon ($FO_{\%} = 71\%$; $W_{\%} = 56\%$) and between two piscivores, Chinook and coho salmon ($FO_{\%} = 69\%$, $W_{\%} = 55\%$). Other instances of bioenergetic diet overlap

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(prey $W_{\%}$) included pink salmon with sockeye salmon ($FO_{\%} = 61\%$, $W_{\%} = 59\%$), coho salmon with Pacific sandfish ($FO_{\%} = 50\%$, $W_{\%} = 59\%$), pomfret with spiny dogfish ($FO_{\%} = 49\%$, $W_{\%} = 68\%$), and Pacific cod with Pacific herring ($FO_{\%} = 58\%$, $W_{\%} = 51\%$; Table 5).

Tabulation of the prey frequencies indicated partitioning among piscivorous and planktivorous predators (Table 4). Among the piscivorous species, coho and Chinook salmon ate the greatest variety of fish, but Chinook salmon ate high $FO_{\%}$ of capelin and fish larvae, whereas coho salmon ate high $FO_{\%}$ of Pacific herring and juvenile salmon. These piscivorous salmon species also frequently ate invertebrate prey. Prey of the piscivorous juvenile sablefish, Pacific hake, and Pacific sandfish were less diverse than those of piscivorous salmon. Planktivorous pink salmon also ate a wide variety of fish prey in low $FO_{\%}$s, and sockeye salmon and Pacific herring also consumed small fish larvae. Planktivorous predators used invertebrate prey categories differentially. Planktivores typically consumed many invertebrate prey categories, with the widest variety consumed by walleye pollock and pink and chum salmon. However, one category usually predominated for a given species: *FO*%s were 65% for euphausiids in walleye pollock, 63% for decapod larvae in pink salmon, 63% for copepods in Pacific herring, and 71% for cephalopods in pomfret. The top prey categories by descending $FO_{\%}$ were decapod larvae, euphausiids, amphipods and pteropods for pink salmon; gelatinous prey, including white granular matter, jellyfish, and oikopleurans for chum salmon; and amphipods, decapod larvae, and pteropods for sockeye salmon.

Prey Seasonality for the Epipelagic Community

The incidence and bioenergetic importance of fish and invertebrate prey categories for the overall epipelagic fish community changed seasonally (Figure 3). No single fish prey category exceeded an $FO_{\%}$ of 25% or a $W_{\%}$ of 30% of the monthly total. Of the prey consumed seasonally, $FO_{\%}$ of Pacific herring, lanternfish, and juvenile salmon prey increased, while fish larvae and capelin prey was relatively high and stable and Pacific sand lance and walleye pollock prey decreased. The seasonal pattern for bioenergetic importance ($W_{\%}$) of common fish prey categories generally tracked the $FO_{\%}$ pattern of incidence, except for Pacific herring and walleye pollock (Figure 3).

Invertebrate prey categories also showed seasonal $FO_{\%}$ peaks of incidence in the overall fish community and generally tracked the pattern for bioenergetic importance, suggesting stable use of abundant prey resources by the predators. This trend was evident for oikopleurans and euphausiids in May, copepods and pteropods in June, decapod larvae in July, and amphipods in July and August (Figure 3). Euphausiid incidence was also high in August, but importance was much reduced after May (when the only predators were planktivorous walleye pollock and the immature Chinook salmon). Overall, higher $FO_{\%}$ for invertebrate prey than for fish prey indicated either higher abundance and availability or more common utilization by epipelagic predators (Figure 3). Some of these small invertebrate prey categories contributed relatively high $W_{\%}$ to predator diets.

The broad monthly size range of fish prey categories (Table 6) in predator guts generally indicated size-selective predation on smaller fish stages (ages 0 and 1) than were captured in the trawls (authors' unpublished data). Although average sizes could not be computed, the length size ranges generally encompassed larvae and age-0 fish (<80 mm), juveniles (<175 mm), and immatures (<250 mm). The size range information for some prey taxa, such as Pacific herring, walleye pollock, and lanternfish, also indicated that multiple age-classes were utilized by predators (Table 6).

Seasonal Diets by Species and Habitat

Seasonal patterns in prey $W_{\%}$ indicated prey partitioning between the most abundant piscivorous and planktivorous predator species and highlighted changes in prey species utilization by month and habitat. Large sample sizes permitted us to describe seasonal food habits of walleye pollock and immature Chinook salmon in strait habitat from May to September; chum, pink, and coho salmon in strait habitat from June to August; and pink salmon and spiny dogfish in coastal habitat from June to August (Table 1; Figure 4). For planktivorous adult pink salmon in all 3 months, the $W_{\%}$ of decapod larvae predominated in strait habitat while the $W_{\%}$ of pteropods predominated in coastal habitat. However, euphausiids, amphipods, and a variety of fish also contributed substantial $W_{\%}$ to pink salmon diet in different months, leading to a different pattern than that indicated by the $FO_{\%}$ data (Table 4). In contrast, for adult chum salmon in all 3 months in strait habitat, gelatinous prey predominated by both $FO_{\%}$ and $W_{\%}$. For planktivorous walleye pollock, euphausiids contributed high $W_{\%}$ from May to September, with lesser $W_{\%}$ from amphipods and copepods. Other prominent prey for walleye pollock included oikopleurans in May, pteropods in June, eulachon and unidentifiable fish in August, and capelin in September.

Striking seasonal differences in fish prey taxa were apparent for piscivorous adult coho salmon and immature Chinook salmon in strait habitat and for the more planktivorous spiny dogfish in coastal habitat. For coho salmon, Pacific herring made up 96% of $W_{\%}$ in June, while juvenile salmon made up 84% of $W_{\%}$ in August. These two prey species and walleye pollock and fish remains contributed high $W_{\%}$ in the other months (Figure 4). For immature Chinook salmon, capelin, sand lance, and euphausiids contributed most $W_{\%}$ in May; capelin remained prominent throughout the season, other fish contributing in different months (Pacific herring in June–August, myctophids in July–August, and walleye pollock in September). Spiny dogfish gut contents were frequently unrecognizable, but cephalopods predominated in June, unidentifiable fish remains in August, and invertebrate remains in July and September. Juvenile salmon contributed to spiny dogfish prey $W_{\%}$ in June and July.

