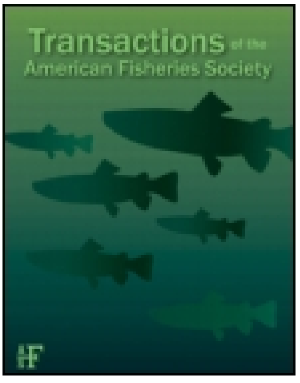

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Nocturnal Feeding of Pacific Hake and Jack Mackerel off the Mouth of the Columbia River, 1998-2004: Implications for Juvenile Salmon Predation

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[Article]

Nocturnal Feeding of Pacific Hake and Jack Mackerel off the Mouth of the Columbia River, 1998–2004: Implications for Juvenile Salmon Predation

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Abstract.—Predation by piscivorous marine fishes has been hypothesized to be a primary source of marine mortality for Pacific Northwest juvenile salmon. During the springs and summers of 1998–2004, we collected predator and prey fishes (forage and juvenile salmonids) at the surface at night off the mouth of the Columbia River. Pacific hake *Merluccius productus* had relatively low percentages of empty stomachs during cool-ocean years (2000 through 2002) and high percentages during 1998, a warm-ocean year. Euphausiids and fishes were the most commonly eaten prey for both species. Pacific hake and jack mackerel *Trachurus symmetricus* appeared to show some diet selectivity, eating some fish, including salmonids, in a higher proportion than found in the environment. Both Pacific hake and jack mackerel ate juvenile salmonids, but at very low amounts. After considering population sizes in the study area, these two predators do not appear to be responsible for the death of large numbers of Columbia River juvenile salmon smolts. However, we may have underestimated the number of salmonids eaten by hake and mackerel due to the limitations of our study. More work needs to be done to identify and quantify predation of juvenile salmon off the Pacific Northwest.

The coastal zone where the Columbia River meets the Pacific Ocean is a very dynamic environment with very strong currents and large fronts (Hickey and Banas 2003; De Robertis et al. 2005; Morgan et al. 2005); each year, approximately 100 million juvenile salmon smolts originating from the Columbia River first encounter the marine environment. This habitat is also where much of the marine mortality of juvenile Pacific salmon is thought to occur, with predation being the primary source of this mortality (Pearcy 1992; Beamish and Mahnken 2001). To examine whether this hypothesis was true, we initiated a study in 1998 to identify the abundance and document the feeding habits of large predatory fishes off the Columbia River.

The movement and feeding patterns of predatory fishes are known to affect fish prey resources (Carpenter and Kitchell 1993; Ware and McFarlane 1995; Bax 1998; Tsou and Collie 2001; Hunt and Stabeno 2002; Worm and Myers 2003). Nevertheless, an extensive analysis of pelagic fish food habits off Oregon and Washington in the 1980s (Brodeur et al. 1987) found only black rockfish *Sebastes melanops* and searun cutthroat trout *O. clarkii* eating salmon smolts off Oregon and Washington. Because these predatory species were not abundant, their feeding would probably account for relatively little juvenile salmon mortality.

We suspected that few instances of juvenile salmonid predation were observed by Brodeur et al. (1987) because nearly all their purse seine sampling occurred during daylight. Many large predatory fishes undertake diel vertical migrations; staying deep during the day but approaching the surface at night. Diel movement in fishes, particularly among clupeids (Blaxter and Holliday 1963) and hakes (Pitcher and Alheit 1995), is common and thought to be related to both reduced predation and an increase in prey availability (Clark and Levy 1988; Bozzano et al. 2005). Juvenile salmonids off the Columbia River, on the other hand, do not undertake diel migrations but remain near the surface (Emmett et al. 2004). By sampling fishes at night at the surface, we were able to observe the interactions of diel-migrating predators with surface-oriented juvenile salmonids, as well as diel-migrating forage fishes, which may act as alternative prey.

During our sampling, only two predatory fishes—Pacific hake *Merluccius productus* and jack mackerel *Trachurus symmetricus*—were abundant enough to possibly affect juvenile salmonid abundance (Emmett et al. 2006). Pacific hake is the most abundant

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predatory fish along the U.S. Pacific coast (Methot and Dorn 1995). Although their 1998–2004 population was lower than their peak abundance during 1987, it is still estimated to be 2.6–4.0 million metric tons (Helser et al. 2004). Pacific hake normally migrate to the Pacific Northwest (Oregon, Washington, and British Columbia) waters in the spring and summer to feed and return to southern California waters in winter to spawn (Bailey et al. 1982; Dorn 1995). Hake feeding habits have been relatively well studied (Alton and Nelson 1970; Livingston 1983; Rexstad and Pikitch 1986; Brodeur et al. 1987; Tanasichuk et al. 1991; Buckley and Livingston 1997; Tanasichuk 1999; Nelson 2004), but none of these studies collected Pacific hake at the surface and only Livingston (1983) and Tanasichuk et al. (1991) collected hake at night. Our study provides diet information from a habitat—near surface, at night—that is regularly used by hake and jack mackerel but has not been previously sampled. Furthermore, although the ecological consequences of hake feeding, movements, and migrations on other fishery resources has been relatively well documented in Canadian waters (Ware and McFarlane 1995, Robinson and Ware 1999; Benson et al. 2002), studies in U.S. waters (Francis 1983; Livingston and Bailey 1985; Rexstad and Pikitch 1986; Jay 1996; Buckley and Livingston 1997) have not been very conclusive. Hannah (1995) did find that Pacific hake predation influences the abundance of ocean shrimp *Pandalus jordani* off Oregon, and recent trophic modeling of the hake population has revealed that hake are major predators in the California Current and may provide a top–down influence on fishery resources (Field 2004; Agostini 2005; Field et al. 2006).

The jack mackerel is perhaps the second most abundant large pelagic predatory fish on the Pacific coast (MacCall et al. 1980; MacCall and Stauffer 1983) and was the second most abundant large pelagic fish off Oregon in 1983 and 1984 (Brodeur and Pearcy 1986; Emmett and Brodeur 2000). Little is known about their migratory behavior; however, juveniles are generally abundant off California, and adults are regularly found from the Gulf of California to Alaska (Blunt 1969; MacCall and Stauffer 1983). There are no current estimates of jack mackerel biomass off the West Coast. In 1983, their spawning biomass was estimated to be 0.64–1.3 million metric tons off southern California, and perhaps biomass is similar outside this area (MacCall and Stauffer 1983). Off of Oregon, no directed commercial fishery currently exists for jack mackerel, but they are the most common bycatch in the commercial Pacific hake fishery (Wiedoff et al. 2003).

Jack mackerel off Oregon and Washington eat primarily euphausiids (mostly *Thysanoessa spinifera* and *Euphausia pacifica*), other crustaceans, and small fishes, but the importance of any particular prey varies annually (Brodeur et al. 1987). For example, juvenile northern anchovy *Engraulis mordax* were important jack mackerel prey in 1982, but not in 1983 and 1984. Euphausiids are usually the most important prey in spring and summer, switching to fish in fall (Brodeur et al. 1987). Carlisle (1971) found that jack mackerel off California fed mainly on euphausiids by weight, but copepods and pteropods were important by number. Other species of *Trachurus* appear to feed similarly, euphausiids being the primary prey and fish being eaten more often as mackerel become larger (Pillar and Barange 1998; Šantić et al. 2005). Their diel feeding behavior varies geographically. Off Chile, *Trachurus murphyi* feeds mostly at night (Bertrand et al. 2004), as does *Trachurus trachurus* in the Adriatic Sea (Jardas et al. 2004), but off South Africa, *Trachurus capensis* feeds primarily during daylight (Pillar and Barange 1998).

The primary goal of our research was to identify the magnitude of large fish predation on juvenile salmon. We also wanted to examine the interannual variability in nocturnal feeding patterns of Pacific hake and jack mackerel, data that are rarely collected. Finally, we investigated how predator feeding patterns could affect ecosystem change (Hanson and Chouinard 2002; Link 2004) and recruitment processes (Mills et al. 2007).

Methods

All fishes for this study were collected by trawling at night from a contracted commercial fishing vessel. Once captured, fishes were processed (identified, measured, counted, and stomachs removed) on deck at sea. Final stomach analysis was conducted in the laboratory.

Study area.—The study area, located just west and north of the mouth of the Columbia River (Figure 1), is a very dynamic physical environment with abundant natural resources. Important commercial fisheries in the area include Pacific salmon (*Oncorhynchus*), Pacific sardine *Sardinops sagax*, flatfishes, and Dungeness crab *Cancer magister*. Detailed biological and physical oceanographic information about the area can be found in Pruter and Alverson (1972), Hickey (1989), and Hickey and Banas (2003); therefore, only a brief synopsis is presented here.

