Review of BASIS Salmon Food Habits Studies

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Davis, N.D., A.V. Volkov, A.Ya. Efimkin, N.A. Kuznetsova, J.L. Armstrong, and O. Sakai. 2009. Review of BASIS salmon food habits studies. N. Pac. Anadr. Fish Comm. Bull. 5: 197–208.

Abstract: The BASIS food habits studies of sockeye, chum, pink, and Chinook salmon conducted in 2002–2006 were summarized. These studies identified important (≥ 10% of prey composition by weight) prey taxa of salmon. Salmon diet composition differed between the western region, where diets contained more zooplankton, and the eastern region, where diets contained more ichthyoplankton and nekton. Salmon feeding conditions, growth, and survival in the eastern region were more favorable in relatively warm years, as compared to cool years. However, warmer conditions may not be favorable for all salmon species, such as chum salmon. These studies significantly increased the available information on salmon food habits during the fall in the western, central, and eastern regions. Salmon diet composition shifted from zooplankton to fish and squid, or to larger sizes of fish prey, with increasing salmon body size, age, or maturity. Continued monitoring of salmon food habits will contribute to understanding how future climate changes will affect salmon populations in the Bering Sea.

Keywords: sockeye, chum, pink, Chinook, food habits, Bering Sea

INTRODUCTION

Shifts in Bering Sea climate-ocean processes and fish assemblages favored by current warming trends (Hunt et al. 2002; Stabeno et al. 2007) prompted the North Pacific Anadromous Fish Commission (NPAFC) to initiate the Bering-Aleutian Salmon International Survey (BASIS) for the period 2002–2006 (NPAFC 2001). The BASIS plan called for trawling surveys across the Bering Sea to be conducted throughout the year to investigate ocean conditions, conduct plankton tows, and sample salmon biological characteristics, including salmon food habits.

Prior to BASIS, the broadest seasonal coverage of salmon food habits sampling was in the western Bering Sea. In the decades before 2000, salmon food habits studies were reported by numerous investigators sampling in the western Bering Sea (e.g., Ito 1964; Andrievskaya 1966; Machidori 1968; Karpenko 1982; Karpenko and Maksimenkov 1988; Chuchukalo et al. 1995; Klovach et al. 1996; Koval and Karpenko 1998; Bugaev and Shaporev 2002; Karpenko et al. 2007). In the central Bering Sea, summer data collections were more frequently reported than fall collections (e.g., Kanno and Hamai 1972; Azuma 1992; Tadokoro et al. 1996; Davis et al. 1998; Davis et al. 2000). Results of food habits studies had not been reported in the eastern Bering Sea since the 1970s (e.g., Nishiyama 1974; Straty 1974; Carlson 1976), and in the Aleutians since the 1990s (Carlson et al. 1998).

Spatial variation among salmon species and life-history groups in the Bering Sea is produced by migrations of juvenile salmon from fresh water to nearshore and coastal areas in the late summer-fall, movement of immature and maturing fish to over-wintering areas, and subsequent springsummer return of immature fish to deep-water feeding areas and maturing fish to near-shore areas for their return to freshwater spawning areas (e.g., Farley et al. in press; Myers et al. in press). Salmon prey organisms also have differing distributions with respect to regions (western, central, eastern Bering Sea) and to temporal-depth distribution (Volkov et al. 2007a; Volkov and Kosenok 2007). Salmon feeding characteristically exhibits both plasticity and selectivity in behavior (Shuntov et al. 2007) that reflect both the flexibility in consuming prey that is available (Naydenko et al. 2007) and selecting prey from preferred items depending on salmon size and life-history stage (Zavolokin et al. 2007).

Our objective was to summarize Russian, Japanese, and U.S. BASIS food habits results from studies of sockeye (*Oncorhynchus nerka*), chum (*O. keta*), pink (*O. gorbuscha*), and Chinook salmon (*O. tshawytscha*) during 2002–2006. This review outlines methods used for routine collection of

food habits data and describes important prey taxa of salmon in the Bering Sea. In addition, we included studies comparing salmon diets across geographical regions, water column depths, between relatively warm and cold time periods, and among seasons. We have also included information on changes in salmon diets associated with salmon body size and maturity stage.

METHODS USED IN BASIS FOOD HABITS STUDIES 2002–2006

During 2002–2006, BASIS trawling cruises surveyed large regions of the western, central, and eastern Bering Sea (Fig. 1). In multiple year surveys, the western Bering Sea was surveyed by the R/V *TINRO*, the central basin was surveyed by the R/V *Kaiyo maru*, and the eastern Bering Sea shelf was surveyed by the F/V *Sea Storm*. In addition, in 2002 the F/V *Northwest Explorer* surveyed westward along the Aleutian chain, in the deep areas of the central basin, and along the eastern Bering Sea shelf. In 2002–2006 the R/V *Wakatake maru* conducted gillnet and longline surveys and monitored salmon food habits in the central region.

Food habits data gathered during the BASIS period used several different approaches. The express method, developed by TINRO Centre, allowed for quick examination of stomach contents while on board the research vessel (Chuchukalo and Volkov 1986; Volkov et al. 1995; Temnykh et al. 2003). At each trawl operation, a maximum of 25 fish per species was grouped into 10-cm fork length (FL) size groups (< 10 cm FL, 10–20 cm FL, 20–30 cm FL, etc.). After associated biological information (i.e., length, weight, maturity, etc.) was collected, stomachs were removed and examined in a fresh condition, without fixation. Contents of the stomachs within each salmon size grouping were combined. In the process of combining stomach contents, the number of empty stomachs and the degree of stomach fullness (based on five categories) of each individual stomach sample was recorded. An average degree of prey digestion characterizing the combined contents of all the stomachs in the size group was noted using a five-step scale based on visual condition of the prey. The total weight of the combined stomach contents was determined, prey species composition was identified to the lowest possible taxonomic level, and the percent composition was measured by weight. Standardization across research vessels was accomplished by placing TINRO specialists on survey vessels operating in each region of the Bering Sea.