Climate Relationship to Interannual Predator Diets

Across the time series, average annual temperatures in the 20-m water column of Icy Strait for the months of May to

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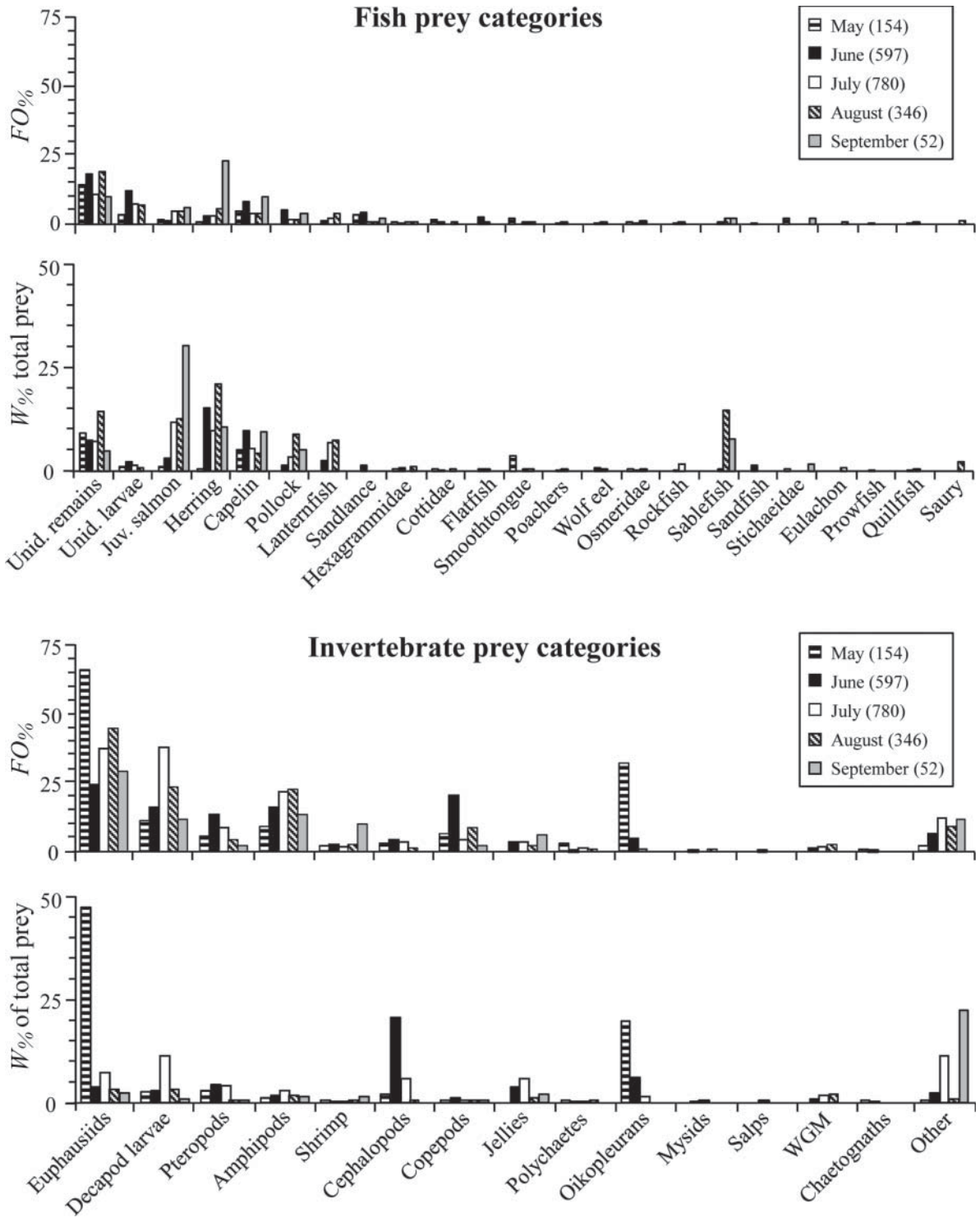


FIGURE 3. Seasonal incidence ($FO_{\%}$) and bioenergetic importance ($W_{\%}$) of fish and invertebrate prey in the epipelagic fish community of Southeast Alaska. Prey are ordered as in Table 4, from those shared by the greatest number of species to those shared by the fewest species among the suite of epipelagic predators. Data were pooled across years and all 18 predator species to identify the times at which prey were important to the community. Monthly total sample size for feeding fish is indicated in the key (unid. = unidentified, juv. = juvenile, jellies = jellyfish, WGM = white granular matter).

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TABLE 6. Monthly prey size range for fish prey categories determined from epipelagic fish predator gut contents; the numbers of records are in parentheses. Size information was pooled across all predators captured in surface trawl hauls in the marine waters of Southeast Alaska over the 15-year period 1997–2011. Categories are listed from those shared by the greatest number of species to those shared by the fewest species among the suite of epipelagic predators. Length measurements were not available from any of the prey records for quillfish, prowfish, or adult salmon. Blanks indicate no measurements.

	Total length (mm) of fish prey categories, by month				
Species	May	Jun	Jul	Aug	Sep
Unidentified larvae	10 (1)	15–60 (19)	10–55 (24)	20–50 (8)	
Juvenile salmon	50–55 (2)	75–145 (6)	98–188 (34)	97–190 (15)	174–199 (3)
Pacific herring	80 (1)	20–290 (12)	45–232 (14)	60–260 (13)	
Capelin		67–115 (35)	60–105 (27)	24–105 (6)	90–100 (2)
Walleye pollock		20–35 (24)	20–235 (14)	30–260 (5)	190 (1)
Lanternfishes		100–115 (3)	30–150 (3)	30–105 (7)	
Pacific sand lance	40–130 (4)	25–100 (7)	50–78 (3)	100 (1)	
Greenlings	15 (1)		65–80 (5)		
Sculpins		30 (1)		10 (1)	
Flatfish		15–25 (4)	25–30 (2)		
Northern smoothtongue			45–110 (2)	60–70 (1)	
Poachers		17 (1)	15–20 (2)		
Wolf-eel		110–130 (2)	250 (1)		
Smelts			30–75 (2)		
Rockfish		20 (1)	40–50 (1)		
Sablefish			120 (1)	150–220 (7)	
Pacific sandfish		65–75 (1)			
Stichaeids	30–40 (1)				
Eulachon				60–100 (1)	
Pacific saury				170–250 (3)	

August ranged from 8.3°C to 10.3°C and averaged 9.3°C (Figure 5a). Six years were colder than average, and 9 years were warmer than average. These temperatures were significantly ($P = 0.02$) correlated with the ENSO MEI (Pearson's product-moment correlation coefficient, $r = 0.59$), indicating that multivariate climate change signals can be teleconnected to Icy Strait. The sign of the MEI value (positive or negative) generally corresponded to the warm versus cold SECM years: seven of the nine warm SECM years had a positive MEI value and five of the six cold SECM years had a negative MEI value (Figure 5a; Wolter 2012).