The study area is strongly affected by three physical factors: ocean currents, upwelling, and Columbia River flows. Ocean currents are generally southerly (California Current) in the spring and summer, and northerly (Davidson Current) in the winter. Upwelling occurs during spring and summer when winds are

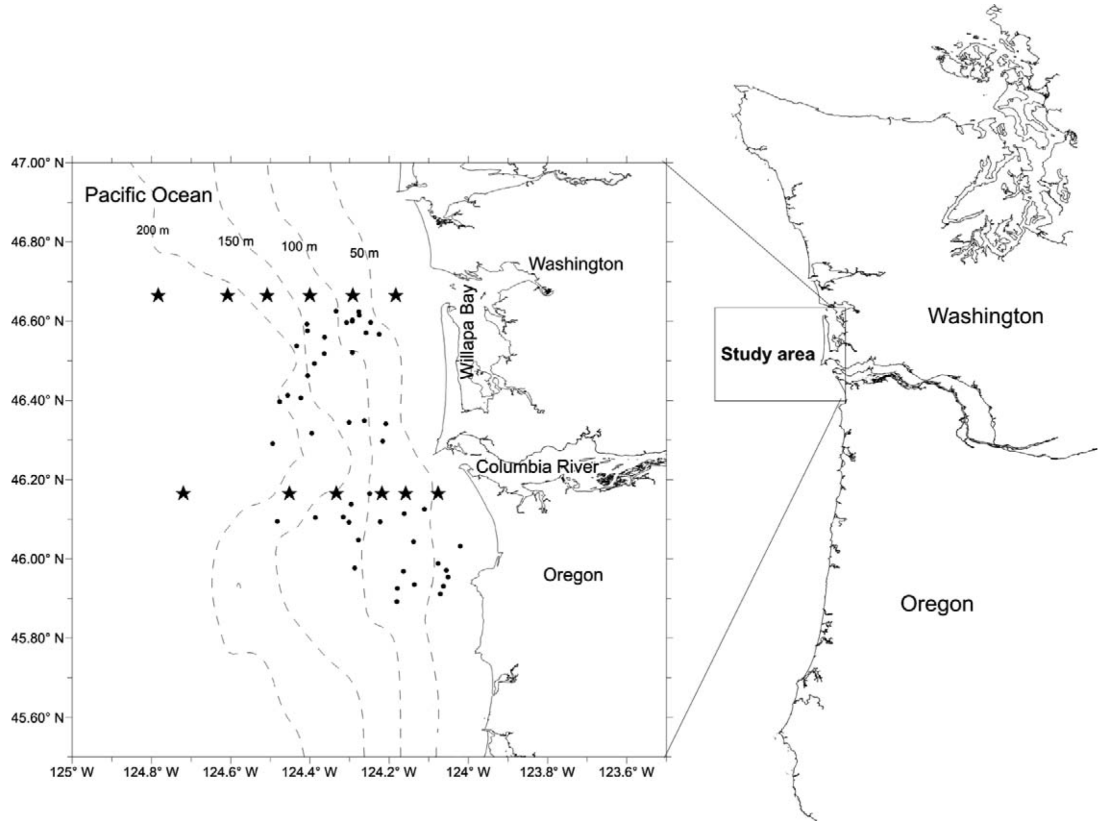

FIGURE 1.—Location of surface trawl stations where Pacific hake and jack mackerel were sampled during spring and early summer of 1998 (dots) and 1999–2003 (stars) in waters off the mouth of the Columbia River, Washington and Oregon.

northwesterly. Downwelling occurs during winter when winds are southwesterly. Upwelling is normally not continuous, but sporadic, with periods of strong upwelling usually followed by a couple of days of relaxation. Columbia River flows usually peak in May–June when snow in interior basins melts. Columbia River juvenile yearling salmon smolt migration peaks in May, and June–July is generally the peak of the subyearling salmon smolt migration. While there are some adult salmon returning year-round, most salmon return to the Columbia River in fall.

Fish sampling.—All stomach samples were collected from 1998 through 2004 at approximately 10-d intervals from late April through July or early August. Although 10 surveys were attempted each year, because of weather or mechanical malfunction, just 9 surveys were conducted in 1998 and 2004 and in 2000 only 8.

Different fishing trawls were used initially to collect fish near the surface at night. In May 1998 a number-4 rope trawl was used. From June 1998 on, a 264-rope trawl with 3-m^2 foam filled doors (built by NET Systems) was used because it was the most effective at fishing at the surface. The 264-rope trawl net was 100-m long and had a fishing mouth opening of approximately 28 m wide by 12 m deep (Emmett et al. 2004). Trawl stretch mesh size ranges from 126.2 cm in the throat of the net near the jib lines to 8.9 cm in the cod end. A 6.1-m-long web liner (0.8-cm stretch knotless web) was sewn into the cod end to capture small fishes and invertebrates. The number-4 rope trawl had mesh sizes similar to those of the 264-rope trawl. All trawls were towed at the surface, except in May 1998, when they were about 5 m below the surface. The net was towed 137 m behind a chartered commercial fishing vessel traveling approximately 1.5 m/s. The trawl was towed for 30 min; however, beginning in 2001 this was often shortened to 15 min because of extremely large tows of forage fish. All trawling was conducted at night when diel migrating predators would interact most with surface-oriented juvenile salmonids (Emmett et al. 2004) and when pelagic trawling for many fishes is most effective (Dotson and Griffith 1996; Krutzikowsky and Emmett 2005). Six trawl tows were usually completed each night.

In 1998 a variety of stations (Figure 1) were sampled every 10 d because we wanted to verify that the fishing gear worked effectively and determine whether predator and forage fishes were widely distributed in the study area. From 1999 to 2004, we sampled 12 designated stations along two transects during each survey. Although the sampling domain was slightly larger in 1998 and was not completely comparable with other years, we believe this difference was relatively small compared with the large change in oceanographic conditions that occurred that year. In 1998 the California Current transitioned from an El Niño to cool-water conditions (Hayward et al. 1999). Because the 1998 data provide valuable contrasting information, we believe they are important to include in this analysis.

The whole catch was initially dumped onto the deck and relatively well mixed. From this mixture, 30 individuals of each species were impartially selected from various areas of the catch were measured, and the remaining individuals were counted. However, when catches of a species were large (generally >200), after measuring the 30 individuals, we estimated the number of fish caught. At least one random basket of that species was counted and weighed to obtain the number of fish per unit weight; this was applied to the total weight caught of that species to estimate the total number caught in the haul.

Minimum estimates of predator and forage fish densities (number fish/10^6 m^3) were determined by dividing the number of fish caught by the distance trawled times the mouth area of the trawl (336 m^2). Net catching efficiency was assumed to be 1. Distance fished was calculated by computing the distance between the beginning and ending trawl location, as determined via the geographic positioning system. Densities of salmon species were calculated by age-class, which we identified by length (Dawley et al. 1986). We use the salmon age convention of Koo (1962; i.e., the number before the period indicates winters in freshwater, and the number after the period indicates winters spent in the ocean). Densities of young of the year (age 0) Pacific hake and rockfish (*Sebastes*) (those <100 mm) were calculated separately from older age-classes (those ≥ 100 mm). Monthly densities of Pacific hake, jack mackerel, and forage fishes were calculated using the delta-distribution method (Pennington 1996), which is appropriate for a species with a very patchy distribution (few relatively large catches and some zero catches). The delta-distribution method uses a lognormal model for the nonzero fish catches to estimate population mean and variance and adjusts these values for the proportion of tows with zero catches (Pennington 1996).

Stomach analysis.—Because the primary objective of this study was to identify whether Pacific hake or jack mackerel were feeding on salmon smolts, which occur rarely, we attempted to analyze as many stomachs as possible. This was accomplished by analyzing stomachs both quantitatively and qualitatively. Stomachs selected for quantitative analysis were dissected from the fish, placed in labeled muslin bags that were placed into a bucket containing a 10% formalin solution. From 1998 through 2003, stomachs (including empty ones) from the 30 Pacific hake and 30 jack mackerel selected and measured per haul were removed and saved for quantitative stomach analysis. Qualitative stomach analysis consisted of cutting open and examining fish stomachs at sea. If fish were found in the stomach, we recorded the information about the predator and placed the stomach in a muslin bag and preserved it in formalin for quantitative analysis. If a stomach did not contain fish, general identification of what the stomach contained was recorded (e.g., euphausiids, shrimp, and digested material) and the stomachs and its contents were discarded. From 1998 through 2003, qualitative stomach analysis was also performed on as many predatory fish as time allowed between sampling efforts (i.e., before the next haul). In 2004, all predator stomachs were analyzed semiquantitatively at sea; stomachs were opened, fish prey identified to species and counted and measured, but all other taxa (e.g., euphausiids or shrimp) were just recorded as present.

In the laboratory, stomachs were first soaked in freshwater, and their contents were subsequently analyzed. Fish prey were identified to the lowest possible taxonomic level, measured for total length (TL; mm), and weighed (0.001 g). For 25% of all stomachs collected, nonfish prey taxa were identified to lowest taxonomic level possible, counted, measured (first 30; mm) and weighed (0.001 g). For the remaining stomachs, nonfish prey items were identified to family and weighed.

Data analysis.—To accurately represent the diet of Pacific hake and jack mackerel populations off the Columbia River, we had to account for differences in catches per haul. As such, all measures of diet (percent empty, frequency of occurrence, etc.) were calculated by haul and then weighted by multiplying these data by the percent of the entire monthly catch that each haul represented, which we then summed. For example, if haul A had 20% empty stomachs and represented 10% of the entire catch and haul B had 50% empty stomachs but represented 90% of the catch for that month, then the percent empty for that month was calculated as $(0.2 \times 0.1) + (0.5 \times 0.9) = 0.47$ (47% empty).