Japanese food habits specialists on board the R/V *Kaiyo maru* used a different method of data collection (Yamamura et al. 2002). After fish measurement, individual salmon stomachs were removed and preserved in a 10% formalin-seawater solution for examination after the cruise. In the laboratory, stomach contents were sorted to the lowest taxon possible and prey items were weighed. Samples of prey items were dried at 52°C in a drying oven for 24 hours and in desiccators for 1.5–2 days, after which prey items were weighed again to

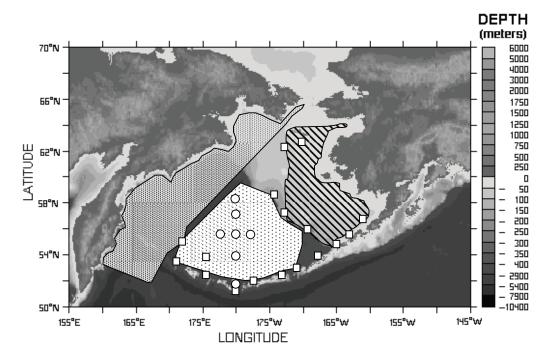


Fig. 1. The regions of the Bering Sea where BASIS cruises collected samples for salmon food habit studies. Map source: http://www.beringclimate.noaa.gov. Dense stippling indicates the western region surveyed by the R/V *TINRO*. Sparse stippling indicates the central region surveyed by the R/V *Kaiyo maru* and the diagonal pattern shows the eastern region surveyed by the F/V *Sea Storm*. Squares indicate approximate survey locations of the F/V *Northwest Explorer* in the Aleutian, central, and eastern regions, and circles indicate approximate survey locations of the R/V *Wakatake maru* in the central region.

the nearest mg. Prey composition was expressed as percentage of dry weight.

Researchers on the F/V *Northwest Explorer* and R/V *Wakatake maru* took yet another approach. They examined a maximum of 10 fish per species per fishing operation (trawl, longline, or gillnet), which were obtained from a range of fish sizes (Ueno et al. 1998). After collecting salmon biological data, fresh fish stomachs were removed and examined individually on board. Total prey weight was calculated as the difference between full stomach weight and weight of the stomach after removal of the contents. Degree of stomach fullness and digestion were recorded and the contents separated into the lowest taxon possible. The percent volume in each prey category was estimated by eye.

Salmon life-history stage was determined for juvenile, immature, and maturing salmon. Juvenile fish have not yet completed one winter at sea because they are caught in the same year that they entered the marine environment. Immature fish have spent at least one winter at sea and will remain at sea for one or more winters before returning to fresh water to spawn. Maturing fish will return to spawn in the current year. Salmon life-history stages were identified on BASIS cruises based one or several of the following characteristics: survey month, fish age, length and weight, and gonad weight or condition (Ishida and Miyaguchi 1958; Ishida et al. 1961; Takagi 1961; Ito et al. 1974).

RESULTS FROM BASIS SALMON FOOD HABITS STUDIES

During the 2002–2006 Bering Sea cruises of the R/V *TINRO*, R/V *Kaiyo maru*, F/V *Sea Storm*, F/V *Northwest Explorer*, and R/V *Wakatake maru* 6,358 sockeye, 13,562 chum, 5,219 pink, and 2,120 Chinook salmon were sampled for their stomach contents (Table 1). Most stomach samples (45.6%) obtained from these studies came from the western region, while 28.8% were from the central region, 25.1% from the eastern region, and 0.6% from the Aleutian Islands region. Differences in the number of samples obtained from various regions occurred for a number of reasons, including the number of survey stations in each region, the number of researchers available for processing food habits samples, and whether stomach contents were combined or fish diet data were based on the examination of individual fish.

Major Prey Items of Salmon in the Bering Sea

Particular taxa of zooplankton, squid, and fish species were shown to be important prey ($\geq 10\%$ of the prey composition by weight) of sockeye, chum, pink, and Chinook salmon in the Bering Sea (Figs. 2, 3). Zooplankton prey, including euphausiids (*Thysanoessa longipes* and *Thy. raschii*) and crab megalopa and zoea, were identified as important prey for all these salmon species (Fig. 2). The hyperiid amphipod, *Themisto pacifica*, was an important component in the diet of sockeye, chum, and pink salmon from the smallest sizes (10 cm FL) to fish up to 60 cm in length. The shelled pteropod, *Limacina helicina*, was also an important component of the diet for a wide size range of sockeye, chum, and pink salmon. Prey items such as medusae and comb jellies, the hyperiid amphipod, *Primno abyssalis*, the unshelled pteropod, *Clione limacina*, and chaetognaths (*Sagitta* spp.) were important in chum salmon diets, exclusively. The euphausiid, *Thy. longipes*, was an important component of stomach contents observed from a wide range of Chinook salmon body sizes (20–70 cm FL).

Squid, Atka mackerel (*Pleurogrammus monopterygius*), lampfishes (*Stenobrachius* spp.), Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), and walleye pollock (*Theragra chalcogramma*) were important nekton ($\geq 10\%$ of the prey composition by weight) in sockeye, chum, pink, and Chinook salmon diets (Fig. 3). Other species of fish identified as significant components ($\geq 10\%$ of the prey composition by weight) of Chinook salmon diets included herring (*Clupea pallasii*), whitespotted greenling (*Hexagrammos stelleri*), prowfish (*Zaprora silenus*), sablefish (*Anoplopoma fimbria*), and rockfishes (*Sebastes* spp).

Salmon Food Habits among Regions

Bering Sea salmon food habits data showed differences between salmon diets collected in the western and eastern Bering Sea (Volkov et al. 2007b; Farley et al. in press). Diets of salmon collected in the western region contained more zooplankton, and those collected from the eastern region contained more ichthyoplankton and nekton.

In the western region, hyperiid amphipods, pteropods, and small squids were the basic prey of planktivorous salmonids, such as sockeye, pink, and chum salmon (Volkov et al. 2007b). Juvenile pink salmon most commonly consumed planktonic crustaceans including hyperiid amphipods (The. pacifica, The. libellula, and P. macropa), euphausiids (Thy. longipes), copepods (Neocalanus plumchrus), and pteropods (L. helicina; Naydenko et al. 2007). Juvenile Chinook salmon in this area consumed zooplankton (Naydenko et al. 2005). Salmon diets contained relatively few euphausiids because of their low abundance in surface waters during the day when salmon were actively feeding (Volkov and Kosenok 2007). Copepods and chaetognaths, while abundant in zooplankton collections, were not important in salmon diets suggesting the habitat provided a high abundance of more preferable food for salmon (Volkov et al. 2007b). Salmon selected prey that were heavily pigmented (e.g., Themisto spp. and L. helicina), large bodied (e.g., young squid, pollock, and Atka mackerel), or possessed luminous photophores (e.g., myctophids and euphausiids; A. Zavolokin, zavolokin@tinro.ru, pers. comm.).