No consistent differences were detected in the diets of the three key predator species between warm versus cold years (Figure 5b). For pink salmon, aggregate diets in these climate periods showed an approximately twofold difference in decapods, euphausiids, and pteropods. However, diets varied interannually and seasonally in each period, and similar prey were utilized in warm and cold years; also prey timing did not appear to shift consistently with temperature (Figure 6). For example, decapod larvae predominated in July across both warm and cold years, pteropods were unusual prey in the strait but occurred in both warm (June 2005) and cold (July 2006) years, and amphipods were prominent in June and August of both warm (2001) and cold (2002) years. Similarly, walleye pollock appeared to utilize approximately twofold more amphipods in the cold-year period and more copepods in the warm-year period (Figure 5b). However, interannual patterns for walleye pollock were again not consistent with a climate effect, even though data spanned fewer years than for pink and Chinook salmon and included substantial night samples between 2001 and 2004. For example, amphipods were eaten from May to August in cold-year 2000 and in warm-year 2001, and seasonal importance occurred earlier in the warm year, yet they appeared only in May of cold-year 2002 (Figure 6). Euphausiid and copepod utilization also varied dramatically between 2001 (warm), 2002 (cold), and 2003 (warm), with no consistent annual pattern between these warm and cold years. For the third key predator species, Chinook salmon, diets were typically predominated by fish in both warm and cold years (Figure 5b) and the invertebrate prey categories were not consistently utilized within warm or cold years (Figure 6).

Overall, diets differed between species and between months but not between years within species (Figure 6). The nonmetric multidimensional scaling analysis supported this strong species and seasonal pattern without a warm–cold year difference in diets (2-d stress = 0.06), and ANOSIM test results corroborated lack of climate effect on diet (global $R = -0.222$, $P > 0.1$). The ANOSIM results indicated significant species differences ($R = 1$, $P = 0.001$) and month differences ($R = 0.778$, $P = 0.003$),

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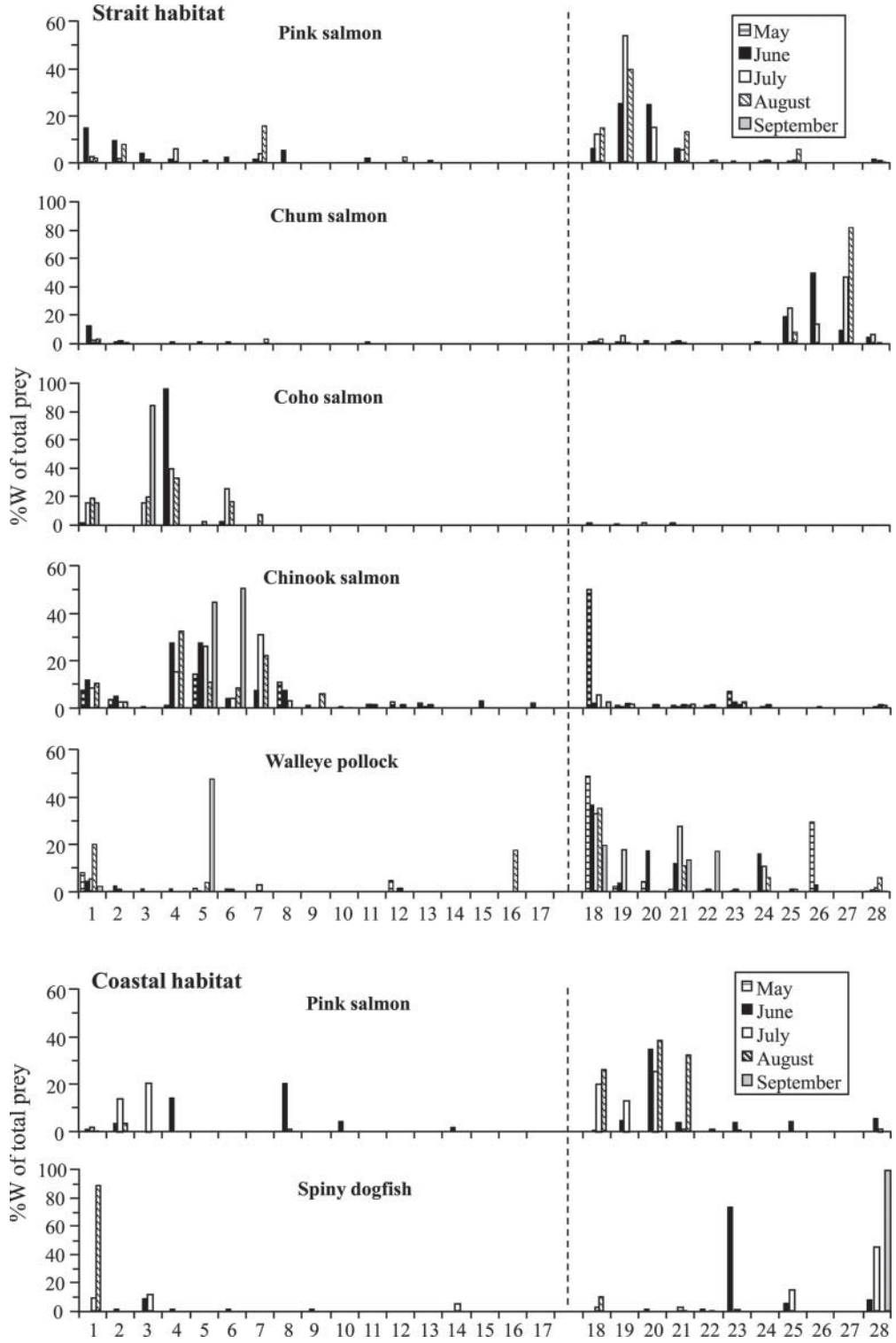


FIGURE 4. Seasonal food habits (percent weight, [$W_{\%}$]) of adult pink, chum, and coho salmon, immature Chinook salmon, and immature walleye pollock in strait habitat and for adult pink salmon and spiny dogfish in coastal habitat of the marine waters of Southeast Alaska. The dashed lines separate fish prey categories (left) from invertebrate prey categories (right). Data from predators collected in surface trawl hauls are pooled across years from 1997 to 2011. Monthly sample sizes are shown in Table 1. Only prey categories constituting $W_{\%}$ of at least 1% for a predator were included. Prey taxa are as follows: 1 = unidentified fish remains, 2 = unidentified fish larvae, 3 = juvenile salmon, 4 = herring, 5 = capelin, 6 = pollock, 7 = lanternfish, 8 = sand lance, 9 = hexagrammids, 10 = cottids, 11 = flatfish, 12 = smoothtongue, 13 = osmerids, 14 = rockfish, 15 = sandfish, 16 = eulachon, 17 = stichaeids; 18 = euphausiids, 19 = decapod larvae, 20 = pteropods, 21 = amphipods, 22 = shrimp, 23 = cephalopods, 24 = copepods, 25 = jellyfish, 26 = oikopleurans, 27 = white granular matter, and 28 = other.