A Kruskal–Wallis test (a nonparametric analysis of variance) was used to identify difference in percent empty stomachs between years and between months. When a significant difference was observed per period ($P < 0.05$), Dunn's multiple-range test (a pair-wise comparison test) was used to identify which year or month differed. Linear regression was used to identify the relationship between percent empty stomachs and predator abundance, and because lengths were not normally distributed, the nonparametric Kruskal–Wallis test was used to identify annual and monthly differences in predator lengths. Before analysis, predator densities were log transformed and percent empty data were arcsine transformed. A Mann–Whitney *U*-test was used to compare medians lengths of euphausiids eaten by Pacific hake and jack mackerel.

The frequency of occurrence of each prey species or prey category was calculated for each month by year by dividing the number of times a prey category occurred by the total number of stomachs. Again, these data were weighted by catch per haul.

To identify whether Pacific hake and jack mackerel were feeding selectively on specific fish species (i.e., eating a fish prey either with greater or less frequency than it was found locally in the environment), we compared the numerical percentage of a fish species in the diet with the numerical percentage of that fish species in the hauls that captured either predator. The selectivity metric we used was the $\log_e$ of the odds ratio (LOR; Gabriel 1978; Schabetsberger et al. 2003). The LOR is symmetrical around zero (no selectivity = prey eaten in the same proportion as it occurred in the local surroundings) and ranges from + 4 to −4, where positive values mean positive prey selection (prey are found at a higher percentage in a fish's diet than are observed in the catch) and negative values mean negative prey selection (numerical proportion of a prey is higher in the catch than in the diet):

$$\mathrm{LOR} = \log_e\left[\frac{d_i(100 - e_i)}{e_i(100 - d_i)}\right]$$

as calculated from the numerical percentages of fish taxon *i* in the predator diet (d_i) and local surroundings (e_i). As stated earlier, the LOR values were calculated by month by summing diet and catch data from each individual haul after these data were weighted (multiplied) by the percentage of predator catch each haul represented per month. This measure of predator selectivity assumes that the surface trawl is catching all predatory and prey fish species with equal efficiency and accurately represents the prey field that the predatory fishes are selecting from. Because equal catch efficiency may not be valid for all prey species, we identified instances of probable biases in trawl catches of prey species.

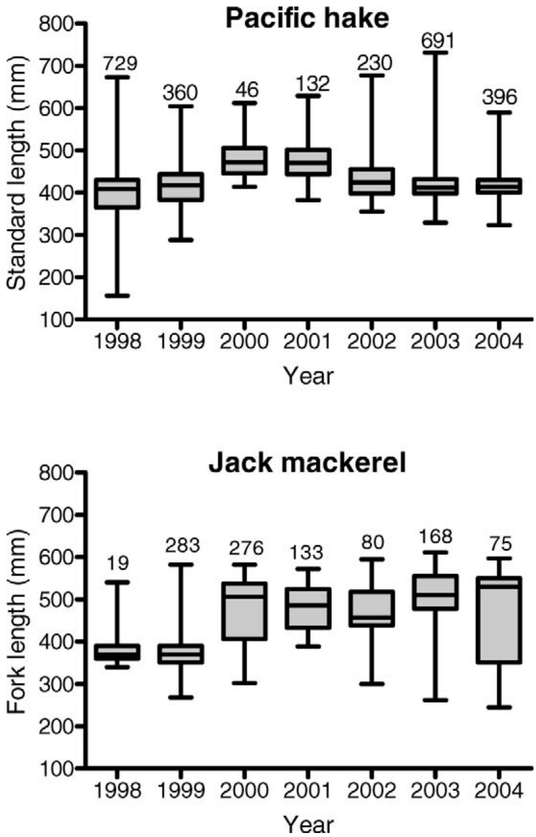

FIGURE 2.—Lengths of Pacific hake and jack mackerel taken (1998–2004) in waters off the mouth of the Columbia River, Washington and Oregon, for feeding analysis. The number above each box plot (median, box is the 25th to 75th percentile, and range) indicates the number of fish measured.

Results

Predator Body Sizes

The size of predators may affect their ability to feed on specific prey items, larger fish generally being able to consume larger prey. Median standard length of Pacific hake examined for stomach analysis differed significantly between years (Kruskal–Wallis, $P < 0.001$; Figure 2). Pacific hake in 1998 were significantly smaller than all other years and were larger in 2000 and 2001 than all other years (Dunn's multiple comparisons test, $P < 0.01$). However, median lengths of Pacific hake were similar in 1999, 2003, and 2004 (Figure 2). Median jack mackerel size also differed

TABLE 1.—Percent frequency of occurrence of prey found in Pacific hake *Merluccius productus* collected off the Columbia River, 1998–2004. Values in parentheses are number of stomachs analyzed and number of stomachs containing food.

Stomach contents	1998 (2,722; 1,136)	1999 (454; 360)	2000 (49; 46)	2001 (193; 135)	2002 (360; 229)	2003 (1,083; 813)	2004 (493; 404)
Plant material	0.1			0.5			
Unidentified invertebrates	10.7						
By-the-wind sailor *Velella velella*							0.2
Annelida	<0.1						
Polychaeta	<0.1						
Gastropoda		0.7					
Olive snail *Olivella* spp.	<0.1						
Cephalopoda	0.1	0.9			0.6		
Squid *Loligo* sp.	0.1					0.2	
Crustacea	0.8	0.9		6.7	0.3	0.1	
Copepoda	0.1						
Calanoida	<0.1						
Mysidae	4.9	1.3		2.1		0.2	
Glass shrimp *Archaeomysis grebnitzkii*	<0.1						
Neomysis	<0.1						
Mysid shrimp *Neomysis kadiakensis*	<0.1			0.5			
Mysid shrimp *Neomysis rayii*	0.5						
Cumacea	1.9	1.3	2.0			0.2	
Isopoda	0.5						
Gnorimosphaeroma oregonensis	<0.1						
Idoteidae	0.1						
Synidotea spp.	0.1						
Synidotea bicuspida	<0.1						
Amphipoda	0.1					0.1	
Gammaridea	<0.1	0.2					
Hyperiidea	<0.1	1.1					
Hyperoche	<0.1						
Parathemisto pacifica	0.1	0.2					
Caprellidea	<0.1						
Euphausiidae	15.1	75.8	87.8	46.1	37.8	49.8	60.6
Pacific krill *Euphausia pacifica*	1.3	12.6	4.1	7.8	0.6	0.3	0.2
Large krill *Thysanoessa spinifera*	1.9	15.0	16.3	10.4	0.3	0.1	
Decapoda	0.1	0.2				0.1	
Caridea	0.1	0.2		0.5	0.3	0.2	0.2
Pandalidae		0.2			0.3		
Shrimp *Pandalus* spp.				0.5			
Pink shrimp *Pandalus jordani*					1.9		
Crangonidae	1.0	1.5		2.1	0.3		
Crangon	0.2	0.4					0.6
Crangon alba	0.1	0.4					
Smooth bay shrimp *Crangon stylirostris*	<0.1	0.2					
Crabs	<0.1						1.2
Callianassidae	0.1	0.2					
Ghost shrimp *Callianassa* spp.						0.1	
Paguridae	<0.1						
Hippidae (megalops)	<0.1						
Brachyura (larvae)	0.7	0.9				0.2	
Cancridae	0.2				0.3		
Rock crab *Cancer* spp. (megalope)	2.0	2.4	10.2	2.6		2.2	
Dungeness crab *Cancer magister* (megalope)	0.7	0.7	2.0	1.6	0.8	0.2	
Pinnotheridae (larvae)	0.3	2.6		0.5			
Fabia zoea		0.2					
Pea crab *Fabia subquadrata*		0.2					
Green shore crab *Hemigrapsus oregonensis* (megalope)	<0.1						
Salpida		0.2					
Osteichthyes	4.7	7.0	20.4	28.0	8.9	6.3	4.5
Fish scales	0.1	0.2				0.1	
Fish bones		0.2			0.3	0.1	
Pacific herring *Clupea pallasi*	1.1	1.1		6.7	1.7	0.5	1.0
Pacific sardine *Sardinops sagax*	0.4				1.1	0.3	
Northern anchovy *Engraulis mordax*	2.3	0.4		1.0	13.9	7.3	17.8
Chinook salmon *Oncorhynchus tshawytscha*	0.1					0.2	0.4
Osmeridae	0.1	0.4		2.1	0.6	0.4	0.6
Night smelt *Spirinchus starksi*	0.1						
Eulachon *Thaleichthys pacificus*					0.3	0.6	
Whitebait smelt *Allosmerus elongatus*	1.6	0.9		5.7	4.4	1.2	2.2
Pacific tomcod *Microgadus proximus*				0.5	1.1	0.4	
Pacific hake *Merluccius productus* (age 0)	<0.1						0.4

TABLE 1.—Continued.