Eastern Bering Sea zooplankton collections were dominated by small-sized copepods, chaetognaths, and ichthyoplankton, primarily larval and juvenile pollock, and crab

able 1. Salmon food habits data collected during BASIS cruises in the western, central, eastern, and Aleutian Islands (< 20 nm from shore) regions of the Bering Sea. Groups (N): number	of groups of stomachs examined by the express method (see text). Stomachs (N): the number of individual stomachs that were combined into groups, or examined individually indicates	no samples examined. *indicates group number not applicable because stomach samples were examined individually.
Table 1. Salmon food habits d	of groups of stomachs examine	no samples examined. *indica

				Sot	Sockeye	U	Chum	ш	Pink	ch	Chinook	Contact
Region	Vessel	Year	Season	Groups	Stomachs	Groups	Stomachs	Groups	Stomachs	Groups	Stomachs	Person
				(N)	(N)	(N)	(N)	(N)	(N)	(N)	(N)	
Western	TINRO	2002	Summer-Fall	66	571	124	834	23	240	24	61	Volkov
		2003	Summer-Fall	151	807	178	1,102	43	514	56	186	Volkov
		2004	Fall	179	986	187	1,208	65	673	82	267	Volkov
		2005	Summer	143	433	225	888	146	873	65	153	Volkov
		2006	Summer-Fall	95	145	151	1,580	48	748	48	154	Volkov
Central	Kaiyo maru	2002	Summer		I	*	395		1		1	Sakai
		2002	Fall		I	*	575		I		I	Sakai
		2002	Fall	*	47	*	238	*	۲-	*	63	Davis
		2003	Summer		I	*	255		I		I	Sakai
		2003	Fall		I	*	189		I		I	Sakai
		2003	Fall	23	463	45	803		I		I	Volkov
		2004	Summer	ę	37	38	544		I	5	30	Volkov
		2006	Spring	27	357	59	849	22	375	4	57	Volkov
	NW Explorer	2002	Fall	*	46	*	166		I	*	34	Davis
	Wakatake maru	2002	Summer	*	139	*	242	*	40	*	89	Davis
		2003	Summer	*	155	*	183	*	168	*	77	Davis
		2004	Summer	*	143	*	180	*	142	*	114	Davis
		2005	Summer	*	112	*	152	*	124	*	27	Davis
		2006	Summer	*	72	*	91	*	35	*	32	Davis
Eastern	NW Explorer	2002	Fall	*	5	*	71		1	*	23	Davis
	Sea Storm	2003	Fall	54	394	50	247	18	175	9	17	Volkov
		2004	Fall	100	677	161	879	96	517	102	329	Volkov
		2005	Fall	103	600	157	581	89	437	84	272	Volkov
		2006	Fall	41	127	309	1,228	26	144	60	119	Valkov
Aleutians	NW Explorer	2002	Fall	*	39	*	65		I	*	16	Davis
	Wakatake maru	2002	Summer	*	2	*	7		I		I	Davis
		2003	Summer		Ι	*	4	*	10		I	Davis
		2004	Summer		I	*	-	*	2		I	Davis
		2005	Summer	*	-		I	*	-		I	Davis
		2006	Summer		I	*	ŝ		I		I	Davie

larvae. These same ichthyoplankton and crab larvae also dominated the contents of salmon stomachs (Naydenko et al. 2007; Volkov et al. 2007b; Farley et al. in press). The small-size fraction (< 1.3 mm) of zooplankton was most abundant in the eastern region, and the large-size fraction (> 3.3 mm) dominated throughout the year in other regions (Volkov et al. 2005). The biomass of the zooplankton forage base, comprising organisms consumed by sockeye, chum, and pink salmon, was determined primarily from the abundance of organisms in the large-size fraction of zooplankton (Volkov et al. 2005). In 2002–2006 differences in zooplankton size composition, taxonomic and trophic structure, and zooplankton production available for fish consumption led researchers to conclude that the eastern Bering Sea was approximately 30% less productive than the western Bering Sea (Volkov et al. 2007a). In 2006–2008 the large-size fraction of zooplankton increased in the eastern Bering Sea affecting salmon diet composition by increasing the proportion of zooplankton, particularly euphausiids, and decreasing nekton in sockeye, chum, pink, and Chinook salmon diets (Volkov et al. 2007b). Sockeye and chum salmon consumed juvenile rockfishes, age-0 pollock, capelin, sand lance, and sablefish (Davis et al. 2004; Naydenko et al 2005; Volkov et al. 2007b; Farley et al. in press), and Chinook salmon consumed young herring, capelin, pollock, rockfishes, and sablefish (Davis et al. 2004).

In the central region the large-size fraction of zooplankton, which included hyperiid amphipods, pteropods, eu-

Zooplankton	10	20	30	40	50	60	70
Medusae and comb jellies							
Epilabidocera amphitrites							
Neocalanus cristatus							
Thysanoessa longipes							
Thysanoessa raschii		//////////////////////////////////////	//////////////////////////////////////			////.	
Thysanoessa inermis	1111	////////	///////////////////////////////////////		,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	////	
Thysanoessa inspinata			/////	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	////	
Thysanoessa spinifera						///.	
Tessarobrachion oculatum				'////	////		
Gammaridae		1111	////				
Themisto pacifica							
Themisto libellula		/////	////				
Primno abyssalis							
Megalopa and Zoea					,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	///.	
Limacina helicina			///////////////////////////////////////				
Clione limacina							
Sagitta							
Appendicularia		/////	///,				

Fork length of salmon predator

Fig. 2. List of the major zooplankton prey items consumed by salmon in the Bering Sea by fork length (cm) of the salmon predator. A prey item is considered major if it comprises at least 10% of the diet by weight for a region and size group. Diagonal pattern = sockeye salmon, gray = pink salmon, vertical pattern = chum salmon, black = Chinook salmon.

Squid and Fish	10	20	30	40	50	60	70	>70
Cephalopods								
Pleurogrammus monopterigius								
Stenobrachius spp.								
Ammodytes hexapterus								
Mallotus villosus								
Theragra chalcogramma								
Hexagrammus stelleri								
Clupea pallasi								
Zaprora silenus								
Anoplopoma fimbria								
Sebastes spp.								

Fork length of salmon predator

Fig. 3. List of the squid and major fish prey items consumed by salmon in the Bering Sea by fork length (cm) of the salmon predator. A prey item is considered major if it comprises at least 10% of the diet by weight for a region and size group. Diagonal pattern = sockeye salmon, gray = pink salmon, vertical pattern = chum salmon, black = Chinook salmon.

phausiids and coelenterates (*Aglantha digitale*; Volkov et al. 2007a), were the common prey items found in the stomach contents of sockeye, chum, and pink salmon (Davis et al. 2004; Volkov et al. 2007b). Fish consumed by immature sockeye, chum, and Chinook salmon in the central Bering Sea differed from fish observed in stomachs collected in the eastern region. In the central region, salmon consumed *S. leucopsarus* and juvenile fish including Atka mackerel, sculpins, and flatfish (Davis et al. 2004; Naydenko et al. 2005). Squid predominated in the diets of Chinook salmon collected from the central basin and fish were the primary prey of Chinook salmon collected on the eastern shelf (Davis et al. 2004).