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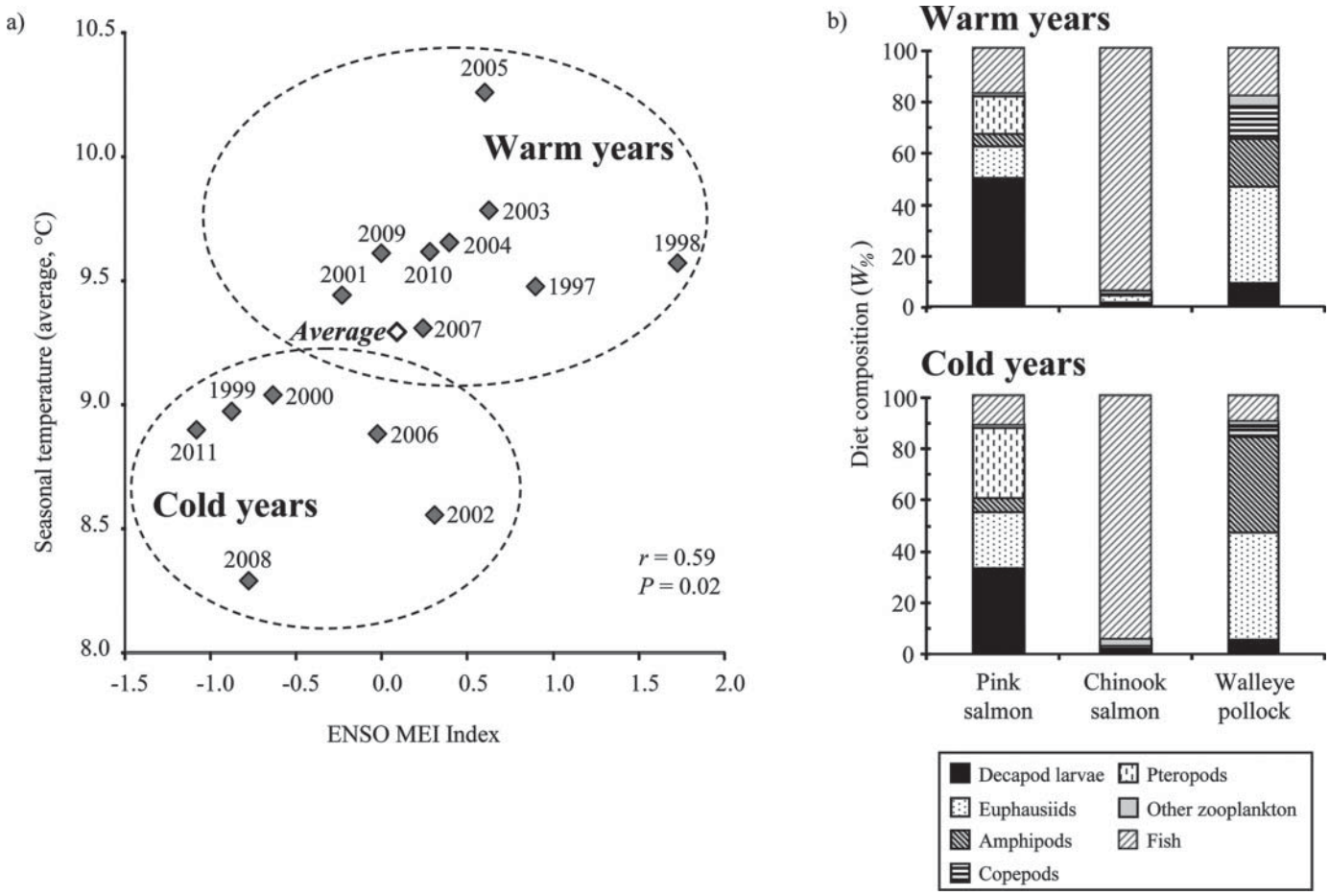


FIGURE 5. Climate and diet relationships in the epipelagic fish community of Southeast Alaska for a 15-year period (1997–2011) as **(a)** the relationship of SECM annual temperature (20-m integrated water column) in Icy Strait with the Multivariate ENSO Index, showing warm versus cold years, and **(b)** diet composition of three key predator species (adult pink salmon, immature Chinook salmon, and immature walleye pollock) in warm versus cold periods (also see Figure 6).

and significant ($P = 0.037$) pairwise tests between all species and months.

DISCUSSION

This paper provides the first description of trophic linkages among the broad epipelagic fish community of Southeast Alaska, information on seasonal and interannual utilization of prey, and an assessment of diet overlap among epipelagic fishes. We provide new data on food habits of spiny dogfish, black rockfish, pomfret, Pacific hake, and other species that will also benefit regional ecosystem models (Coyle et al. 2011). Our finding that diets in warm versus cold years do not clearly reflect climate effects is not completely surprising because interannual diets varied substantially and many different prey categories were used by epipelagic fish predators. Predators shared some prey categories and partitioned others, moderate diet overlap was common but lower than some other reports (Landingham et al. 1998; Kaeriyama et al. 2004; Orlov 2004), and seasonal shifts in timing of prey utilization were apparent in some years. Such flexibility can allow switching of prey resources during climate change, as suggested for high-seas salmon (Kaeriyama et al. 2004). Zooplankton prey are abundant in this region (Orsi et al. 2004); however, our observations suggest that trophic overlap could increase if prey suites are compressed by climate change. We also documented the occurrence of some unusual predators, unusual prey in diets, and unusual diet overlap. Together, these observations suggest that escalating climate change could affect trophic interactions, increase competition by changing predator community composition, and affect carrying capacity of local marine environments for fish production in Southeast Alaska through trophic linkages (Litzow and Ciannelli 2007; Coyle et al. 2011).

