

STOMACH CONTENTS AND FOOD CONSUMPTION ESTIMATES OF PACIFIC HAKE, *MERLUCCIIUS PRODUCTUS*¹

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ABSTRACT

Analysis of 466 stomachs of Pacific hake, *Merluccius productus*, collected during August 1983 off the coasts of Washington and Oregon indicates euphausiids comprise the most important food resource in terms of percent by weight, numbers, and frequency of occurrence for the species at that time of year. The importance of fish in the Pacific hake diet increases with the size of the hake, constituting 87% of the diet by weight in the largest individuals. Weak evidence of a nocturnal feeding pattern was observed. This indistinct nocturnal feeding pattern could have been caused by poor food availability due to El Niño. Estimates of food consumption by Pacific hake indicate that this species may have a substantial impact on some commercially valuable species such as pink shrimp, *Pandalus jordani*, even though pink shrimp is a fairly minor component of the diet. A statistically significant negative relationship between Pacific hake catch-per-unit-effort (CPUE) and pink shrimp CPUE off the west coast of the United States, using a lag of 2 years, was found.

Pacific hake, *Merluccius productus*, constitute an important component of the California Current ecosystem off the west coast of North America. It is estimated that a standing stock of approximately 1.5 million metric tons (t) exists off the Pacific coast between central California and Vancouver Island (Bailey et al. 1982). This biomass represents a substantial prey base for a variety of fish in the ecosystem: great white sharks, *Carcharodon carcharias*; soupfin sharks, *Galeorhinus zyopterus*; Pacific electric ray, *Torpedo californica*; bonito, *Sarda chiliensis*; albacore, *Thunnus alalunga*; bluefin tuna, *Thunnus thynnus*; rockfishes, *Sebastes* spp.; sablefish, *Anoplopoma fimbria*; lingcod, *Ophiodon elongatus*; dogfish, *Squalus acanthias*; and arrowtooth flounder, *Atheresthes stomias* (Bailey et al. 1982). Pacific hake also constitute a major prey item for a number of marine mammals, including the California sea lion, *Zalophus californianus*; northern sea lion, *Eumetopias jubatus*; northern fur seal, *Callorhinus ursinus*; saddleback dolphin, *Delphinus delphis*; Pacific whiteside dolphin, *Lagenorhynchus obliquidens*; and northern right whale dolphin, *Lissodelphis borealis* (Fiscus 1979).

Pacific hake also have an important impact on species below them in the food chain. Best (1963) described Pacific hake as opportunistic feeders. Their diet includes numerous species of crustacea, particularly euphausiids, several genera of shrimp, crab megalopae, and a variety of fish including Pacific herring, *Clupea harengus pallasi*; rockfish; sablefish; and flatfish (Livingston 1983). Pacific hake may compete for food resources with a host of other species that feed on the abundant euphausiid resource (Tyler and Percy 1975; Karpov and Cailliet 1978; Brodeur and Percy 1984), including commercially prized salmonids (Peterson et al. 1982).

At the top of the trophic structure is the commercial fishing fleet, comprised mainly of foreign joint-venture fishing boats that have harvested, on average, 127,000 t of Pacific hake per year since 1966 (R. C. Francis⁴).

Pacific hake migrate seasonally along the west coast of North America (Swartzman et al. 1983) and spawn in winter in the warm waters off southern California and the Baja peninsula. During the spring and summer, the adults migrate as far north as Vancouver Island to feed. The Pacific hake tend to stratify along the coast by size, with the largest individuals traveling farthest from the spawning areas and smaller juveniles remaining off the coast of California. In autumn, the adults return to the southern spawning areas (Bailey et al. 1982).

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⁴R. C. Francis, Fisheries Research Institute, University of Washington, Seattle, WA 98195, pers. commun. May 1985.

The pink shrimp, *Pandalus jordani*, fishery off Oregon was one of the most economically viable fisheries during the late 1970s with landings in excess of 26,000 t in 1978. Subsequent to that time, pink shrimp landings have declined, with slightly over 2,000 t being landed in 1984 (Saelens and Zirges 1985). The purpose of this study was to describe the dietary habits of the Pacific hake and, in particular, to determine whether predation by Pacific hake on pink shrimp could explain some of the fluctuations seen in pink shrimp landings.