If salmon consumption of zooplankton does not significantly affect the salmon's forage base, then recent increases in salmon abundance are unlikely to change the trophic relationships in the Bering Sea (Naydenko 2009). Patterns in food habits characteristics may represent adaptive strategies intended to lessen density-dependent interactions and maximize utilization of available feeding grounds (Sviridov et al. 2004).

Salmon Food Habits Associated with Water Depth

Patterns in salmon prey composition have been associated with different water column depths. Sockeye salmon caught in shallow waters of the western Bering Sea contained more chaetognaths and copepods than sockeye salmon collected from deeper waters, where more amphipods, euphausiids, and squids were observed in stomach contents (Temnykh et al. 2003; Naydenko et al. 2005). In the shallow northern areas of the western Bering Sea *The. libellula* predominate in diets of young chum salmon, while in deeper southern areas and the deep water of the central Bering Sea basin, *The. pacifica* is more common (Temnykh et al. 2003; Davis et al. 2004).

The ratio of euphausiids and fish offal, identified as originating from pollock (Buser et al. 2009), observed in Chinook salmon stomach contents was significantly higher in samples collected at shallow depths (< 200 m), and the ratio of squid was significantly higher in salmon collected at deeper depths (201 to 600 m; Davis et al. 2009). Changes in prey composition of salmon diets among habitats of differing water depths likely reflect changes in the distribution and abundance of salmon prey organisms available in those habitats.

Shifts in Salmon Food Habits Associated with Relatively Warm and Cool Years

The five years of BASIS (2002 – 2006) captured variation in environmental conditions in the Bering Sea including relatively warm and cool years. Oceanographic indices formulated from eastern Bering Sea shelf conditions show that 2002 to 2005 were relatively warm years, and 2006 was a relatively cool year (Fig. 4). These indices show levels of water column stability, nutrient conditioning, and the influence of thermal conditions on distributions of fishes. The switch from warm to cool years during the BASIS study period provided a natural experiment to measure effects on salmon food habits in response to climate and ecosystem change.

Warmer spring sea surface temperatures on the eastern Bering Sea shelf were associated with increased marine growth and survival of juvenile western Alaska sockeye salmon and changes in primary prey composition of juvenile sockeye salmon during relatively warm years (2002– 2003), as compared to cool years (2000–2001; Farley et al. 2007). When cool springtime conditions prevailed in the eastern region, Pacific sand lance was an important component (by weight) of juvenile salmon diets. However, when warm springtime conditions prevailed, age-0 pollock were the primary prey and sockeye salmon had an improved body condition (Farley et al. 2007). Similarly, later comparisons of juvenile salmon collected in the southeast and northeast Bering Sea shelf showed a shift in diets for all species across the shelf in a cool year (2006; Farley et al. in press). Under cool conditions, the importance of sand lance dramatically increased in the diets of juvenile salmon in both areas, while the importance of age-0 pollock (southeast and northeast areas) and euphausiids and other zooplankton (northeast area) was reduced. Authors concluded cold spring sea surface temperatures on the eastern Bering Sea shelf contribute to lower growth and survival for western Alaska juvenile salmon (Farley et al. in press).

Environmental changes are likely to have complex effects on different salmon species from inter-specific interac-

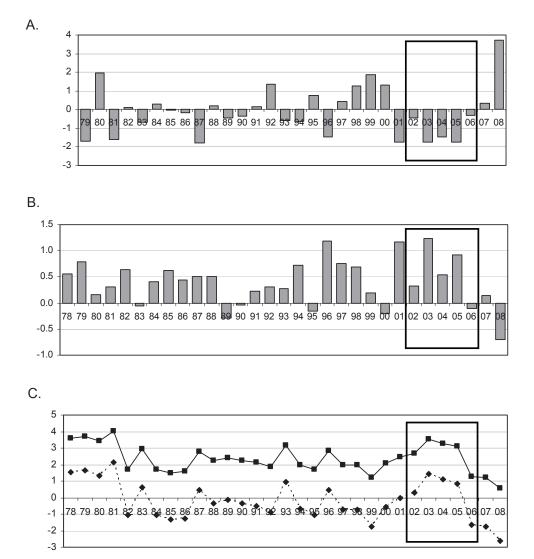


Fig. 4. Several eastern Bering Sea shelf climate indices show that 2002–2005 were characterized as relatively warm years, and 2006 was a cool year. Rectangular boxes highlight the BASIS years 2002–2006. Data source for indices: http://www.beringclimate.noaa.gov. A. Ice cover index shows the average ice concentration anomalies from January 1 to May 31 at locations between 56° to 58°N, 163° to 165°W, normalized relative to values from 1981 to 2000. B. Winter (January to March) sea surface temperature anomalies in the 5° by 5° grid centered at 55°N, 170°W, normalized relative to values from 1950 to 2000. C. May sea surface temperatures (solid line) and anomalies (dotted line) in the area 54° to 60°N, 161° to 172°W. Anomalized relative to values from 1961 to 2000.

tions, prey availability, and bioenergetics (Beauchamp et al. 2007). For example, abundance of several species of large medusae, which consume some of the same prey as chum salmon, was higher in relatively warm years (2004, 2005) than in relatively cool years (2006, 2007) suggesting possible increased food competition between jellyfish and chum salmon in warming climate conditions (Cieciel et al. 2009). Using average total lipid content as a measure of chum body condition, researchers showed a significant negative correlation between sea surface temperature and lipid content of chum salmon muscle (T. Kaga, tkaga@fra.affrc.go.jp, pers. comm.). Increased water column stability and observed shifts to increased abundance and biomass of smaller-sized zooplankton taxa in relatively warm years might affect the feeding conditions of higher trophic levels in the eastern Bering Sea (Coyle et al. 2008).

Salmon Food Habits among Seasons

The 2002–2006 BASIS cruises significantly increased data collection of salmon food habits data during the fall season in all regions (Fig. 5; NPAFC 2003; Temnykh et al.

2003; Farley et al. 2004; NPAFC 2004; Farley et al. 2005; Glebov et al. 2005; NPAFC 2005; Farley et al. 2006; Glebov et al. 2006; Kuznetsova 2006; NPAFC 2006; Naydenko et al. 2007; Temnykh et al. 2007; Volkov et al. 2007b; Farley et al. in press). New food habits data were obtained from the Aleutians area in summer and fall (Murphy et al. 2003; Davis et al. 2004), and temporal coverage in the central Bering Sea was extended to spring (Azumaya et al. 2003, 2005).

In the eastern region in 2007, the percentage of empty stomachs observed was higher in Chinook salmon stomach samples collected in winter (45%) than in summer (8%), suggesting longer time periods between meals in winter (Davis et al. 2009). The diversity of squid species observed in Chinook salmon diets was higher in winter than summer, when more fish (particularly juvenile walleye pollock) were consumed (Davis et al. 2009).