Ecosystem diet studies reflect complex community relationships and are important for identifying trophic links, particularly during periods of climate change. Climate change can have broad impacts on key trophic interactions in marine ecosystems by changing relationships of the biophysical environment with seasonal abundance, composition, timing, and utilization of prey (Brodeur et al. 2005; Mackas et al. 2007; Coyle et al.

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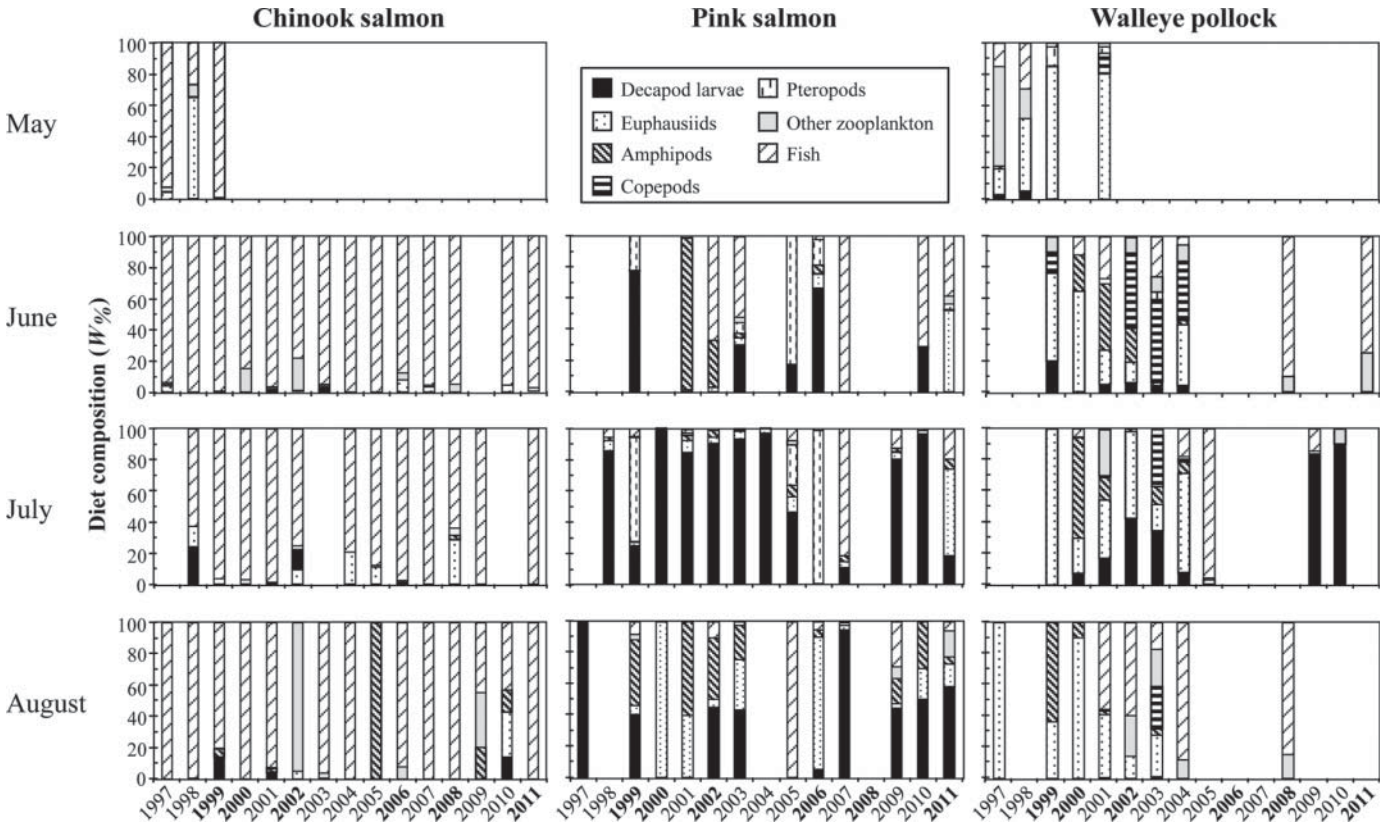


FIGURE 6. Interannual diet composition (percent weight [*W*%]) in June, July, and August for three key epipelagic predator species (adult pink salmon, immature Chinook salmon, and immature walleye pollock) in marine waters of strait habitat in Southeast Alaska, 1997–2011, in both cold (bold) years and warm years.

2011). Community diet studies therefore have the potential to detect changes in the degree of match–mismatch between predators and prey, identify shifts in predator trophic overlap at multiple trophic levels (Sydeman and Bograd 2009), and point to trophic cascades in response to climate change (Casini et al. 2009). This is important because climate change can also induce phenological shifts with fitness consequences (Taylor 2008; Sydeman and Bograd 2009; Walther 2010). However, relatively few studies have examined climate effects on food webs with multiple predators (Beamish et al. 2004; Orlov 2004; Yatsu et al. 2008; Coyle et al. 2011) and even fewer have examined community diets (Brodeur and Pearcy 1994; Miller and Brodeur 2007). Therefore, fish community diet studies, such as ours, that provide baseline understanding of trophic links and their interannual variation are important in order to identify ecosystem effects of climate change. They also provide data for trophic models (Tsou and Collie 2001; Yatsu et al. 2008; O'Gorman and Emmerson 2009; Rose et al. 2008) and can corroborate stable isotope studies (Kaeriyama et al. 2004; Johnson and Schindler 2009).

Effects on North Pacific fisheries production by climate-induced changes in trophic interactions have been identified by studies that monitored diet (Beamish et al. 2004; Kaeriyama et al. 2004; Yatsu et al. 2008; Coyle et al. 2011). For example, diet composition of Bering Sea juvenile salmon and pollock shifted between warm (2003–2006) and cool years (2006–2009), reflecting zooplankton composition and abundance changes, as well as temperature shifts (Coyle et al. 2011). Both the salmon species (pink, chum, and sockeye) and larval and juvenile walleye pollock ate more fish in the warm years and more euphausiids and large copepods during the cool years. Overall, these shifts in energy flow led to poor recruitment in fisheries. Conversely, Beamish et al. (2004) found that the climate regime shift in 1998 led to increased salmon production in the Strait of Georgia ecosystem. Unlike the later period in the Bering Sea (Coyle et al. 2011), juvenile salmon diet composition did not show dramatic interannual shifts between 1997 and 2002; instead, feeding intensity and frequency increased, size increased, and survival was greater after the change in climate (Beamish et al. 2004). Similarly, a regional comparison of juvenile salmon diets from 2000 to 2002 (Brodeur et al. 2007) showed that prey composition and feeding intensity varied more spatially than year to year, which suggests that climate change may not uniformly affect diets of the same species across regions. Likewise, Yatsu et al. (2008) concluded that climate effects on pink salmon, walleye pollock, and other North Pacific fish vary with life history strategy and local environmental conditions, zooplankton phenological shifts, and stochastic episodic

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events in both top–down and bottom–up processes. In dynamic ecosystems such as Southeast Alaska (Weingartner et al. 2009), the effects of climate variation on epipelagic trophic interactions are likely to be complex, varied, and difficult to distinguish from natural variation, particularly if annual temperature changes are moderate. We found no climate effect on predator diets in our region, where average summer temperatures in the 20-m water column varied only 2 degrees between warm and cold years.