Stomach contents	1998 (2,722; 1,136)	1999 (454; 360)	2000 (49; 46)	2001 (193; 135)	2002 (360; 229)	2003 (1,083; 813)	2004 (493; 404)
Rockfish *Sebastes* spp. (age 0)	0.1		2.0			0.2	0.4
Cottidae	<0.1						
Agonidae	<0.1						
Sturgeon poacher *Agonus acipenserinus*	<0.1						
Cyclopteridae						0.1	
Shiner perch *Cymatogaster aggregata*	0.1						
Pacific sand lance *Ammodytes hexapterus*		0.9			0.3		
Chub mackerel *Scomber japonicus*	<0.1						
Pleuronectiformes		0.4					0.2
Sanddab *Citharichthys* spp.	<0.1	0.7					
Pacific sanddab *Citharichthys sordidus*	0.1					0.2	
Speckled sanddab *Citharichthys stigmaeus*		0.2					
Pleuronectidae				0.5			
Slender sole *Lyopsetta exilis*[a]	<0.1						
Digested material	6.6	6.6	65.3	18.7	3.3	1.8	0.4

[a] Formerly placed in *Eopsetta*.

significantly among years (Kruskal–Wallis, $P < 0.001$; Figure 2); in 1998–1999 they were significantly smaller than all other years, and in 2003 they were larger than other years (Dunn's multiple-range test, $P < 0.05$).

Number of Stomachs Examined and Empty

We examined a total of 5,320 Pacific hake and 2,082 jack mackerel stomachs for this study (Tables 1, 2). The number of Pacific hake stomachs collected and analyzed ranged from 2,722 in 1998 to 40 in 2000. The greatest catches and largest number of jack mackerel stomachs taken were in 1999 (496), the fewest were in 2004 (115). For both predators, the number of stomachs analyzed was proportional to their numbers in the catch.

To identify temporal (daily, monthly, annual) patterns in predator fish feeding, we documented the percentage and variation of empty stomachs by species, hour, month, and year. Combining all stomach data for all years together by hour of capture revealed that both Pacific hake and jack mackerel had relatively high percentages of empty stomachs at sunset but relatively low values by sunrise (Figure 3). These hourly data indicate that hake and mackerel actively fed at night after migrating to the surface at sunset.

The overall percentages of empty stomachs were highest in 1998 and lowest in 2000 for both Pacific hake (65% and 6%) and jack mackerel (86% and 32%; Figure 4). In April and May 1998, we may have overestimated the percentages of empty hake stomachs because fishes were collected at middepth rather than at the surface (sampling gear issue). Only hake showed significant annual differences in percentages of empty stomachs, 1998 exceeding 1999 (Kruskal–Wallis, $P = 0.05$). On a monthly basis, hake had significantly more empty stomachs in June (Kruskal–Wallis, $P = 0.0003$; Dunn's multiple-range test, $P < 0.05$) than in the other months. For jack mackerel, percentages of empty stomachs showed no significant annual differences (Kruskal–Wallis, $P = 0.063$), but there were fewer empty stomachs in June than in other months (Kruskal–Wallis, $P = 0.0007$; Dunn's multiple-range test, $P < 0.05$). Jack mackerel had higher percentages of empty stomachs than Pacific hake, both annually and monthly (Figure 4).

There was a significant positive linear relationship ($P < 0.001$, $R^2 = 0.55$) between monthly densities of Pacific hake and the percentages of empty stomachs. The addition of monthly forage fish densities (prey abundance) in a multiple regression model did not improve the simple regression model (extra sum of squares F-test, $P = 0.29$). There was no relationship between monthly densities of jack mackerel and the percentages of empty stomachs ($P = 0.5047$).

Stomach Contents

Euphausiids, primarily *Thysanoessa spinifera* and *Euphausia pacifica,* were the prey items occurring most frequently in Pacific hake and jack mackerel stomachs (Tables 1, 2). We did not identify all euphausiids to species in all stomachs. As such, *T. spinifera* and *E. pacifica* are reported as separate taxa categories and are not also included in the euphausiid categories in Tables 1 and 2. Euphausiids (including *T. spinifera* and *E. pacifica*) were most commonly eaten in 1999 and 2000, when they were found in nearly all hake stomachs that contained food. Fishes were the second most frequently occurring prey found in hake and mackerel during most years. However, decapods (primarily crab megalopae and zoea) were also important prey, especially for mackerel from 1999 to

TABLE 2.—Percent frequency of occurrence of prey found in jack mackerel *Trachurus symmetricus* collected off the Columbia River, 1998–2004. Values in parentheses are number of stomachs analyzed and number of stomachs containing food.

Stomach contents	1998 (130; 21)	1999 (496; 283)	2000 (407; 276)	2001 (428; 134)	2002 (239; 80)	2003 (268; 166)	2004 (115; 76)
Plant material				0.9			
Unidentified invertebrates							0.9
Phaeophycophyta						0.4	
By-the-wind sailor		0.4				13.8	
Ctenophora		0.2					
Annelida			0.2				
Polychaeta		0.4	0.5				
Mollusca				0.5			
Gastropoda		0.4					
Lacunidae		0.2					
Cerithiopsidae			0.2				
Epitoniidae			0.2				
Eulimidae			0.2				
Sea slug *Corolla spectabilis*				0.2			
Cephalopoda			1.5		1.3		1.7
Loligo spp.						1.9	
California market squid *Loligo opalescens*		0.2					
Crustacea	0.8			15.2			
Calanoida		4.6		1.2	0.4		
Thoracica		0.2					
Mysidae		1.0	0.7				
Cumacea		0.2		0.2			
Idoteidae		0.2					
Amphipoda		1.0					
Gammaridea		2.0		0.2			
Hyperiidea		0.8	0.2	0.2			
Hyperia spp.		0.6					
Hyperiella		0.2					
Vibiliidae		1.2					
Vibilia spp.		0.2					
Euphausiidae	13.1	46.0	63.9	28.0	23.8	31.7	7.8
Pacific krill	0.8	4.6	7.1	11.7		0.4	
Large krill	1.5	5.2	10.1	13.8		0.4	
Decapoda				0.2	2.1	0.4	
Caridea				1.9			
Pandalidae		1.6		1.4			
Pink shrimp				2.8			
Crangonidae			0.2	0.2			
Crangon alaskensis			0.2				
Crabs				0.2	1.7		
Callianassidae		0.2					
Paguridae		0.4					
Porcellanidae		4.0					
Hippidae (megalops)		0.2					
Brachyura (megalops)		0.2		0.2			
Majidae		1.0					
Graceful decorator crab *Oregonia gracilis*		1.0					
Cancridae		0.8					
Cancer spp. (megalope)		7.3	8.6	7.2		9.0	0.9
Dungeness crab		4.0	2.7	4.7			
Pinnotheridae zoea		3.6					
Fabia zoea		0.4					
Pea crab		1.8					
Grapsidae		0.2					
Osteichthyes unidentified		1.8	2.5	0.9		0.4	19.1
Pacific sardine							7.8
Northern anchovy			0.2			0.7	20.0
Chinook salmon						0.4	0.9
Osmeridae		0.8	0.5	0.2			
Whitebait smelt			3.7	0.7			
Myctophidae		0.2					1.7
Gadidae		0.4					
Pacific tomcod						1.5	
Pacific hake (age 0)							20.9
Scorpaenidae		0.2					
Sebastes spp. (age 0)			2.5				1.7
Hexagrammidae		0.2	0.2				
Cottidae		0.4			0.8		

TABLE 2.—Continued.

Stomach contents	1998 (130; 21)	1999 (496; 283)	2000 (407; 276)	2001 (428; 134)	2002 (239; 80)	2003 (268; 166)	2004 (115; 76)
Cyclopteridae			0.5				
Snailfish *Liparis* spp.			0.5				
Pacific sand lance		0.2	0.2		1.7		
Pleuronectiformes		0.6		0.2			
Pacific sanddab			0.2				
Rex sole *Glyptocephalus zachirus*[a]			0.2				
Digested material	0.8	19.6	42.8	8.4	2.5	9.3	2.6

[a] Formerly *Errex zachirus*.

2003. Fishes were most frequently found in hake stomachs in 2001 (45%) and 2002 (32%), years when hake were relatively large in size (Figure 2) but not abundant. The frequency of occurrence (FO) of fishes in mackerel stomachs ranged widely, from 0% (1998) to 72.2% (2004).

Pacific hake consumed a large variety of prey items in 1998 (62) but only eight different taxa in 2000. Jack mackerel consumed a large number of taxa in 1999 (45) and few in 1998. For both predator species, the number of prey taxa increased with increased number of stomachs sampled. We suspect that the increased in prey taxa was related to the increased opportunity of

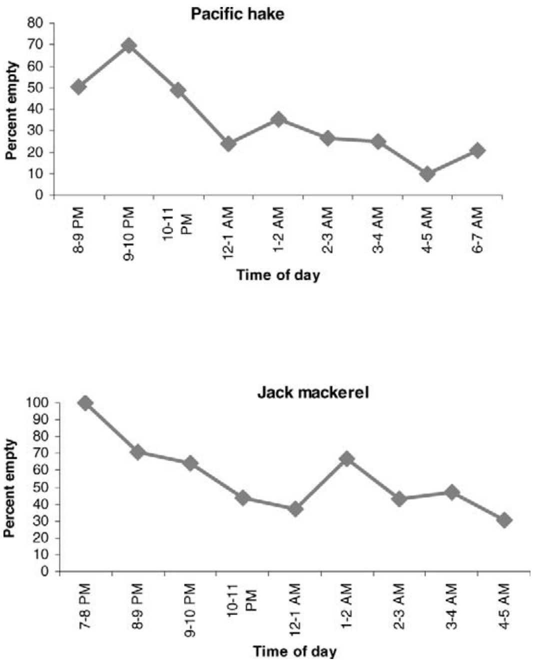

FIGURE 3.—The average percent of empty stomachs in Pacific hake and jack mackerel, by time of day, captured off the mouth of the Columbia River, Washington and Oregon, 1998–2004.