In the central region, sockeye salmon consumed a higher proportion of euphausiids in fall than summer, and squids present in summer stomach samples disappeared in the fall samples (Davis et al. 2004). In 2002–2003, chum salmon shifted from consuming zooplankton, mostly euphausiids in summer, to lampfishes in fall (NPAFC 2005). Chinook

	Decade	Spring	Summer	Fall	Winter		Year	Spring	Summer	Fall	Winter
Western	1950-59					Western	2002				
	1960-69						2003				
	1970-79						2004				
	1980-89						2005				
	1990-99						2006				
	2000-01										
Central	1950-59		<u> </u>			Central	2002				
Central	1960-69					Central	2002				
	1970-79						2003				
	1980-89						2004				
	1990-99						2006				
	2000-01						2000				
Eastern	1950-59					Eastern	2002				
	1960-69						2003				
	1970-79						2004				
	1980-89						2005				
	1990-99						2006				
	2000-01										
Ale	4050 50					Aleutiene	0000 [
Aleutians	1950-59					Aleutians	2002				
	1960-69						2003				
	1970-79		├ ──┤				2004				
	1980-89						2005				
	1990-99		┞───┤				2006				
	2000-01										

Before BASIS

BASIS 2002-2006

Fig. 5. Shaded boxes indicate the time period by decade (before BASIS) and BASIS years (2002–2006) when salmon food habits data were collected by season in the western, central, eastern, and Aleutian Islands regions of the Bering Sea. Spring = March–May, summer = June–August, fall = September–November, winter = December–February.

salmon stomach samples collected during the summer contained euphausiids, squid, and fish, however, in fall stomach samples contained primarily squid (Davis et al. 2004; Myers et al. in press).

Salmon Food Habits Associated with Salmon Biological Characteristics

Patterns in salmon food habits have been associated with variations in body size, age, or maturity of the salmon predator. For example, as chum salmon grow they prey more intensively on lampfish, pollock, Atka mackerel, sand lance, or capelin, depending on the geographic area (Naydenko et al. 2005).

In the western region, small chum salmon (< 20 cm FL) fed mostly on hyperiid amphipods (The. pacifica) and large chum salmon (> 50 cm FL) fed mostly on fish (Atka mackerel; Temnykh et al. 2003). In the western region and more southerly waters off Kamchatka, medusae consumption was a distinctive feature of chum > 51 cm. This might reflect adaptations by maturing chum, which could require more easily digested prey (Dulepova and Dulepov 2003). Sockeye salmon < 50 cm FL preyed on hyperiid amphipods, euphausiids, pteropods, and juvenile squid, while larger fish preyed more intensively on nekton (Naydenko et al. 2005). Chinook salmon juveniles consumed mostly plankton, including large crab larvae and euphausiids, and larger fish consumed few zooplankton (Naydenko et al. 2005). The diurnal feeding activity of immature salmon (< 30 cm FL) had similar feeding rhythms, regardless of whether they were nekton or zooplankton consumers, with most activity occurring between mid-day and dusk (Volkov and Kosenok 2007). Older immature and maturing individuals had less defined diurnal patterns (Volkov and Kosenok 2007).

Juvenile sockeye, chum, and pink salmon in the eastern region preyed on nektonic animals including, larvae and age-0 walleye pollock, sand lance, capelin, and bottom fish larvae. All sizes of chum salmon consumed larval and age-0 pollock, crab larvae, and coelenterates (Naydenko et al. 2005; Volkov et al. 2007a). Prevalence of fish in the diet of juvenile sockeye, chum, and pink salmon was associated with the high concentration of juvenile fish prey, especially age-0 pollock (Kuznetsova 2006). Small Chinook (≤ 40 cm FL) salmon preyed predominately upon fish (sand lance, juvenile pollock, larval fishes) and large individuals (≥ 60 cm FL) preyed almost exclusively on squid (Naydenko et al. 2005).

In the eastern region, pteropods often dominated the diets of ocean age-1 and older sockeye and chum salmon (NPAFC 2004). In Bristol Bay juvenile sockeye up to 10 cm FL fed mostly on copepods. Larger juveniles (10–30 cm FL) consumed mainly juvenile pollock, pteropods, copepods, hyperiid amphipods, euphausiids, and crab megalopa (Kuznetsova 2006), whereas large sockeye salmon (50 to 60 cm FL) consumed mostly euphausiids. The proportion of fish (juvenile pollock and capelin) in the diet of pink salmon increased with pink salmon body size (Kuznetsova 2006). Examining Chinook salmon winter diets, investigators found that the ratio of euphausiids to fish body weight was significantly higher in immature than maturing fish (Davis et al. 2009).

CONCLUSIONS

In 2002-2006 BASIS food habits studies of sockeye, chum, pink, and Chinook salmon identified important prey taxa of salmon including, euphausiids, crab megalopa and zoea, hyperiid amphipods, pteropods, chaetognaths, gonatid squids, Atka mackerel, lampfishes, Pacific sand lance, capelin, walleye pollock, herring, whitespotted greenling, prowfish, sablefish, and rockfish. Monitoring the abundance and distribution of these prey organisms using a standardized method will be useful for evaluating the feeding status of salmon in the Bering Sea. Investigations comparing salmon diets among areas of the Bering Sea showed the largest difference in salmon diets between the western and eastern regions. Diets of salmon collected in the western region contained more zooplankton, while salmon collected in the eastern region contained more ichthyoplankton and nekton. Salmon stomach samples collected from deep waters contained more prey species that were either deep dwelling or vertically migrating themselves. Studies showed salmon feeding differed in relatively warm years, as compared to cooler years, suggesting some salmon species will do better under warming climate conditions than others.

The BASIS food habits studies significantly increased the available information on salmon food habits during the fall in the western, central, and eastern regions. Limited studies suggest salmon food habits vary by season but more studies in the same sampling area in more than one season are required. Salmon prey composition shifts with increasing salmon body size, enabling large salmon to feed on relatively large-size fish such as young pollock, Atka mackerel, and lampfishes. As sea temperatures and environmental variability increase in the future, it is important that we continue to monitor salmon food habits, growth, and body condition if we are to understand how these changes will affect salmon populations in the Bering Sea.