Planktivores and Piscivores

We found that fish and invertebrate prey resources were partitioned among members of the epipelagic fish community of Southeast Alaska, but piscivory was not strictly associated with larger size. We used piscivore and planktivore definitions and predator size classifications that closely aligned with those used in trophic models (Stobberup et al. 2009). Large, medium, and small predator groups all included both piscivores and planktivores. For example, among the large predators, pink and chum salmon were planktivorous, in contrast to their conspecifics; among the medium-sized predators, juvenile sablefish were piscivorous, but walleye pollock were planktivorous; and among the small predators, Pacific herring were planktivorous, while Pacific sandfish were piscivorous (Table 3; Figure 2). However, the most piscivorous species frequently ate invertebrate prey also, whereas planktivorous species ate little fish prey. Guts of the piscivorous species were also fuller than those of planktivorous species, suggesting that differences in feeding intensity and dietary nutrition could affect their growth. The diets of many of these species have seldom been described in a community context or from these habitats (Rogers et al. 1980; Beacham 1986; Sturdevant et al. 1999). In particular, trophic links reported between juvenile salmon and many piscivorous fish have largely been anecdotal rather than systematic (Heard 1991; Beamish et al. 1992; Sturdevant et al. 2009, 2012), and our study is one of few that reports on simultaneous use by multiple marine predator species (Nagasawa 1998; Emmett and Krutzikowsky 2008).

Predatory fishes typically select for prey size rather than species, and juvenile salmon are one of several forage species with relatively large size and variable nutritional value that are available to predators (Payne et al. 1999; Emmett and Krutzikowsky 2008; Vollenweider et al. 2011). In Southeast Alaska, juvenile salmon are the most abundant forage species captured in daytime epipelagic trawls (summer), but other forage species predominate the nighttime catch (Orsi et al. 2004, 2007). In our study, these large juvenile salmon were preyed on most frequently by juvenile sablefish that were only two to three times longer than their prey and were selective for salmon species and size (Sturdevant et al. 2009). Juvenile salmon were next most frequently eaten by adult coho salmon ($FO_{\%}$ and $W_{\%}$), which were closer to six times the juvenile salmon in length and presumably more capable of capturing and handling these prey. This observation contrasts with the low rate of predation by adult coho salmon on juvenile salmon reported in commercial troll studies (Reid 1961; Wing 1985) in coastal areas where juvenile salmon may be more dispersed. Our observations are primarily from strait habitat, but we also observed incidents of predation by adult coho and pink salmon on juvenile salmon in coastal habitat. Other studies have shown conspecific interactions between additional salmon life stages, such as juvenile coho salmon predating on pink and chum salmon fry (Heard 1991; Nagasawa 1998).

Adult salmon were key predators in the epipelagic ecosystem of Southeast Alaska, and our results from the inside waters of Southeast Alaska support those from stable isotope analyses of salmon in the ocean, which distinguished the trophic feeding levels of piscivorous Chinook and coho salmon from those of planktivorous pink, chum, and sockeye salmon (Kaeriyama et al. 2004; Johnson and Schindler 2009). This partitioning of prey resources by salmon species is already evident in the juvenile stages during early marine life history (Brodeur et al. 2007). Food habits of adult and immature salmon in our study were similar to those reported from the Strait of Juan de Fuca (Beacham 1986). However, the degree of piscivory in coho and Chinook salmon was stronger in Southeast Alaska than in Washington, with a more diverse suite of fish prey categories, and the $FDG_{\%}$ of fish was higher. We also observed a strong difference between fish prey of adult coho and immature Chinook salmon, similar to early diet reports comparing adult coho and Chinook salmon from commercial troll catches in Southeast Alaska (Reid 1961; Wing 1985). The most frequent prey in Reid's (1961) study were Pacific herring, Pacific sand lance, prowfish, and sablefish, whereas in our study Pacific herring, capelin, lanternfish, and juvenile salmon were consumed most frequently. Wing (1985) identified a wider variety of prey species that included all of the fish species and principal invertebrates (euphausiids, decapod larvae) that we did. Diet differences between the studies could have been due to predator life stage, size (Beacham 1986), or location and season differences, or could be related to climate change during these decades. For example, community composition and distribution of demersal fish (Anderson and Piatt 1999), pelagic nekton (Brodeur et al. 2005), and plankton communities (Mackas et al. 2007) were dramatically reorganized following ocean climate regime shifts and large-scale changes in ecosystem dynamics during this period. Trophic effects of such community shifts were linked to salmon and pollock production (Beamish et al. 2004; Coyle et al. 2011). Unfortunately, however, our data on prey utilization by the epipelagic fish community of Southeast Alaska does not precede either of these regime shifts for direct comparison of changes over time.

Incidence of Juvenile Salmon

The importance of predation on juvenile salmon that we report differs from other studies and highlights additional sources of predation that juvenile salmon may encounter beyond the near-shore stage of greatest vulnerability (Willette et al. 2001). We found juvenile salmon were utilized most by juvenile sablefish and adult coho salmon predators. However, juvenile