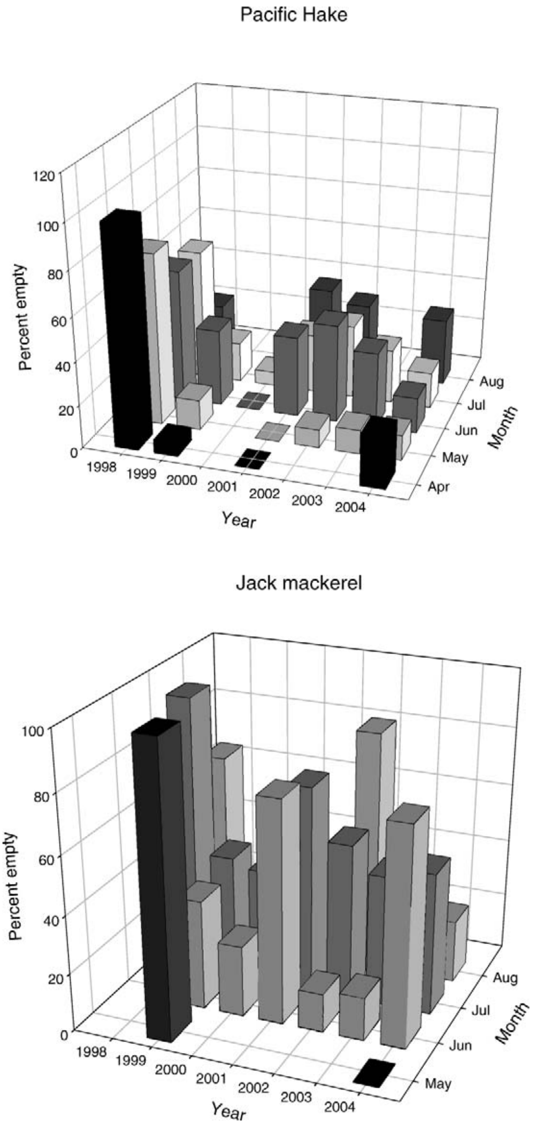

FIGURE 4.—Percent of empty stomachs in Pacific hake and jack mackerel, by year and month, collected off the Columbia River, Washington and Oregon, 1998–2004.

TABLE 3.—Number of salmon observed in Pacific hake and jack mackerel stomachs collected off the Columbia River, Washington and Oregon, 1998–2004. All lengths are fork lengths, except hake, which were standard lengths.

Predator collection data			Salmon eaten[a]	
Length (mm)	Date	Distance from shore (km)	Age	Fork length (mm)
Pacific hake				
430	13 Jun 1998	10.0	0.0	100
439	27 Jun 1998	16.3	0.0	87
390	21 May 2003	37.0	1.0	135
415	08 Jul 2004	27.8	0.0	96
376	18 Jul 2004	37.0	0.0	109
Jack mackerel				
490	08 Jul 2003	16.7	0.0	100
545	07 Jul 2004	46.3	0.0	85

[a] Each predator consumed just one salmon and all salmon eaten were Chinook salmon.

predators to consume rare or uncommon taxa at larger sample sizes.

Many of the fishes found in Pacific hake stomachs were partially digested and not identifiable to species (Table 1). However, of the identifiable fishes, northern anchovy had a higher FO than any other fish prey. Northern anchovy were found in 17.8% of hake stomachs in 2004 and 13.9% in 2002. Other important fish prey for hake included whitebait smelt *Allosmerus elongatus*, Pacific herring *Clupea pallasii*, and Pacific sardine. Only five salmon were eaten by Pacific hake, all of which were juvenile Chinook salmon *Oncorhynchus tshawytscha*; four were age 0.0 and one was age 1.0. Their FOs were 0.1% in 1998, 0.2% in 2003, and 0.4% in 2004. Hake cannibalism occurred in 1998 and 2004 but was limited (Table 1).

Jack mackerel ate only a large number of fishes in 2004 (Table 2). During other years, the FO of fishes

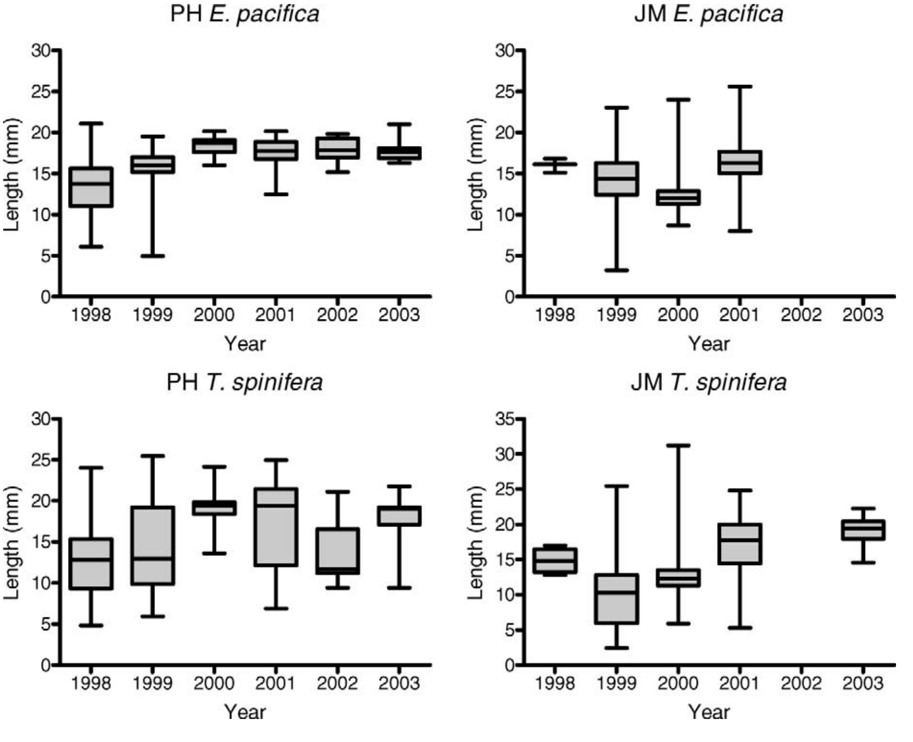

FIGURE 5.—Box plots (median, box is the 25th to 75th percentile, and range) of the lengths of two euphasids (*Euphausia pacifica* and *Thysanoessa spinifera*), by year, found in the stomachs of Pacific hake and jack mackerel off the mouth of the Columbia River, Washington and Oregon, 1998–2003.

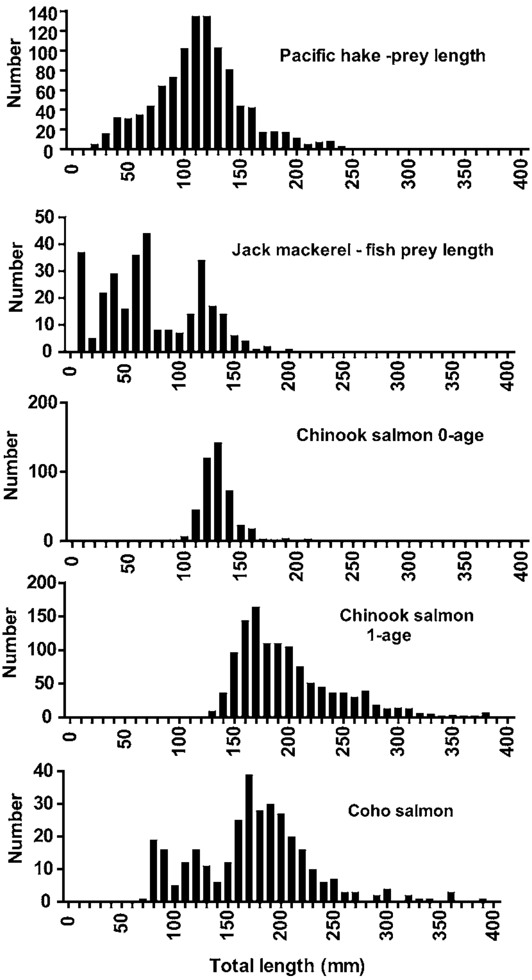

FIGURE 6.—Length frequency of prey fish consumed by Pacific hake and jack mackerel (top two panels) collected during spring and early summer off the Columbia River, Washington and Oregon, 1998–2004, compared with length frequencies of juvenile salmonids collected in the same area and time (bottom three panels).

was less (≤12%). Nevertheless, mackerel consumed a wide variety of fish species (Table 2). In 2004, they ate a large number of age-0 Pacific hake (FO of 20.9%). However, age-0 Pacific hake were not eaten in any other year. Jack mackerel also ate a large number of northern anchovy (FO of 20.0%) in 2004. During other years, important fish prey of mackerel included osmerids (in 1999 and 2001), age-0 rockfish (2000 and 2004), and Pacific sand lance *Ammodytes hexapterus* (2002). Two age-0.0 Chinook salmon were found in mackerel stomachs, one in 2003 (FO = 0.4%) and one in 2004 (FO = 0.9%).