MATERIALS AND METHODS

In August and September 1983, during the National Marine Fisheries Service (NMFS) West Coast Groundfish Survey, Pacific hake stomachs were sampled from 41 hauls taken during daylight hours between Coos Bay, OR, and Grays Harbor, WA (Fig. 1). Tows were of 0.5-h duration using a Nor'easter[®] high-opening bottom trawl equipped with roller gear which has an approximate horizontal opening of 13.4 m and vertical opening of 8.8 m. Further details of the sampling regime can be found in Gunderson and Sample (1980) and Weinberg et al. (1984). Between 5 and 15 individuals of each sex from a 5 cm size class (30-34 cm, 35-39 cm, 40-44 cm, 45-49 cm, 50-54 cm, 55+ cm) were sampled from each haul where practical. A total of 466 stomachs were extracted at sea and placed in cheesecloth bags. Stomachs with evidence of regurgitated contents were not included in the sample. Stomachs were preserved in a 10:1 solution of seawater to Formalin.

Stomach Content Analysis

In the laboratory, stomachs were transferred to ethyl alcohol and examined under a dissecting microscope. Stomach fullness and degree of digestion were visually estimated and given a qualitative rating (0-4 from empty to distended, and from unrecognizable to recently consumed). Contents were identified to the lowest taxon and enumerated. Wet weight of each taxon was also determined.

Diet composition was characterized by percent of total number of food items (%*N*), percent of total diet by weight (%*W*), and frequency of occurrence in nonempty stomachs (FO). An index of relative importance (IRI) was then derived from these values $IRI = FO (\%N + \%W)$ (Pinkas et al. 1971).

The data were further stratified by sex, time of

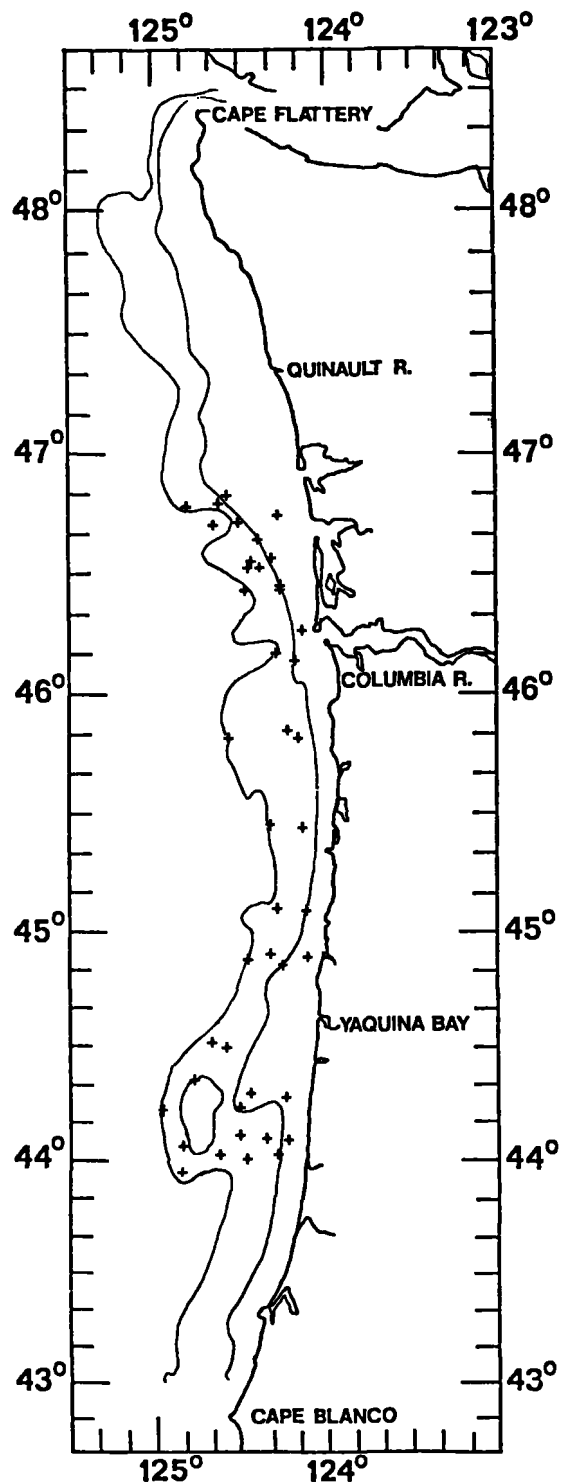


FIGURE 1.—Stations where Pacific hake stomachs were taken during 1983 NMFS West Coast Groundfish Survey; 100 and 200 m isobaths are also shown.

[®]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

collection (morning, afternoon, and evening), depth of capture (0-100 m, 100-200 m, >200 m), and size. Chi-square tests of homogeneity (Ostle and Mensing 1975) were performed on the frequency of occurrence data for each prey species in these categories.