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sablefish were episodic predators present in strait habitat only in 1999 (Sturdevant et al. 2009), while coho salmon were common and consistent predators from year-to-year (M. Sturdevant, unpublished data), even though overall salmon prey $FO_{\%}$ and $W_{\%}$ values were lower than for sablefish. The age-0 sablefish we captured in coastal habitat in 1997–1998 were strictly planktivorous. We are also not aware of other studies documenting predation on juvenile salmon by pomfret or Pacific sandfish or cannibalism by adult pink salmon (Heard 1991), but predation by generally planktivorous walleye pollock on pink salmon fry has previously been reported for near-shore habitats (Armstrong and Winslow 1968 in Clausen 1983; Willette et al. 2001). Pacific sandfish in our study were larger and more piscivorous than reported in other Alaskan studies (Paul et al. 1997; Thedinga et al. 2006), and we documented predation from samples captured in inshore habitat (salmon fry, 50–55 mm) and coastal habitat (juvenile salmon, 130 mm), but not in strait habitat. Conversely, we observed no predation on juvenile salmon by Pacific hake (small sample; piscivorous) and jack mackerel (empty gut), unlike observations off the coast of British Columbia and the Pacific Northwest, where these species are common, interact with the forage fish community, and feed at low levels on juvenile salmon (Tanasichuk et al. 1991; Emmett and Krutzikowsky 2008). For spiny dogfish, heavy predation on juvenile salmon has been reported near inshore hatchery release sites (Beamish et al. 1992), whereas our observations occurred remotely in both strait and coastal habitat. Juvenile salmon were the most frequently occurring identifiable fish prey for spiny dogfish ($FO_{\%} = 5\%$, $W_{\%} = 16\%$) in our study, but only 51% of dogfish had been feeding. We also confirmed spiny dogfish predation on maturing salmon (Beamish et al. 1992), but not on Pacific hake (Tanasichuk et al. 1991). In contrast to predation by juvenile sablefish, adult salmon, or Pacific sandfish in inshore and strait habitats, the summer predation by spiny dogfish and adult salmon on juvenile salmon in coastal habitat potentially may impact salmon stocks migrating up the Pacific coast (Orsi et al. 2007). Similarly, the seasonal incidence of prey is probably influenced by migratory timing of predator species (Beamish et al. 1992; Orsi et al. 2007; Csepp et al. 2011).

Other Trophic Linkages

Our study documents additional unexpected trophic links in the epipelagic fish community. One such unexpected trophic link was for Pacific cod feeding on zooplankton since these large-mouthed predators typically eat fish and macroinvertebrates (Clausen 1981). Another is the high diet overlap between planktivorous adult pink salmon and walleye pollock, despite variable diet overlap reported for planktivorous juveniles of these species (Willette et al. 1997; Purcell and Sturdevant 2001). Other examples of unexpected trophic links include unusually large predator–prey size ratios (Scharf et al. 2000), such as a 190-mm Pacific sandfish with a 130-mm pink salmon in its gut (Icy Point, August 2011), a 357-mm sablefish with a 250-mm wolf-eel in its gut (Cape Edward, July 1999), a 316-mm Chinook salmon with an unmeasured quillfish in its gut (Icy Strait, July 1999), and a 378-mm Chinook salmon with ten 100-mm wolf-eels in its gut (Upper Chatham Strait, June 1999). Such predation events may depend on prey volume rather than body length (Weitkamp and Sturdevant 2008; Sturdevant et al. 2009). While we have no way to confirm absence of feeding in the net, we are confident that most observations were not due to feeding in the net because (1) juvenile salmon were present in sablefish guts from trawls that did not also capture these prey, (2) we observed a high frequency of nonfeeding predators in the same hauls, (3) no wolf-eels were present in any hauls in strait habitat when the Chinook salmon (above) had consumed 10 individuals, and captures of >1–2 wolf-eels are rare in the entire time series (authors' unpublished data), and (4) commonly, advanced prey digestion indicated that feeding occurred considerably before predator capture.

We also noted the absence of certain fish prey species from predator diets, such as Pacific spiny lumpsucker *Eumicrotremus orbis*, smooth lumpsucker *Aptocyclus ventricosus*, and crested sculpin *Blepsias bilobus*, that are commonly captured in the trawls (Orsi et al. 2007). Larger sizes of fish prey species such as wolf-eel or prowfish that occurred with low %FO in the piscivore diets were captured in low numbers in the same trawls (Orsi et al. 2007). Piscivorous predators of lanternfish, northern smoothtongue, Pacific herring, and walleye pollock may have consumed them during the night when these fish prey migrated to the surface. Alternatively, predators could have consumed life stages that have not developed strong vertical migration, or they may have fed in deeper waters than the trawl fished during the day (Orsi et al. 2004, 2007; Emmett and Krutzikowsky 2008). Chinook salmon, for example, often contained quite digested specimens of these taxa that were probably eaten the night before we sampled. Lack of predation by Dolly Varden was also unexpected since this species is known for predation impact on juvenile salmon in near shore habitats (Heard 1991).

The appearance of unusual species in our trawl samples may reflect gear selectivity as well as climate change effects on distribution that are related to the movement of water masses (Orsi et al. 2006, 2007, 2009; Weingartner et al. 2009). Samples were limited for common but typically demersal species, such as Pacific cod and rockfish (Csepp et al. 2011), for large-size vertical migrators such as adult walleye pollock (Orsi et al. 2004; 2007), and for species like pomfret and mackerel (coastal habitat) or hake (strait habitat) that were probably transported with shifting water masses during ENSO events (Orsi et al. 2006; Csepp et al. 2011). The diet overlap between pomfret and spiny dogfish, planktivory of Pacific cod, and appearance of piscivorous sablefish in habitat advantageous to unusual predation on juvenile salmon (Sturdevant et al. 2009) provide additional evidence that climate change affected predator community composition or distribution and expanded trophic interactions. Conversely, absence of diet overlap between commonly co-occurring species, such as walleye pollock and Pacific herring (Willette et al. 1997), probably simply reflects limited samples.

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Predators can serve as autonomous prey samplers that indicate when prey taxa are abundant and available to predation (Wing 1985; Roseneau and Bird 1997; Link 2004), particularly when direct data on prey abundance is not available. The Nordic trawl passes most larval and age-0 fish, and daytime fishing does not representatively sample the vertically migrating species in deeper water, such as lanternfish and walleye pollock (Orsi et al. 2004). Gaining understanding of seasonal prey resources and their sizes from piscivores may be particularly useful for ichthyoplankton prey, which are difficult to sample representatively with a single gear type (Brodeur et al. 2011) and because the timing of larval fish taxa varies (Haldorson et al. 1993). Fish larvae occurred in predator guts in all months except September, even though local abundance of larval fish species common in the diets (including Pacific sand lance, walleye pollock, Pleuronectidae, Agonidae, and others) peaks in spring prior to the majority of our trawling effort; osmerid larvae peak later, in June (Haldorson et al. 1993). The planktivory we observed in May for typically piscivorous Chinook salmon (see also Weitkamp and Sturdevant 2008) suggests that fish larvae were not yet abundant (Haldorson et al. 1993) or that euphausiids were exceptionally abundant prey.