ACKNOWLEDGEMENTS

We thank the following institutions and individuals for their support of BASIS food habits investigations: Pacific Research Institute of Fisheries and Oceanography (TINRO-Centre), Kamchatka Research Institute of Fisheries and Oceanography (KamchatNIRO), Russian Federal Research Institute of Fisheries and Oceanography (VNIRO), Hokkaido National Fisheries Research Institute and National Salmon Resources Center (Fisheries Research Agency), Auke Bay Laboratories (Alaska Fisheries Science Center), Pacific Biological Station (Fisheries and Oceans Canada), School of Aquatic and Fishery Sciences (University of Washington), Faculty of Fisheries Sciences (Hokkaido University), Tomonori Azumaya, Edward Farley, Masa-aki Fukuwaka, Oleg Ivanov, Vladimir Karpenko, Nataliya Klovach, Natalya Kosenok, Maxim Koval, Ellen Martinson, Kentaro Morita, James Murphy, Katherine Myers, Svetlana Naydenko, Shunpei Sato, Vyacheslav Shuntov, Alexander Slabinskiy, Olga Temnykh, Robert Walker, Orio Yamamura, and Alexander Zavolokin. Our manuscript was improved by thoughtful suggestions of two anonymous reviewers. Early support for BASIS studies was provided to US authors by the National Oceanic and Atmospheric Administration (NOAA) contract 50-ABNF-1-00002 and the Yukon River Drainage Fisheries Association. Support for manuscript preparation by N. Davis and J. Armstrong was funded by award #NAO4NMF4380162 from NOAA, U.S. Department of Commerce, administered by the Alaska Department of Fish and Game (ADFG) for the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative (http://www.aykssi.org/). The statements, findings, conclusions, and recommendations are those of the authors and do not necessarily reflect the views of NOAA, the U.S. Dept. of Comm., or ADFG.

REFERENCES

- Andrievskaya, L.D. 1966. Food relationships of the Pacific salmon in the sea. Vopr. Ichthiologii 6: 84–90. (Translated from Russian by Bureau of Comm. Fish., Seattle, 1966).
- Azuma, T. 1992. Diel feeding habits of sockeye and chum salmon in the Bering Sea during the summer. Nippon Suisan Gakkaishi 58: 2019–2025.
- Azumaya, T., S. Urawa, O. Yamamura, M. Fukuwaka, A. Kusaka, T. Nagasawa, T. Nomura, S. Moriya, and A. Urano. 2003. Results of the survey by *Kaiyo maru* in the Bering Sea, 2002. N. Pac. Anadr. Fish Comm. Doc. 717. 12 pp. (Available at www.npafc.org).
- Azumaya, T., T. Nomura, N. Tanimata, O. Sakai, T. Onuma, and S. Sato. 2005. Results of the survey in the Bering Sea in 2004. N. Pac. Anadr. Fish Comm. Doc. 843. 13 pp. (Available at www.npafc.org).
- Beauchamp, D.A., A.D. Cross, J.L. Armstrong, K.W. Myers, J.H. Moss, J.L. Boldt, and L.J. Haldorson. 2007.
 Bioenergetic responses by Pacific salmon to climate and ecosystem variation. N. Pac. Anadr. Fish Comm. Bull. 4: 257–269. (Available at www.npafc.org).
- Bugaev, A.V., and R.A. Shaporev. 2002. Results of marine research on the RMS *Moskam-alfa* in 2001. N. Pac. An-adr. Fish Comm. Doc. 607. 20 pp. (Available at www. npafc.org).
- Buser, T.J., N.D. Davis, I. Jiménez-Hidalgo, and L. Hauser. 2009. Genetic techniques provide evidence of Chinook salmon feeding on walleye pollock offal. N. Pac. Anadr. Fish Comm. Bull. 5: 225–229. (Available at www.npafc. org).
- Carlson, H.R. 1976. Foods of juvenile sockeye salmon, On-

corhynchus nerka, in the inshore coastal waters of Bristol Bay, Alaska, 1966–67. Fish. Bull. 74: 458–462.

- Carlson, H.R., E.V. Farley, K.W. Myers, E.C. Martinson, J.E. Pohl, and N.M. Weemes. 1998. Survey of salmon in the southeastern Bering Sea, Gulf of Alaska, and northeastern Pacific Ocean April–May, 1998. N. Pac. Anadr. Fish Comm. Doc. 344. 33 pp. (Available at www. npafc.org).
- Chuchukalo, V.I., and A.F. Volkov. 1986. Guide book of fish feeding study. TINRO, Vladivostok. 32 pp. (In Russian).
- Chuchukalo, V.I., A.F. Volkov, A.Ya. Efimkin, and N.A. Kuznetsova. 1995. Feeding and daily rations of sockeye salmon (*Oncorhynchus nerka*) during the summer period. N. Pac. Anadr. Fish Comm. Doc. 125. 9 pp. (Available at www.npafc.org).
- Cieciel, K., E.V. Farley, Jr., and L.B. Eisner. 2009. Jellyfish and juvenile salmon associations with oceanographic characteristics during warm and cool years in the eastern Bering Sea. N. Pac. Anadr. Fish Comm. Bull. 5: 209–224. (Available at www.npafc.org).
- Coyle, K.O., A.I. Pinchuk, L.B. Eisner, and J.M. Napp. 2008. Zooplankton species composition, abundance and biomass on the eastern Bering Sea shelf during summer: The potential role of water-column stability and nutrients in structuring the zooplankton community. Deep-Sea Res. II 55: 1775–1791.
- Davis, N.D., K.W. Myers, and Y. Ishida. 1998. Caloric value of high-seas salmon prey organisms and simulated salmon ocean growth and prey consumption. N. Pac. Anadr. Fish Comm. Bull. 1: 146–162. (Available at www.npafc.org).
- Davis, N.D., K.Y. Aydin, and Y. Ishida. 2000. Diel catches and food habits of sockeye, pink, and chum salmon in the central Bering Sea in summer. N. Pac. Anadr. Fish Comm. Bull. 2: 99–109. (Available at www.npafc.org).
- Davis, N.D., J.L. Armstrong, and K.W. Myers. 2004. Bering Sea diet overlap in fall 2002 and potential for interactions among salmon. N. Pac. Anadr. Fish Comm. Doc. 779. 30 pp. (Available at www.npafc.org).
- Davis, N.D., K.W. Myers, and W.J. Fournier. 2009. Winter food habits of Chinook salmon in the eastern Bering Sea. N. Pac. Anadr. Fish Comm. Bull. 5: 243–253. (Available at www.npafc.org).
- Dulepova, E.P., and V.I. Dulepov. 2003. Interannual and interregional analysis of chum feeding features in the Bering Sea and adjacent Pacific waters of eastern Kamchatka. N. Pac. Anadr. Fish Comm. Doc. 728. 8 pp. (Available at www.npafc.org).
- Farley, E.V., Jr., J.M. Murphy, A. Middleton, L. Eisner, J. Moss, J. Pohl, O. Ivanov, N. Kuznetsova, M. Trudel, M. Drew, C. Lagoudakis, and G. Yaska. 2004. Eastern Bering Sea (BASIS) coastal research (August–October 2003) on juvenile salmon. N. Pac. Anadr. Fish Comm. Doc. 816. 29 pp. (Available at www.npafc.org).