Consumption Estimates

Using the size-specific prey consumption information derived from this study, Pacific hake population abundance estimates from the 1983 NMFS survey (Weinberg et al. 1984; Francis fn. 4) and bioenergetics estimates from Francis (1983), trophic calculations were performed to estimate ecosystem-level impacts of prey consumption by Pacific hake in the Columbia INPFC (International North Pacific Fisheries Commission) statistical area in 1983.

Biomass estimates were derived from two distinct surveys. The bottom trawl survey estimated the benthic component of the population. Details of these estimates can be found in Weinberg et al. (1984). The pelagic component of the population was estimated by hydroacoustic methods. Size composition of the pelagic segment of the population was estimated from companion midwater trawls conducted from the hydroacoustic vessel. Biomass estimates for each of the five size classes sampled were determined from estimated numbers in each centimeter size interval and length-weight regressions (Francis fn. 4).

Using a mean body weight for each size class, the percent of total body weight consumed daily was calculated based on the equations of Francis (1983). This total biomass consumption was then broken down into the constituent prey categories found in the stomachs of fish sampled using the percent of the diet by weight. These calculations were repeated for each of the five classes, and both the pelagic and benthic components of the population, to derive daily consumption estimates.

Residence times provided by Francis (1983) for each age class within each statistical area were converted to residence time by size class to account for the migratory behavior of Pacific hake. This provided consumption rate estimates summed over the length of time Pacific hake are found in the Columbia statistical area. An example of the calculations used to estimate total consumption of each prey item category is shown in Table 1.

Pacific Hake-Pink Shrimp Interaction

The relationship between the abundance of Pacific hake and pink shrimp was examined via regression

TABLE 1.—Calculations used to compute total consumption of *Thysanoessa spinifera*. Column E1 = $A \times B/100 \times C/100$. Column E2 = $E1 \times D$. Biomass is combined benthic and pelagic components of the population, BWD is percent body weight consumed per day, W is percent of the diet by weight composed of *T. spinifera*, and Days is number of days each size class resides in the Columbia INPFC Area. Note total biomass differs from value given in text due to biomass of population <35 cm in length.

Size class (cm)	(A)	(B)	(C)	(D)	(E1) (E2) Consumption	
	Biomass (1,000 t)	%BWD	%W	Days	Daily (1,000 t)	Seasonal (1,000 t)
35-39	331.252	1.10	14.7	80	0.540	42.85
40-44	69.126	0.98	9.4	69	0.060	4.20
45-49	21.272	0.84	17.2	45	0.030	1.38
50-54	17.640	0.65	14.9	42	0.020	0.72
55+	8.936	0.40	6.4	41	0.002	0.09
Total	448.226				0.652	49.24

analysis. Data from Francis et al. (unpubl. data) on Pacific hake catches in U.S. waters from 1967 to 1982 were converted to catch per unit effort (CPUE) based on the number of days of effort of foreign stern-trawling factory ships (BMRTs). Pounds per hour of pink shrimp taken in the equivalent of single-rigged shrimp trawls (SRE) in California, Washington, and Oregon from 1968 to 1984 (Saelens and Zirges 1985) were used as the dependent variable in regression analyses.

Two regressions were performed. The first used hake CPUE in year i to predict shrimp CPUE in year i , while the second involved a 2-yr lag (i.e., Pacific hake CPUE in year i versus shrimp CPUE in year $i + 2$).

RESULTS

Stomach Content Analysis

A breakdown of the stomach contents by size class of Pacific hake is presented in Table 2. Euphausiids dominate the diet of small hake while decapods and fish become increasingly important as Pacific hake increase in size. Considering percent of the diet by weight, the importance of euphausiids monotonically decreases from 100 to 7.9% with increasing predator size. Likewise, the importance of fish rises from 0 to 87.1% with increasing predator size. Pink shrimp comprise only a minor portion of the diet, the largest percentage being 4.9% for the largest size class. Commercially important herring comprise nearly one-third of the diet of the larger size classes.

A previously unreported prey item, the ghost shrimp, *Callinassa* sp., appeared in the diet of the Pacific hake sampled in this study. These burrow-

TABLE 2.—Summary of stomach contents of *Merluccius productus* collected during the 1983 NMFS Pacific Coast Groundfish Survey. T = <0.1%.