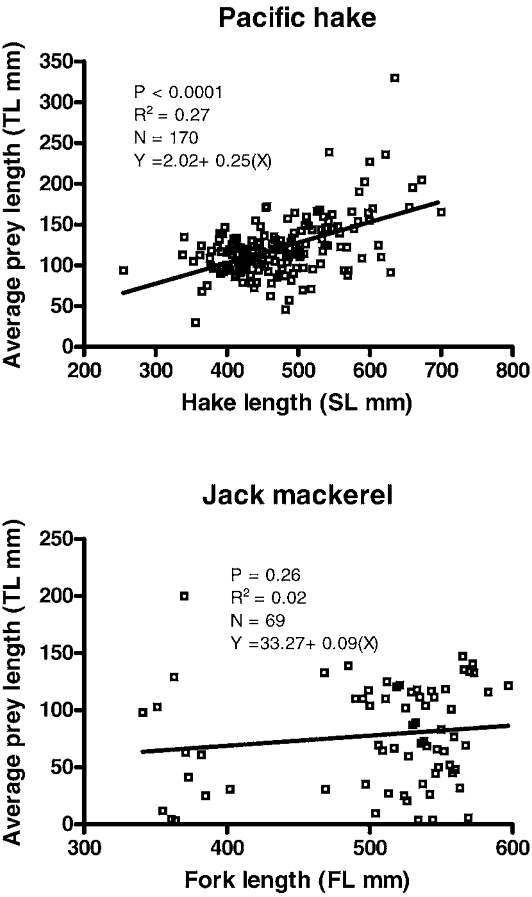

FIGURE 7.—Maximum lengths of fish prey consumed by Pacific hake and jack mackerel, collected off the Columbia River, Washington and Oregon, 1998–2004.

Salmon Eaten

Although seven Chinook salmon (ages 0.0 or 0.1) were found in Pacific hake and jack mackerel stomachs, no other salmonids were found. Two of the Chinook salmon were eaten in 1998, two in 2003, and three in 2004; one salmon was eaten in May, two in June, and four in July. Salmon were eaten at both nearshore locations (10 km) and offshore locations (46.3 km). The Chinook salmon eaten ranged from 85 to 135 mm fork length (FL), and all but one were less than 109 mm (i.e., age 0.0; Table 3). Pacific hake that ate salmon averaged 410 mm standard length (range, 376–439 mm). The two jack mackerel that ate salmon were 490 and 545 mm FL.

Euphausiid Lengths

Both Pacific hake and jack mackerel ate a wide range of sizes (length) of euphausiids annually (Figure

TABLE 4.—Prey selection, $\log_e$ of the odds ratio (LOR), for fish prey categories from Pacific hake stomachs versus trawl catches (values in cells) by month and year. Percent fish prey and catch were weighted by the number of Pacific hake per trawl. Black cells (LOR = 0.01 to 4) indicate when fish taxa were found in stomachs at higher percentages than in trawl catches (positive per selection). Gray cells (LOR = −0.01 to −4) indicate when fish prey taxa were found in stomachs less than trawl catchs (negative selection). Shaded cells with no values indicate prey that were found only in stomachs (black) or trawls (gray). Empty cells indicate prey taxa were not found in stomachs or trawls. An asterisk indicates that fish prey were not identifiable to specific taxa.

	1998				1999			2000	2001		
Pacific hake and prey species	May	Jun	Jul	Aug	May	Jun	Jul	Jul	Jun	Jul	Aug
Number Pacific hake caught	508	7,803	3,434	2,218	1,102	500	576	88	33	181	61
Number of Pacific hake stomachs examined	387	920	841	453	116	116	186	46	27	132	31
Number of Pacific hake eating fish	50	106	69	28	16	13	20	11	9	57	3
Prey						*					*
American shad *Alosa sapidissima*											
Pacific herring		1.68	-0.77		-1.30		1.96		1.72	-0.78	
Pacific sardine		-3.22	-0.51								
Northern anchovy	4.11	1.41	2.31	-1.02	0.35		2.00		3.57		
Coho salmon *Oncorhynchus kisutch* (age 1)											
Sockeye salmon *O. nerka* (age 1)											
Chinook salmon (Age 0)											
Chinook salmon (Age 1)											
Osmeridae											
Surf smelt											
Eulachon											
Whitebait smelt		5.64		2.22	-0.96				-0.56	0.53	
Pacific tomcod											
Pacific hake (age 0)											
Sebastes spp. (age 0)											
Cottidae											
Agoniidae											
Cyclopteridae											
Sablefish											
Shiner perch											
Pacific sand lance											
Chub mackerel											
Pleuronectiformes											
Citharichthys spp.											
Rex sole											

5). Pacific hake consistently ate *E. pacifica* and *T. spinifera* that were larger on average than those consumed by jack mackerel (Mann–Whitney, $P < 0.001$). Pacific hake ate a less variable size range of both euphausiids species than did jack mackerel. During most recent years, hake fed mostly on large *E. pacifica*, but this was not true for *T. spinifera*. This may have been related to availability of small *E. pacifica*, but we did not have any information on euphausiid abundance.

Prey Fish Lengths

The size of fish eaten by Pacific hake was unimodal, ranging from 18 to 330 mm TL, (mean length = 109 mm; (Figure 6). In contrast, the lengths of fishes eaten by jack mackerel were smaller (2–200 mm) and their size frequency distribution was irregular. Overall, Pacific hake ate significantly larger fish than jack mackerel (Mann–Whitney, $P < 0.0001$).

Large Pacific hake ate both small and large fishes. However, the average length of fish eaten by hake increased with hake size (regression, $P < 0.0001$, $R^2 = 0.27$; Figure 7). The average sized fish eaten by a 400-mm (standard length) hake was 102 mm (TL), whereas a 600-mm Pacific hake consumed a fish that averaged 153 mm. Jack mackerel also ate a very wide size range of fishes (Figure 7). However, there was no relationship between maximum size of fish eaten and mackerel size (regression, $P = 0.2645$, $R^2 = 0.02$). The largest fish consumed was 200 mm (TL); it was unidentifiable to species.

Selection of Fish Prey

During all years, there were many instances when the species of prey fishes observed in the catch were not found in the stomachs of Pacific hake captured in the same hauls (Table 4). For example, American shad *Alosa sapidissima* commonly occurred in surface hauls in most years but was never found in any Pacific hake stomachs. Conversely, there were many fishes observed in hake stomachs that did not appear in the hauls. Pacific sand lance, for example, was observed in

TABLE 4.—Extended.

	2002				2003			2004			
Pacific hake and prey species	May	Jun	Jul	Aug	May	Jun	Jul	May	Jun	Jul	Aug
Number of Pacific hake caught	11	104	1,688	59	1,697	909	4,657	40	213	2,085	116
Number of Pacific hake stomachs examined	11	104	156	35	199	346	452	40	75	148	54
Number of Pacific hake eating fish	8	56	29	8	8	91	74	5	23	66	26
Prey											
American shad *Alosa sapidissima*											
Pacific herring	0.76	-2.48	3.23		-3.61	-2.75	0.63		0.93	-1.58	1.08
Pacific sardine			-0.79	-2.56		-2.14	-1.22				
Northern anchovy	-0.37	1.40	1.07	2.71		1.50	0.52	13.12	1.92	-1.16	0.44
Coho salmon *Oncorhynchus kisutch* (age 1)											
Sockeye salmon *O. nerka* (age 1)											
Chinook salmon (Age 0)		2.51								5.31	
Chinook salmon (Age 1)											
Osmeridae											
Surf smelt											
Eulachon			0.82		5.84	-0.45	-1.25			3.59	
Whitebait smelt	-0.29	0.01	2.94		-0.65	0.70	1.93				
Pacific tomcod		0.08	-2.28				4.94				
Pacific hake (age 0)											0.07
Sebastes spp. (age 0)						5.07			1.02		
Cottidae											
Agoniidae											
Cyclopteridae											
Sablefish											
Shiner perch											
Pacific sand lance											
Chub mackerel											
Pleuronectiformes											
Citharichthys spp.											
Rex sole											

the Pacific hake stomachs in 1999 and 2002 but not in any hauls. Nevertheless, when a fish species was prevalent in the environment, it was usually observed in Pacific hake stomachs, but rarely in the same proportion as in the local environment. This implies that hake fed selectively. For example, although northern anchovy were common in hauls and in Pacific hake stomachs, it was usually eaten in a larger proportion than found in the local environment (i.e., in hauls). Hake positively selected northern anchovy in 14 of 20 months of sampliing, and they very were strongly positively selected in May 2004 (LOR = 13.12). Other fish prey that hake seemed to prefer included whitebait smelt, eulachon *Thaleichthys pacificus*, and age-0 rockfish (Table 4). Hake had strong positive selection for age-0 rockfish in June 1998, July 2000, June 2003, and June and July 2004. For adult hake, selection was positive for age-0 hake in August 2004 but negative in August 1998 and July 2004.