- Farley, E.V., Jr., J. Murphy, L. Eisner, A. Middleton, J. Pohl, J. Moss, K. Cieciel, O. Ivanov, N. Kuznetsova, and H. George. 2005. Eastern Bering Sea (BASIS) coastal research (Aug–Oct 2004) on juvenile salmon. N. Pac. Anadr. Fish Comm. Doc. 914. 27 pp. (Available at www. npafc.org).
- Farley, E.V., Jr., J. Murphy, A. Middleton, L. Eisner, J. Pohl,
 O. Ivanov, N. Kusnetsova, K. Cieciel, M. Courtney, and
 H. George. 2006. Eastern Bering Sea (BASIS) coastal
 research (August–October 2005) on juvenile salmon.
 N. Pac. Anadr. Fish Comm. Doc. 992. 26 pp. (Available at www.npafc.org).
- Farley, E.V., Jr., J.M. Murphy, M. Adkison, and L. Eisner. 2007. Juvenile sockeye salmon distribution, size, condition, and diet during years with warm and cool spring sea temperatures along the eastern Bering Sea shelf. J. Fish Biol. 71: 1145–1158.
- Farley, E.V., Jr., J.M. Murphy, J. Moss, A. Feldmann, and L. Eisner. In press. Marine ecology of western Alaska juvenile salmon. *In* Pacific salmon: ecology and management of western Alaska's populations. *Edited by* C.C. Krueger and C.E. Zimmerman. Am. Fish. Soc. Symp. 70, Bethesda, MD.
- Glebov, I.I., O.S. Temnykh, V.V. Sviridov, and A.N. Starovoytov. 2005. Cruise report of the 2004 R/V *TINRO* BASIS survey in the western Bering Sea, September–October. N. Pac. Anadr. Fish Comm. Doc. 901. 47 pp. (Available at www.npafc.org).
- Glebov, I.I., O.S. Temnykh, and V.V. Sviridov. 2006. Cruise report of the R/V *TINRO* BASIS survey in the western Bering Sea, June–July 2005. N. Pac. Anadr. Fish Comm. Doc. 985. 67 pp. (Available at www.npafc.org).
- Hunt, G.L. Jr., P. Stabeno, G. Walters, E. Sinclair, R.D. Brodeur, J.M. Napp, and N.A. Bond. 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep Sea Res. II 49: 5821–5853.
- Ishida, T., and K. Miyaguchi. 1958. On the maturity of Pacific salmon (*Oncorhynchus nerka*, *O. keta*, and *O. gorbuscha*) in offshore waters with reference to the seasonal variation of gonad weight. Bull. Hokkaido Reg. Fish. Res. Lab. 18: 11–22. (In Japanese with English abstract, Fish. Res. Bd. Can. Transl. Ser. No. 190).
- Ishida, R., K. Takagi, and S. Arita. 1961. Criteria for the differentiation of mature and immature forms of chum and sockeye salmon in northern areas. Int. N. Pac. Fish. Comm. Bull. 5: 27–47.
- Ito, J. 1964. Food and feeding habit of Pacific salmon (Genus *Oncorhynchus*) in their oceanic life. Hokkaido Suisan Shikenjo Hokoku (Bulletin of the Hokkaido Regional Fisheries Research Laboratory) 29: 85–97. (In Japanese, Fish. Res. Bd. Can. Transl. Ser. No. 1309).
- Ito, J., K. Takagi, and S. Ito. 1974. The identification of maturing and immature Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) in the offshore stage and some related information. Far Seas Fish. Res. Lab. Bull. 11:

68-75.

- Kanno, Y., and I. Hamai. 1972. Food of salmonid fish in the Bering Sea in summer of 1966. Bull. Fac. Fish., Hokkaido Univ. 22: 107–128. (In Japanese with English abstract).
- Karpenko, V.I. 1982. Biological peculiarities of juvenile coho, sockeye, and Chinook salmon in coastal waters of east Kamchatka. Soviet J. Mar. Biol. 8(6): 317–324.
- Karpenko, V.I., and V.V. Maksimenkov. 1988. Preliminary data on the interactions between Pacific salmon and herring during early ontogeny. J. Ichthyol. 28(5): 136–140.
- Karpenko, V.I., A.F. Volkov, and M.V. Koval. 2007. Diets of Pacific salmon in the Sea of Okhotsk, Bering Sea, and northwest Pacific Ocean. N. Pac. Anadr. Fish Comm. Bull. 4: 105–116. (Available at www.npafc.org).
- Klovach, N.V., L.A. Rzhannikova, and S.B. Gorodovskaya. 1996. Biological characteristics of the chum salmon *Oncorhynchus keta* during the summer period of foraging in the sea. J. Ichthyol. 36(8): 591–599.
- Koval, M.V., and V.I. Karpenko. 1998. Feeding of Pacific salmon during anadromous migrations in the Kamchatkan waters. N. Pac. Anadr. Fish Comm. Doc. 365. 5 pp. (Available at www.npafc.org).
- Kuznetsova, N.A. 2006. Feeding of Pacific salmon in the eastern Bering Sea. N. Pac. Anadr. Fish Comm. Doc. 987. 9 pp. (Available at www.npafc.org).
- Machidori, S. 1968. Vertical distribution of salmon (Genus *Oncorhynchus*) in the Northwestern Pacific III. Bull. Hokkaido Reg. Fish. Res. Lab. 34: 1–11. (In Japanese with English summary).
- Murphy, J., N. Davis, O. Ivanov, M. Rohr, S. Elmajjati, and W. Barber. 2003. Cruise report of the 2002 Northwest Explorer BASIS survey in the Bering Sea, September– October. N. Pac. Anadr. Fish Comm. Doc. 676, Rev. 1. 23 pp. (Available at www.npafc.org).
- Myers, K.W., R.V. Walker, N.D. Davis, J.L. Armstrong, and M. Kaeriyama. In press. High seas distribution, biology, and ecology of Arctic-Yukon-Kuskokwim salmon: direct information from high seas tagging experiments, 1954–2006. *In* Pacific salmon: ecology and management of western Alaska's populations. *Edited by* C.C. Krueger and C.E. Zimmerman. Am. Fish. Soc. Symp. 70, Bethesda, MD.
- Naydenko, S.V. 2009. The role of Pacific salmon in the trophic structure of the upper epipelagic layer of the western Bering Sea during summer-autumn 2002–2006.N. Pac. Anadr. Fish Comm. Bull. 5: 231–241. (Available at www.npafc.org).
- Naydenko, S.V., A.Ya. Efimkin, A.F. Volkov, N.A. Kuznetsova, and N.S. Kosenok. 2005. Food habits and trophic position of Pacific salmon in the Bering Sea epipelagic communities in autumn 2000–2004. N. Pac. Anadr. Fish Comm. Doc. 876. 30 pp. (Available at www. npafc.org).