Prey category	30-34 cm			35-39 cm			40-44 cm			45-49 cm			50-54 cm			>55 cm		
	FO ¹	%N ²	%W ³	FO	%N	%W	FO	%N	%W	FO	%N	%W	FO	%N	%W	FO	%N	%W
Euphausiacea																		
<i>Thysanoessa spinifera</i>	—	—	—	14.9	15.0	14.7	27.5	10.6	9.4	32.5	79.6	17.2	52.4	65.1	14.9	61.9	62.3	6.4
<i>Euphausia pacifica</i>	25.0	16.7	17.1	56.4	73.7	72.7	68.1	78.5	70.8	10.4	9.0	2.2	19.5	18.7	3.9	33.3	23.4	1.3
Unidentified	100.0	83.3	82.9	33.0	10.4	6.2	33.3	10.3	10.7	31.2	9.2	2.5	35.4	12.4	1.9	19.0	9.0	0.2
Decapoda																		
<i>Pandalus jordani</i>	—	—	—	1.1	T	0.2	—	—	—	1.3	0.1	0.1	—	—	—	19.0	2.3	4.9
<i>Sergestes similis</i>	—	—	—	2.1	0.7	2.9	5.8	0.3	2.5	—	—	—	—	—	—	—	—	—
<i>Pasiphaea pacifica</i>	—	—	—	—	—	—	1.5	T	2.0	—	—	—	—	—	—	14.3	1.5	0.4
<i>Crangon</i> sp.	—	—	—	—	—	—	—	—	—	2.6	0.1	0.2	4.9	1.1	12.0	—	—	—
<i>Callinassa</i> sp.	—	—	—	—	—	—	—	—	—	11.7	0.7	13.4	8.5	1.1	14.5	—	—	—
Osteichthyes																		
<i>Engraulis mordax</i>	—	—	—	—	—	—	—	—	—	1.3	0.1	1.5	2.4	0.3	2.7	—	—	—
<i>Clupea harengus</i>	—	—	—	—	—	—	2.9	0.1	3.8	3.9	0.2	34.7	3.7	0.2	28.4	—	—	—
<i>Thaleichthys pacificus</i>	—	—	—	—	—	—	1.4	T	0.6	9.1	0.4	23.0	1.2	0.1	T	—	—	—
Osmeridae	—	—	—	—	—	—	—	—	—	1.3	0.1	T	1.2	0.1	2.8	—	—	—
Gadidae	—	—	—	—	—	—	—	—	—	1.3	0.1	1.2	2.4	0.2	2.4	4.8	0.2	83.6
Pleuronectidae	—	—	—	—	—	—	—	—	—	1.3	0.2	0.1	2.4	0.2	14.5	9.5	0.6	3.4
Agonidae	—	—	—	—	—	—	—	—	—	—	—	—	1.2	0.1	0.4	—	—	—
Myctophidae	—	—	—	0.8	T	1.5	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified	—	—	—	5.3	0.2	1.8	5.8	0.2	0.3	9.1	0.4	3.6	7.3	0.5	1.8	14.3	0.6	0.1
Number of stomachs (empty)		11 (7)			120 (26)			97 (28)			118 (41)			93 (11)			27 (6)	
Number of prey items		6			2,006			2,029			1,921			1,206			478	
Weight of stomach contents (g)		0.4			77.0			78.0			376.5			319.3			293.0	

¹Frequency of occurrence in non-empty stomachs.²Percent of diet by number of items.³Percent of diet by weight of stomach contents.

ing animals were found in stomachs of Pacific hake taken at tows stations between 8.3 and 15.6 km (4.5 and 8.5 mi) offshore but not in immediate proximity to estuaries where ghost shrimp are most often found.

Chi-square tests (Table 3) illustrate the patterns in prey consumption by various stratifications of the data. There was little statistical difference in stomach contents of males compared with females. The analysis of prey categories by depth is essentially an inshore-offshore comparison as isobaths run roughly parallel to the coastline in the study area. Statistically significant differences were found in depth of capture for both species of euphausiids found in this study. *Thysanoessa spinifera* was more important in the diet of fish taken close to shore whereas *Euphausia pacifica* was important for fish taken further offshore. Eulachon, *Thaleichthys pacificus*, was found in stomachs more often in shallow waters than at depth. These animals, being anadromous, are often found in bays and estuaries, i.e., close to shore.

A significant difference exists in the presence of the two species of euphausiids in stomachs collected at different times of the day. The data collected in this study show that *T. spinifera* were seldom found in stomachs collected after 1600 h while *E. pacifica*

TABLE 3.—Chi-square analysis of difference in stomach content by prey category and various factors.