Pacific hake nearly always had negative selection for Pacific herring and Pacific sardine, meaning they occurred less frequently in hake stomachs than they did in the hauls that also caught hake. However, schooling fishes such as herring and sardine have very patchy distributions, which may influenced this LORs. There were negative LORs in 21 out of 25 months for Pacific herring, and 22 out of 23 months for Pacific sardine. Hake also exhibited negative selection for juvenile salmonids, except juvenile Chinook salmon during June 1998, May 2003, and July 2004.

Over the 7-year study period the diet of Pacific hake changed as fish prey (northern anchovy, whitebait smelt, and Pacific herring) became more abundant. Linear regression analysis indicated a positive functional response between average monthly densities of northern anchovy in the local environment and their percent by number in the hake diet ($P = 0.002$, $R^2 = 0.48$), indicating that, in general, hake ate northern anchovy more frequently when they were more abundant. Hake also ate Pacific herring ($P = 0.0091$, $R^2 = 0.25$) and whitebait smelt ($P = 0.0236$, $R^2 = 0.18$) more frequently when they were more abundant in the

TABLE 5.—Prey selection, $\log_e$ of the odds ratio (LOR), for fish prey categories in jack mackerel stomachs versus trawl catches. Percent fish prey and catch were weighted by the catch of Pacific hake by individual trawl. Black cells (LOR = 1.23 to 13.95) indicate when fish taxa were found in stomachs at higher percentages than in trawl catches (positive selection). Gray cells (LOR = −1.11 to −5.09) indicate when fish prey taxa were found in stomachs less than trawl catchs (negative selection). Shaded cells with no values indicate prey that were found only in stomachs (black) or trawls (gray). Empty cells indicate prey taxa were not found in stomachs or trawls. An asterisk indicates that fish prey were not identifiable to specific taxa.

	2002				2003			2004			
Pacific hake and prey species	May	Jun	Jul	Aug	May	Jun	Jul	May	Jun	Jul	Aug
Number of Pacific hake caught	11	104	1,688	59	1,697	909	4,657	40	213	2,085	116
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Number of Pacific hake eating fish	8	56	29	8	8	91	74	5	23	66	26
Prey											
American shad *Alosa sapidissima*											
Pacific herring	0.76	-2.48	3.23		-3.61	-2.75	0.63		0.93	-1.58	1.08
Pacific sardine			-0.79	-2.56		-2.14	-1.22				
Northern anchovy	-0.37	1.40	1.07	2.71		1.50	0.52	13.12	1.92	-1.16	0.44
Coho salmon *Oncorhynchus kisutch* (age 1)											
Sockeye salmon *O. nerka* (age 1)											
Chinook salmon (Age 0)		2.51								5.31	
Chinook salmon (Age 1)											
Osmeridae											
Surf smelt											
Eulachon			0.82		5.84	-0.45	-1.25			3.59	
Whitebait smelt	-0.29	0.01	2.94		-0.65	0.70	1.93				
Pacific tomcod		0.08	-2.28				4.94				
Pacific hake (age 0)											0.07
Sebastes spp. (age 0)						5.07			1.02		
Cottidae											
Agoniidae											
Cyclopteridae											
Sablefish											
Shiner perch											
Pacific sand lance											
Chub mackerel											
Pleuronectiformes											
Citharichthys spp.											
Rex sole											

local environment. These data indicate that hake diets are positive indicators for the local abundance of prey species.

Jack mackerel were much less piscivorous than Pacific hake, and many fish species observed in the environment were rarely found in jack mackerel stomachs. This included American shad, Pacific herring, Pacific sardine (found only in 2004), 1.0-age Chinook salmon, juvenile coho salmon, longfin smelt *Spirinchus thaleichthys*, night smelt *Spirinchus starksi*, eulachon, Pacific tomcod *Microgadus proximus* (only found in 2003), lingcod *Ophiodon elongatus*, agonids, and sanddabs *Citharichthys* spp. (only in 2000; Table 5). Jack mackerel had positive selection for age-0 rockfishes, especially in 2000 and 2004. They also had strong positive selection for age-0 Pacific hake in July and August 2004. Other strongly selected fishes included Osmeridae (smelts), Myctophidae (lanternfishes), and Pleuronectiformes (larval flatfish).

Jack mackerel generally did not show positive selection for forage fish (northern anchovy, Pacific herring, or osmerids). There was a negative LOR for northern anchovy in 11 of 13 months, and a negative LOR for whitebait smelt in 8 of 9 months (Table 5). Jack mackerel showed negative selection for 0.0-age Chinook salmon in 13 of 15 months, but positive selection for 0.0-age Chinook salmon in July 2003 and 2004.

As with Pacific hake, there was a positive linear relationship between whitebait smelt densities in the local environment and their percent by number in jack mackerel diets ($P = 0.0125$, $R^2 = 0.47$). However, there was no relationship between any other forage fish densities and percent by number in mackerel diet (all $P > 0.05$).

Discussion

Previous diet studies of Pacific hake and jack mackerel off the Northwest coast have been conducted primarily during daylight and from fish collected at depth by bottom or midwater trawls. Although Tanasicuk et al. (1991) reported that Pacific hake feed sporadically between dawn and dusk and Livingston (1983) showed evidence for night and crepuscular feeding, there have been questions whether Pacific hake are primarily nocturnal feeders (Alton and Nelson 1970; Outram and Haegele 1972; Livingston 1983; Rexstad and Pikitch 1986; Tanasichuk et al. 1991; Buckley and Livingston 1997). We suggest that these unequivocal results regarding night feeding probably resulted from scientists not sampling Pacific hake that had migrated to the surface. Our data support the argument that both species feed during both day and night but that feeding increases at night. Pacific hake appear to be better night feeders (lower percent empty) than jack mackerel. Our data indicate that to properly quantify feeding habits of diel-migrating fishes it is important to observe nocturnal surface feeding habits. Surface trawling at the surface at night has the added attribute of effectively sampling diel migrating forage fishes, something that is usually unavailable from other sampling efforts. Past studies may have underestimated prey consumption by Pacific hake by not considering near-surface night feeding.

Jack mackerel had consistent higher percentages of empty stomachs than Pacific hake. Brodeur et al. (1987) found similar percentage empty stomachs from daytime samples and a wide variation of primary prey, depending on the year. We suspect that jack mackerel are highly dependent on prey patches and have much faster digestion rates than Pacific hake.

Salmon composed a very small portion of Pacific hake and jack mackerel diets. This was not surprising, given that juvenile salmon compose only a very small percentage of the small fish or forage fish in the study area (Emmett et al. 2006). The calculated LOR values indicated that juvenile salmonids were selected more frequently than would be expected from their prevalence in the local environment. We suspect, however, that juvenile salmon were not actually selected for and that the high LOR values resulted from lower surface trawl catch efficiencies for salmon at night (Krutzikowsky and Emmett 2005). We suspect that hake and mackerel ate primarily 0.0-age Chinook salmon, as opposed to other salmonids, because these salmon enter the ocean at a relatively small size (usually $\leq$120 mm FL) compared with 1.0-age Chinook and coho salmon (about 150 mm upon ocean entry; Dawley et al. 1986; Fisher and Pearcy 1988). We also suspect that no coho salmon were eaten by either predator because they are relatively large smolts and move out of the study area quickly or because coho salmon move very close to the surface at night (Krutzikowsky and Emmett 2005), which would reduce their availability to subsurface predators. More research needs to be conducted on the detailed vertical distribution of juvenile salmon during their first few months at sea.

If we divide the number of salmon observed in Pacific hake or jack mackerel per month (X_s) by the total number of stomachs analyzed (N_s) and multiply by the estimated abundance of Pacific hake or jack mackerel population (N_p) in the study area expanded over 30 d we can calculate a minimum estimate of the number of Chinook salmon eaten (C) by these two predators per month in the study area:

$$C = (X_s/N_s) \times N_p \times 30.$$

For Pacific hake we derived the following estimates for the number of juvenile salmon eaten: 7.42×10^5 in June 1998, 1.15×10^6 in May 2003, and 6.38×10^6 in July 2004. For jack mackerel the estimates were 1.21×10^5 in July 2003 and 4.42×10^5 in July 2004. The larger estimated numbers consumed by Pacific hake reflects their much larger population size. These estimates of juvenile salmonids eaten by Pacific hake and jack mackerel in the study area are relatively small compared with the number of smolts leaving Oregon and Washington rivers. Approximately 100 million salmon smolts (roughly half are 0-age Chinook salmon) leave the Columbia River annually (W. Muir, National Oceanic and Atmospheric Administration, Cook, Washington, personal communication). However, our estimates of Pacific hake and jack mackerel abundance and, thus, predation, are probably low. Our study area (and thus Pacific hake and mackerel population estimates) composed only a very small portion of juvenile salmonid habitat in the Northwest (see Brodeur et al. 2004, 2005). Furthermore, we considered only the area around the Columbia River, other areas, especially north along the Washington shelf, may have high predator densities. We also assumed a net efficiency of 1, which it probably is not true for either species. If net efficiency was ½ (i.e., ½ the fish in front of the net were actually caught), then our population and predation levels would double.