- Naydenko, S.V., A.Ya. Efimkin, and A.E. Lazhentsev. 2007. Regional diversity of juvenile pink salmon diet in autumn in the Bering, Okhotsk, and Japan seas. N. Pac. Anadr. Fish Comm. Bull. 4: 117–126. (Available at www.npafc.org).
- Nishiyama, T. 1974. Energy requirement of Bristol Bay sockeye salmon in the central Bering Sea and Bristol Bay. *In* Oceanography of the Bering Sea with emphasis on renewable resources. *Edited by* D.W. Hood and E.J. Kelley. Occas. Publ. No. 2. Inst. Mar. Sci., Univ. Alaska, Fairbanks, AK. pp. 321–343.
- North Pacific Anadromous Fish Commission (NPAFC). 2001. Plan for NPAFC Bering–Aleutian Salmon International Survey (BASIS) 2002–2006. N. Pac. Anadr. Fish Comm. Doc. 579, Rev. 2. 27 pp. (Available at www.npafc.org).
- NPAFC. 2003. Annual Report of the Bering-Aleutian Salmon International Survey (BASIS), 2002. N. Pac. Anadr. Fish Comm. Doc. 684. 38 pp. (Available at www.npafc. org).
- NPAFC. 2004. Annual Report of the Bering-Aleutian Salmon International Survey (BASIS), 2003. N. Pac. Anadr. Fish Comm. Doc. 769. 78 pp. (Available at www.npafc. org).
- NPAFC. 2005. Annual Report of the Bering-Aleutian Salmon International Survey (BASIS), 2004. N. Pac. Anadr. Fish Comm. Doc. 857. 105 pp. (Available at www. npafc.org).
- NPAFC. 2006. Annual Report of the Bering-Aleutian Salmon International Survey (BASIS), 2005. N. Pac. Anadr. Fish Comm. Doc. 1009. 94 pp. (Available at www. npafc.org).
- Shuntov, V.P., O.S. Temnykh, and I.I. Glebov. 2007. Some aspects of international program BASIS (2002–2006) implementation by Russia. Izv. TINRO 151: 3–34. (In Russian with English abstract).
- Stabeno, P.J., N.A. Bond, and S.A. Salo. 2007. On the recent warming of the southeastern Bering Sea shelf. Deep Sea Res. II 54: 2599–2618.
- Straty, R.R. 1974. Ecology and behavior of juvenile sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay and the eastern Bering Sea. *In* Oceanography of the Bering Sea with emphasis on renewable resources. *Edited by* D.W. Hood and E.J. Kelley. Occas. Publ. No. 2. Inst. Mar. Sci. Univ. Alaska, Fairbanks, AK. pp. 285–320.
- Sviridov, V.V., I.I. Glebov, and V.V. Kulik. 2004. Spatio-temporal variability in biological characteristics of Pacific salmon in the western Bering Sea. N. Pac. Anadr. Fish Comm. Doc. 753. 17 pp. (Available at www.npafc.org).
- Tadokoro, K., Y. Ishida, N.D. Davis, S. Ueyanagi, and T. Sugimoto. 1996. Change in chum salmon (*Oncorhynchus keta*) stomach contents associated with fluctuation of pink salmon (*O. gorbuscha*) abundance in the central subarctic Pacific and Bering Sea. Fish. Oceanogr. 5: 89–99.
- Takagi, K. 1961. The seasonal changes in gonad weight of

sockeye and chum salmon in the North Pacific Ocean, especially with reference to mature and immature fish. Bull. Hokkaido Reg. Fish. Res. Lab. 23: 17–34. (Transl. Bur. Commer. Fish., Br. Foreign Fish., Washington D.C.).

- Temnykh, O.S., A.N. Starovoytov, I.I. Glebov, G.V. Khen, A.Ya. Efimkin, A.M. Slabinsky, and V.V. Sviridov. 2003. The results of trawling survey in the epipelagic layer of the Russian economic zone in the Bering Sea during September–October, 2002. N. Pac. Anadr. Fish Comm. Doc. 682, Rev. 2. 39 pp. (Available at www. npafc.org).
- Temnykh, O.S., I.I. Glebov, V.V. Sviridov, S.V. Laboda, A.L. Figurkin, N.A. Kuznetsova, and A.M. Slabinskii. 2007. Cruise report of the R/V *TINRO* survey in the western Bering Sea, August–October 2006. N. Pac. Anadr. Fish Comm. Doc. 1065. 26 pp. (Available at www.npafc. org).
- Ueno, Y., N.D. Davis, M. Sasaki, and I. Tokuhiro. 1998. Japan-U.S. cooperative high-seas salmonid research aboard the R/V *Wakatake maru* from June 9 to July 25, 1998. N. Pac. Anadr. Fish Comm. Doc. 326. (Available at www.npafc.org).
- Volkov, A.F., and N. Kosenok. 2007. Similarity of diurnal rhythms of Pacific salmon feeding in the western Bering Sea. N. Pac. Anadr. Fish Comm. Bull. 4: 327–333. (Available at www.npafc.org).
- Volkov, A.F., V.I. Chuchukalo, and A.Ya. Efimkin. 1995. Feeding of Chinook and coho salmon in the northwestern Pacific Ocean. N. Pac. Anadr. Fish Comm. Doc. 124. 12 pp. (Available at www.npafc.org).
- Volkov, A.F., A.Ya. Efimkin, N.A. Kuznetsova and A. M. Slabinsky. 2005. Hydrobiological investigations by the TINRO-Centre under the BASIS-2003 Program: zooplankton and Pacific salmon feeding. N. Pac. Anadr. Fish Comm. Tech. Rep 6: 35–37. (Available at www. npafc.org).
- Volkov, A.F., A.Ya. Efimkin, and N.A. Kuznetsova. 2007a.
 Plankton communities in the Bering Sea and some areas of the North Pacific in 2002–2006. Izv. TINRO 151: 338–364. (In Russian with English abstract).
- Volkov, A.F., A.Ya. Efimkin, and N.A. Kuznetsova. 2007b. Results of the BASIS studies on Pacific salmons feeding habits in 2002–2006. Izv. TINRO 151: 365–402. (In Russian with English abstract).
- Yamamura, O., S. Honda, O. Shida, and T. Hamatsu. 2002. Diets of walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan: ontogenetic and seasonal variations. Mar. Ecol. Prog. Ser. 238: 187–198.
- Zavolokin, A.V., A.Ya Efimkin, A.M. Slabinskiy, and N.S. Kosenok. 2007. Food supply and trophic relationships of Pacific salmon (*Oncorhynchus* spp.) and Atka mackerel (*Pleurogrammus monopterygius*) in the western Bering Sea in fall 2002–2004. N. Pac. Anadr. Fish Comm. Bull. 4: 127–131. (Available at www.npafc.org).