Prey category	Factor			
	Sex df = 1	Depth df = 2	Time df = 2	Size df = 4
<i>Thysanoessa spinifera</i>	2.48	15.65***	23.67***	36.69***
<i>Euphausia pacifica</i>	1.42	17.45***	6.23*	76.90***
<i>Pandalus jordani</i>	0.48	1.02	3.53	39.60***
<i>Sergestes similis</i>	0.02	28.07***	0.12	9.86*
<i>Pasiphaea pacifica</i>	0.80	17.47***	3.92	34.39***
<i>Crangon</i> sp.	0.02	6.40*	3.07	8.27
<i>Callinassa</i> sp.	0.05	3.69	9.14*	20.30***
<i>Engraulis mordax</i>	0.46	0.68	3.87	3.99
<i>Clupea harengus</i>	0.76	3.95	10.14**	4.30
<i>Thaleichthys pacificus</i>	0.72	9.35**	4.14	16.71**
Osmeridae	2.24	1.44	2.49	2.33
Gadidae	0.01	0.16	2.20	5.44
Pleuronectidae	4.55*	1.45	2.21	12.49*

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

were often found in stomachs collected during that time (Fig. 2a).

To further examine the diel feeding pattern of Pacific hake, the percent of all stomachs in each of two fullness categories (<25% full; >75% full) was calculated by time of day. A three-point moving average was computed for each fullness category, and the resulting averages plotted (Fig. 3). There

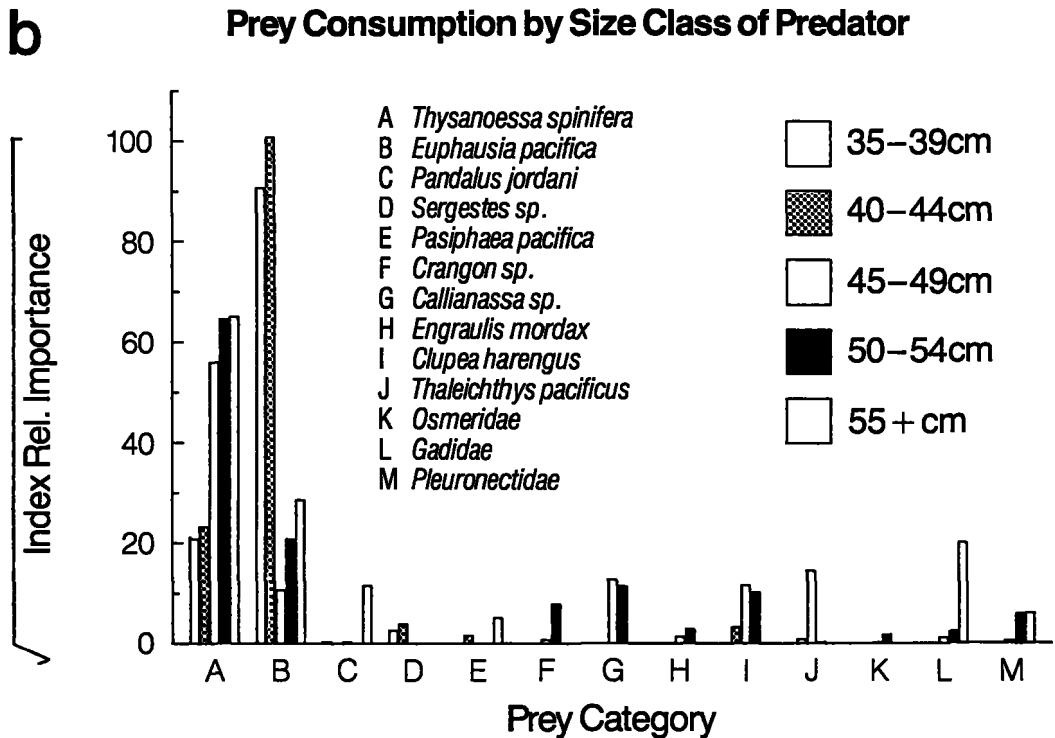
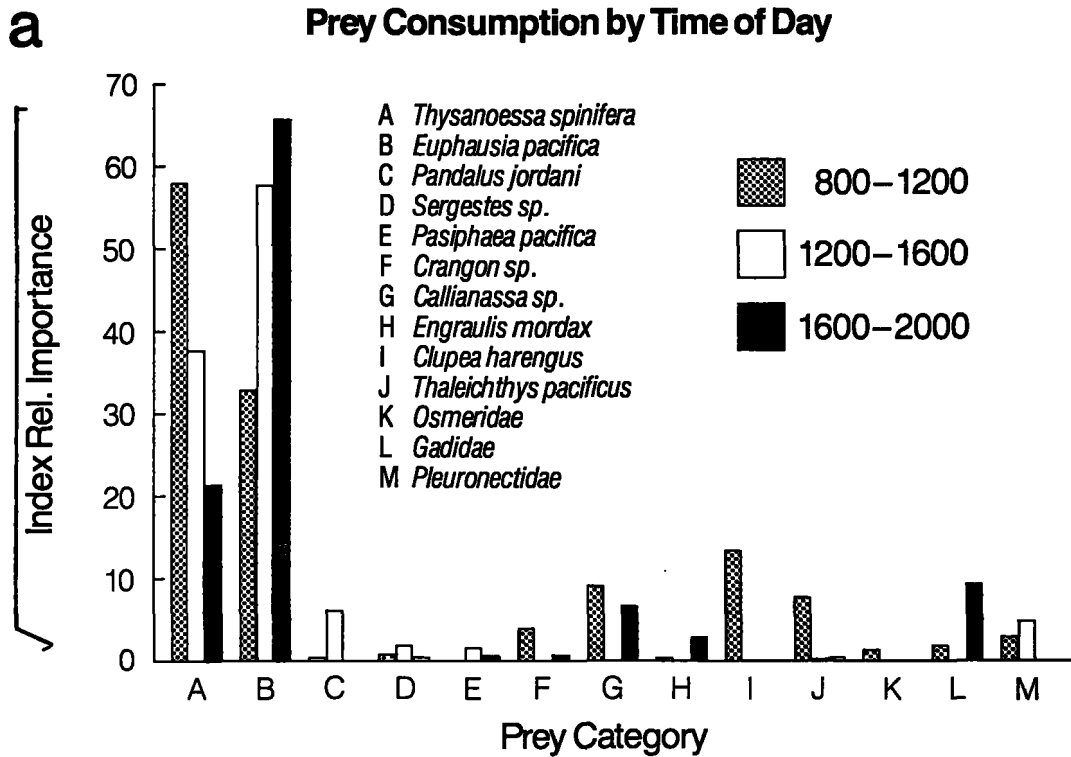