The food habit data indicate that Pacific hake and jack mackerel may not be a major source of juvenile salmon marine mortality off the Columbia River during most years. However, there is a relative strong negative relationship between Pacific hake densities off the Columbia River and juvenile salmon marine survival (Emmett et al. 2006), indicating that hake predation on salmonids may be important. It is possible that we did not identify hake and mackerel predation well during this study. For example, if hake and mackerel are finding and feeding on patches or concentrations of salmonids, and we did not sample at those areas and times, we could have missed a significant portion of the salmonid predation that was occurring.

We suspect that fish predation on salmon may be higher during warm years, when euphausiid abundance is probably lower off Oregon and Washington (Tanasichuk 1999, 2002; Mackas et al. 2001, 2004; Brinton and Townsend 2003). Future research should collect stomachs from predatory fishes in marine areas where juvenile salmon are known to congregate and should also document euphausiid abundance. There are also other large fish predators, such as the jumbo squid *Dosicdicus gigas*, known to be common off the Northwest coast during warm periods (Cosgrove 2005), that we did not effectively capture in our surface trawl. Additional sampling techniques should be used to collect other juvenile salmonid predators in the marine environment (e.g., gill net, hook and line, purse seine and paired trawl).

Predators are known to affect prey resources, especially when prey resources are low (Krebs 1978). In Canadian waters, Pacific hake feeding had a significant effect on Pacific herring abundance (Ware and McFarlane 1995). Our data indicates that Pacific hake may affect the abundance of northern anchovy, whitebait smelt, and possibly Pacific herring off Oregon and Washington. Pacific hake positively selected northern anchovy and whitebait smelt during most months and years. In 1998, when Pacific hake densities in the study area were very large, these and other forage fish populations were extremely low, but Pacific hake still consumed relatively large numbers of anchovy. We estimate that in May 1998 alone, Pacific hake consumed over 3.5×10^8 northern anchovy in the study area. In 1999, however, Pacific hake densities were low, and they consumed few anchovy; 1 year later anchovy densities increased. By 2003, after 3 years of low Pacific hake and jack mackerel predation pressure, anchovy and other forage fish numbers were about two orders of magnitude greater (Emmett et al. 2006). In spring 2003, Pacific hake again became abundant, and northern anchovy densities quickly declined that summer (unpublished data). A similar decline in northern anchovy and forage fish abundance occurred when Pacific chub mackerel *Scomber japonicus* and jack mackerel became abundant off Oregon in 1983–1984 (Emmett and Brodeur 2000). These were also years of poor salmon ocean survival, supporting Pearcy's (1992) hypothesis that forage fish play an important role for juvenile salmonids by acting as alternative prey. Avian predation on juvenile salmonids in the Columbia River estuary also tends to decline as forage fishes become more abundant (D. Lyons and D. Roby, Oregon State University, Department of Fish and Wildlife, personal communication).

The feeding selectivity analysis indicated that Pacific hake and jack mackerel are very selective fish feeders, eating certain fish prey either at amounts much greater or much less than its prevalence in the local environment. However, our analysis assumed that the surface trawl catches adequately reflected what hake and mackerel saw as available prey. This assumption may not hold for all potential prey under all conditions. First, the trawl probably does not catch all sizes of fishes with equal efficiency, and second, turbidity and light are known to strongly affect predatory fish reaction distances (De Robertis et al. 2003; Mazur and Beauchamp 2003). Unfortunately, we were unable to address these factors during our study. Nevertheless, the relatively consistent positive and negative selection of some fish species by hake and mackerel supports the argument that these predators are actively selecting specific fish prey.

Pacific hake off Canada and the Columbia River consume primarily adult euphausiids. In Canada, the consumption of euphausiids by hake did not measurably affect euphausiid populations (Tanasichuk 1999, 2002). However, Tanasichuk (2002) noted that if Pacific hake and Pacific herring diets were combined, euphausiid populations could have been affected by their feeding. In our study area, besides finding euphausiids in Pacific hake stomachs, we also found euphausiids in the stomachs of jack and chub mackerel, Pacific herring, northern anchovy, Pacific sardine, and whitebait smelt (R. Emmett, personal observation). Unfortunately we did not undertake systematic food habit studies of all these species, nor did we sample the euphausiid populations. However, we suspect the combined effect of lower ocean productivity and increased fish predation during the 1998 El Niño and the warm, poor upwelling years (2003 and 2004) could have decreased euphausiid abundance. The decrease in euphausiids has large ecosystem consequences, one of which is to encourage Pacific hake and jack mackerel to move nearshore where they are more likely to feed on fishes (Benson et al. 2002). During the El Niño year of 1998, hake showed relative high percentage of empty stomachs (Figure 4) and consumed fewer fish prey compared with other years. Nelson (2004) found that Pacific hake less than 50 mm FL (taken from the bottom and midwater) ate fewer euphausiids in 1998, but the diet of larger hake, which ate mostly fishes, was relatively unaffected.

Besides being predators, Pacific hake and jack mackerel may also be food competitors with juvenile salmonids because euphausiids and small fishes are also important prey for juvenile salmonids off Oregon (Peterson et al. 1982; Emmett et al. 1986; Brodeur and Pearcy 1990; Schabetsberger et al. 2003). High densities of Pacific hake, as we observed 1998, 2003, and 2004, may have not only increased predation rates on salmonids directly, but also indirectly, by reducing salmonid food supply and thus growth rates, ultimately lengthening the time the salmonids are available to size-selective predators. As stated earlier, juvenile salmonids differ from forage fishes in that they do not undertake diel vertical migrations (Emmett et al. 2004) but have a life history strategy of outgrowing predation by actively feeding during daylight hours (Schabetsberger et al. 2003; Railsback et al. 2005).

Although still in dispute, there are studies indicating that marine predators can control the abundance of prey populations and community structure (Pace et al. 1999; Worm and Myers 2003). We were unable to directly show that predation by Pacific hake and jack mackerel caused any appreciable decrease in the euphausiid and forage fish populations off the Columbia River region. This would have required additional information on euphausiid and forage fish population dynamics. Nevertheless, the large changes in forage fish densities off Oregon observed from 1998 through 2003 (Emmett et al. 2006) appear to be related, at least in part, to fluctuations in predatory fish densities. The abundance of forage fishes and euphausiids in the Pacific Northwest undoubtedly affects upper trophic levels in the northern California Current ecosystem. Future research should attempt to collect simultaneous information on the abundance and feeding habits of Pacific hake and jack mackerel for a series of 24-h periods, collecting fish and prey from their daytime deepwater to surface habitats. These data would provide valuable information on total amount of prey consumed and whether fish and can exercise top–down control of forage fish and euphausiids populations.

Mills et al. (2007) found that top predator diets are useful indicators of rockfish recruitment off California. We suggest that adult Pacific hake and jack mackerel nocturnal diets are useful indicators of rockfish and Pacific hake recruitment off Oregon. The occurrence of age-0 Pacific hake in jack mackerel stomachs (2004) and adult Pacific hake stomachs (1998 and 2004) provided independent confirmation that Pacific hake spawned and recruited off Oregon in those years because it is unlikely that juveniles of their size could have been transported that far north from the normal spawning grounds off southern California. The occurrence of age-0 rockfish in jack mackerel stomachs (1999, 2000, and 2004) indicated that rockfish recruitment was relatively good during those years. However, it is also possible that survival of rockfish larvae can be hindered by pelagic fish feeding, as gadids were in the Georges Bank ecosystem (Garrison et al. 2000) or Pacific herring were on the west coast of Canada (Ware and McFarlane 1995). Because nearly all Pacific Northwest marine fishes have pelagic life stages, future research should attempt to identify whether the feeding of pelagic fishes affects recruitment processes of other fishes. This could be accomplished by establishing a long-term pelagic fish abundance and stomach analysis program, which could be used in a multispecies virtual population analysis model (Livingston and Jurado-Molina 2000; Tsou and Collie 2001) to estimate the effects of predation on recruitment of Pacific Northwest fishes and euphausiids.

The nocturnal feeding of Pacific hake and jack mackerel off the Columbia River varied significantly within and among years (1998–2004). Pacific hake ate mostly euphausiids, but fishes were very important, especially during warm ocean years (1998, 2003, and 2004). Both hake and mackerel rarely ate juvenile salmonids, but feeding by these species could have substantial impact because of their large population sizes. However, predation by hake and mackerel on juvenile salmon did not appear to account directly for the majority of juvenile salmon marine mortality off the Columbia River. Additional research needs to be conducted in other coastal areas where predation impacts on juvenile salmon by predatory fishes may be more significant (e.g., as juvenile salmon move from the turbid Columbia river plume environment to usually less turbid coastal waters).

During years when Pacific hake and jack mackerel are abundant, their feeding could significantly reduce the abundance of euphausiid and forage fishes. This, in turn, could reduce juvenile salmonid growth rates, thereby effectively increasing their predation rates. Future work should continue to monitor and fully quantify these predator–competitor–prey relationships, utilizing nighttime predator stomach samples.

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