The monthly size range for fish prey categories consumed by predators generally suggests that vulnerability and mortality are highest for age-0 and age-1 prey fish in these waters (Tsou and Collie 2001) and that prey quality differs between months based on life stage, an important factor in determining the energy content and nutritional value of prey (Anthony et al. 2000; Vollenweider et al. 2011). Prey size data are not sufficient to determine if the increase in seasonal importance ($W_{\%}$) for some of the prey fish was due to growth instead of higher prey incidence ($FO_{\%}$). Prey species can also outgrow vulnerability to some predators or change habitat, which would decrease incidence in the diets even when they are still present in local waters.

Prey Seasonality for the Epipelagic Community

Together, data on fish $FO_{\%}$ and seasonal importance $W_{\%}$ to epipelagic predators provide a more complete picture of community trophic links and prey nutritional importance than either single measure. The community seasonal analysis showed that the most important invertebrate prey were euphausiids, decapod larvae, amphipods, and pteropods. Seasonal patterns of utilization these taxa in the diets generally mimicked their availability in plankton (Sturdevant et al. 2004, 2011), but our study excludes abundant planktivorous forage species, such as juvenile salmon and other forage species. Forage species consume more plankton (Landingham et al. 1998; Sturdevant et al. 1999) than most of the large predators we examined, including the predominant taxa (copepods; Park et al. 2004). Therefore, our study does not represent community utilization of small prey taxa in proportion to their abundance, the full spectrum of their predators, or the species that probably overlap most with planktivorous walleye pollock. Nonetheless, the bioenergetic importance of frequently consumed invertebrate prey, such as euphausiids and decapod larvae, occasionally rivaled that of fish prey (Weitkamp and Sturdevant 2008) for the large predators. Fish larvae were utilized as frequently as juvenile salmon, Pacific herring, capelin, and walleye pollock, but the latter categories contributed greater $W_{\%}$ despite similar $FO_{\%}$ because of their larger size. Thus, these large categories may be more important in overall bioenergetics of the epipelagic community (Stobberup et al. 2009). However, the importance of smaller-sized fish and invertebrate prey in diets may be underestimated because they are likely to be digested and evacuated more quickly than large fish prey (Elliott 1991; Temming et al. 2002). Our results for uncommon species should also be considered preliminary because of limited sample size and identification limitations of digested fish prey.

Climate Relationship to Interannual Predator Diets

A relationship between climate indices and local temperatures in Icy Strait had not been established prior to this study, even though our data have been used to relate local environmental conditions to adult salmon harvest (Wertheimer et al. 2011; Orsi et al. 2012). Interannual climate signals were detected in Icy Strait temperatures, despite the changing tidal connection to Pacific Coast waters; the complexity of Southeast Alaska waterways; and monthly extremes in rainfall, glacial melt, and stream flow that can influence marine surface temperatures in different directions (Weingartner et al. 2009). The annual SECM temperatures varied by 2°C on average. By comparison, the MEI climate index incorporates six environmental variables (including sea surface temperature) to represent comprehensive environmental change and to track ocean–atmosphere climate variation. Positive and negative values of the MEI generally represent the warm (El Niño) and cold (La Niña) ENSO phases, respectively (Wolter 2012). However, the lack of SECM temperature correspondence in years when the MEI was near neutral could be related to variation in monthly temperature patterns between years (Orsi et al. 2011), as well as the cumulative intensity of the MEI for a given year. For example, in the warmest or coldest years, all 4 months were anomalously warm or cold; the net sum of these monthly anomalies was as great as ± 4°C for 2005 (warm) or 2008 (cold). In contrast, only 3 months followed the pattern for the warm years of 2001, 2004, and 2010; the months of May, June, and July, respectively, were actually colder than average in these overall warm years.

Diets differed minimally between warm and cold years, and our interannual diet data did not consistently reflect climate change signals. Nonetheless, the diets suggest some seasonal shifts in timing of prey utilization between years. This is to be expected because local zooplankton prey fields do vary interannually with strong seasonal patterns and differential effects of temperature on the taxa (Park et al. 2004; Orsi et al. 2011; Sturdevant et al. 2011). We speculate that the absence of a clear climate–diet signal is related to prey life history and reproduction pulses, which could depend on annual magnitude and monthly timing of temperature events in warm or cold years. For example, the predominant amphipods consumed (*Themisto*

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pacifica and *T. libellula*) reproduce year-round, as affected by temperature-related generation times, brood sizes, and overlapping occurrence (Yamada et al. 2004). Thus, presence of multiple species prey categories such as amphipods in fish diets could equalize across temperature events between warm and cold years, rather than simply showing presence or absence. Future analyses should address climate-related zooplankton patterns for the SECM time series, and future sampling would benefit from an assessment of forage fish and larval fish prey. Targeted sampling of predators at more times of the day would also help to address the limitations of our data to quantify prey utilization and fully identify trophic links. Future research could also apply a modeling approach to examine for finer-scale differences in diet response to climate change, which is outside the scope of this study.

In summary, we provided evidence of the complexity within the trophic links of the epipelagic fish community in coastal waters of Southeast Alaska, as demonstrated by prey partitioning, seasonal and habitat changes in diet, and shifting predation linkages between life history stages of some species. We presented an interannual time series of the diets of three key predator species during warm and cold climate periods, but did not detect a relationship between diet variation and climate change. In contrast to many diet studies, our diet metrics included both the $W_{\%}$ and $FO_{\%}$ for prey categories. The $W_{\%}$ provided information on the predominant nutritional sources used by epipelagic predators, while the $FO_{\%}$ highlighted trophic links and sources of predation vulnerability. Modeling studies have shown that the relationship between the $FO_{\%}$ and $W_{\%}$ diet indices is highly significant, and prey type (especially for fish) is an important variable that determines the strength of the relationship (Stobberup et al. 2009). However, even when these metrics point to different prey utilization trends, it is important to consider both because of the ecosystem trophic links indicated and because high $FO_{\%}$ of low weight (energy) prey could indicate that they are bioenergetically important at other times and places or could be during climate change. Diet monitoring studies can be used to identify potential prey resources that are unsampled in many surveys and will help identify key marine predators, potential sources of mortality in fish and plankton populations, trophic links in marine food webs, and potential sources of competition if marine prey resources for seabirds, marine mammals, and fish predators become limited in changing marine ecosystems. Continued monitoring of predator diets during climate change, even if sampling is opportunistic rather than targeted toward certain species, will provide useful information that will enable researchers to detect effects on trophic linkages, inform stable isotope studies, and provide data for studies that model other ecological interactions in Southeast Alaska.

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