FIGURE 2.—Index of relative importance for major prey categories by a) time of collection and b) size of Pacific hake. Square root transformation used for scaling purposes.

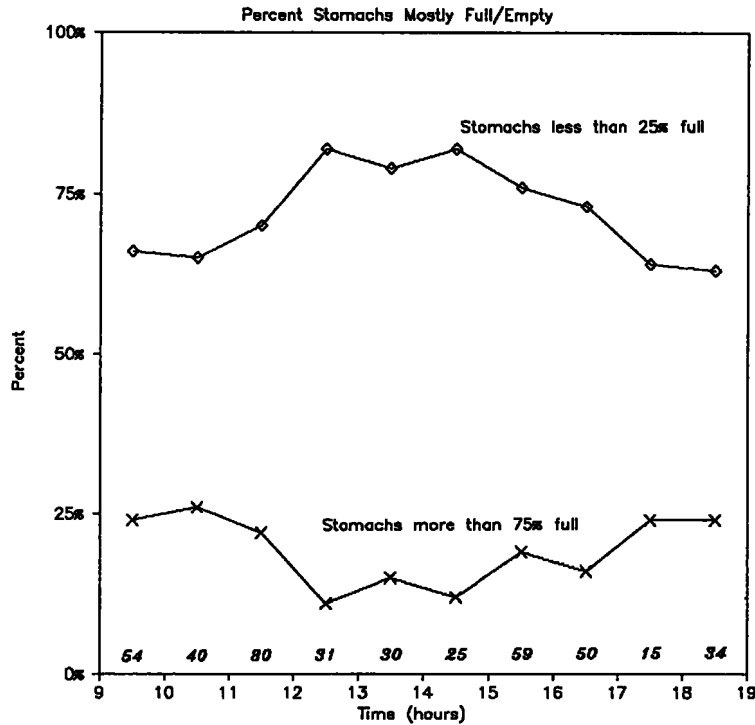


FIGURE 3.—Diel pattern of stomach contents of Pacific hake as demonstrated by percent of stomachs <25% full (upper curve) and >75% full (lower curve). Three-point moving average used to smooth the curves. Sample sizes shown above x-axis.

is a weak indication that these fish exhibit a pattern of feeding more heavily at night than during the day. For a predator feeding nocturnally, the expected pattern of this curve would be low percentages of empty stomachs early and late in the day, and high percentages of empty stomachs at midday. No tows were made between the hours of 2000 and 0700 thus direct evidence of nocturnal feeding was not available.

Comparison of stomach contents by size class showed the greatest amount of variation (Table 3, Fig. 2b) because of the shift in diet composition from euphausiids in early life stages to fishes in later stages.

The estimated consumption by Pacific hake in the Columbia statistical area over all prey categories is 4,651 t/d (Table 4). The amount of euphausiids consumed (over 4 kt/d), exceeds that of all other prey categories combined, but several commercially valuable species are also consumed in significant quantities. Consumption of pink shrimp is estimated at over 9.2 t/d, and almost 120 t/d of herring are consumed. Residence time for each size class of Pacific hake was derived from data presented by

Francis (1983) (size class 1: 80 d; size class 2: 69 d; size class 3: 45 d; size class 4: 42 d; and size class 5: 41 d) to extrapolate estimates of annual prey consumption from the daily consumption rate in the Columbia area. The annual consumption of pink shrimp, based on these data, is estimated at 659.3 t.

Pacific Hake-Pink Shrimp Interaction

The regression of Pacific hake CPUE versus pink shrimp CPUE resulted in a nonsignificant correlation ($r^2 = 0.114$, $df = 15$, $P = 0.185$). However, the regression performed with a 2-yr lag (hake CPUE in year i versus shrimp CPUE in year $i + 2$) showed a significant negative correlation between the variables ($r^2 = 0.418$, $df = 15$, $P = 0.005$). Note that the significance of the latter analysis stems largely from data obtained in recent years (Fig. 4).

DISCUSSION

One of the most striking patterns found in the data is the distinct change in diet composition that Pacific

TABLE 4.—Diet composition by size class on a daily basis (t) and on seasonal basis (kt). Values based on biomass for the Columbia INPFC area estimated from bottom trawl survey (Weinberg et al. 1984) and hydroacoustic survey (Francis, see text fn. 4). T = <0.1 t/d or 0.05 kt seasonally.

Prey category	Size 1		Size 2		Size 3		Size 4		Size 5		Totals	
	Daily	Season	Daily	Season	Daily	Season	Daily	Season	Daily	Season	Daily	Season
Euphausiacea												
<i>Thysanoessa spinifera</i>	535.1	42.5	64.0	4.4	30.6	1.4	17.2	0.7	2.3	.01	649.2	49.1
<i>Euphausia pacifica</i>	2,646.4	210.4	481.8	33.2	3.9	0.2	4.5	0.2	0.5	T	3,137.1	244.0
Unid. euphausiid	225.7	17.9	72.8	5.0	4.5	0.2	2.2	0.1	0.1	T	305.2	23.3
Total euphausiid	3,407.3	270.9	618.6	42.7	39.0	1.7	23.9	1.0	2.8	0.1	4,091.6	316.4
Decapoda												
<i>Pandalus jordani</i>	7.3	0.6	0.0	0.0	0.2	T	0.0	0.0	1.8	0.1	9.2	0.7
<i>Sergestes</i> sp.	105.8	8.4	17.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	122.6	9.6
<i>Pasiphaea pacifica</i>	0.0	0.0	13.6	0.9	0.0	0.0	0.0	0.0	0.1	T	13.8	1.0
<i>Crangon</i> sp.	0.0	0.0	0.0	0.0	0.4	T	13.8	0.6	0.0	0.0	14.2	0.6
<i>Callinassa</i> sp.	0.0	0.0	0.0	0.0	23.9	1.1	16.7	0.7	0.0	0.0	40.6	1.8
Osteichthyes												
<i>Engraulis mordax</i>	0.0	0.0	0.0	0.0	2.7	0.1	3.1	0.1	0.0	0.0	5.8	0.2
<i>Clupea harengus</i>	0.0	0.0	25.9	1.8	61.8	2.8	32.8	1.4	0.0	0.0	120.5	5.9
<i>Thaleichthys pacificus</i>	0.0	0.0	4.1	0.3	41.0	1.8	0.1	T	0.0	0.0	45.1	2.1
Omeridae	0.0	0.0	0.0	0.0	0.4	T	3.2	0.1	0.0	0.0	3.6	0.2
Gadidae	0.0	0.0	0.0	0.0	2.1	0.1	2.8	0.1	30.2	1.2	35.1	1.4
Pleuronectidae	0.0	0.0	0.0	0.0	0.2	T	16.7	0.7	1.2	0.1	18.1	0.8
Agonidae	0.0	0.0	0.0	0.0	0.0	0.0	0.5	T	0.0	0.0	0.5	T
Myctophidae	54.6	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	54.6	4.3
Unid. fish	65.5	5.2	2.0	0.1	6.4	0.3	2.1	0.1	T	T	76.1	5.7
Grand total	3,640.2	289.4	681.2	47.0	178.0	8.0	115.7	4.8	36.2	1.5	4,651.4	350.7

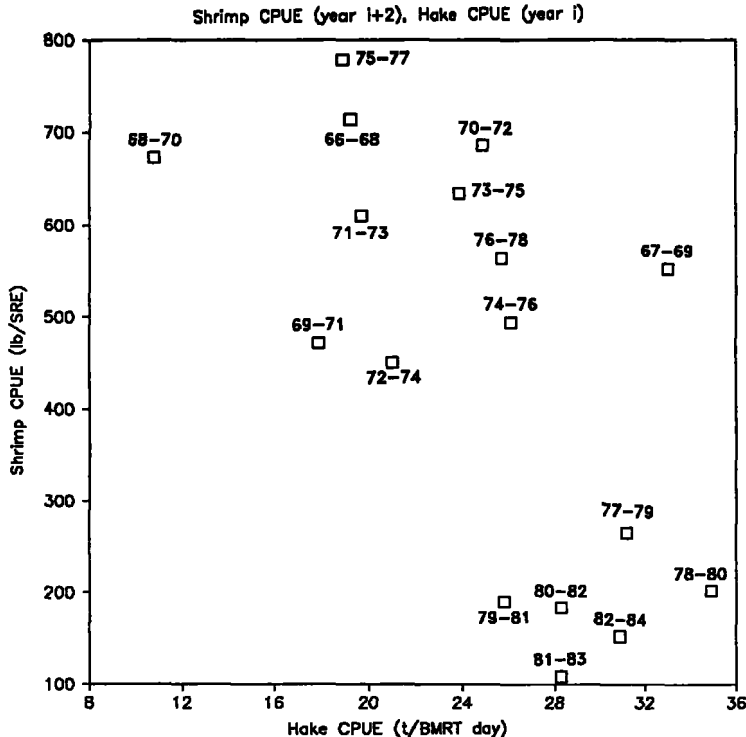


FIGURE 4.—Pink shrimp CPUE in year $i + 2$ (y -axis) plotted against Pacific hake CPUE in year i (x -axis). Regression expression is $y = 1029 - 23.23x$ ($r^2 = 0.418$). Numbers on the plot represent the years of the CPUE data.

hake undergo as they increase in size. *Thysanoessa spinifera* appears to be more important to larger hake whereas *Euphausia pacifica* is more important to smaller individuals. Pink shrimp and glass shrimp, *Pasiphaea pacifica*, were consumed almost exclusively by fish >55 cm. Eulachon and pleuronectids were also predominantly consumed by larger hake. Cannibalism was also observed among larger individuals.

Diel Feeding Pattern

A number of previous researchers have postulated that species in the genus *Merluccius* exhibit a diel feeding pattern (Outram and Haegle 1972; Bowman and Bowman 1980). Alton and Nelson (1970) as well as Livingston (1983) described Pacific hake as nocturnal predators that migrate vertically to feed near the surface during hours of darkness and dive to deeper water during daylight hours. Brinton (1967) and Alton and Blackburn (1972) showed that this same vertical migration pattern exists for the two species of euphausiids found in this study. If the Pacific hake follow the euphausiids on their vertical diel migration, the expectation is that the relative proportion of both species of euphausiids in the diet should not vary significantly by time of day. As reported above, our findings conflict with this expectation.

To further examine this apparent deviation, we considered potentially confounding factors; such as differences in the distributions of the euphausiid species and various size classes of Pacific hake. Brinton (1962) reported that *T. spinifera* is a neritic species and *E. pacifica* is a more oceanic species. Analysis of length-frequency data from the cruise during which this study was conducted shows that Pacific hake of different size classes segregate by depth. Pacific hake <40 cm in length made up 37% of the catch in <100 m of water, but these same size classes comprised 62% of the catch taken in >100 m of water. Hence, the smaller individuals were found in greater abundance in the habitat associated with *E. pacifica*.

This phenomenon of smaller fish occurring in deeper water and consequently consuming greater quantities of *E. pacifica* explains the apparent difference in importance of the two species of euphausiids by time of day (Fig. 2a). Only 7% of the non-empty stomachs taken before 1200 h were from fish <40 cm in length whereas of the fish sampled after 1600 h, 34% were <40 cm in length. Thus, we regard the observed differences in consumption of *T. spinifera* and increasing importance of *E. pacifica* by

time of day as spurious, confounded by the differences in the diets and distributions of various size classes of Pacific hake.

This study coincided with the strong presence of El Niño in 1983 which may have altered the normal migration pattern of Pacific hake and consequently the residence time estimates, and may also have affected the abundance of the prey base. Hence, there may be some error in the consumption estimates presented herein. Miller et al. (1984) noted a decline in the relative abundance of *T. spinifera* off the Oregon coast during 1983 in comparison with other years. Thus, feeding to satiation during evening hours may have been impossible; consequently, feeding occurred whenever euphausiids were encountered. Additional circumstantial evidence of aberrant feeding behavior of Pacific hake in 1983 is their severely depressed growth (Francis and Hollowed 1985). Food resources may only have been sufficient for maintenance metabolism with little energy remaining for growth. These observations may explain why the diel feeding pattern observed was weak.

Trophic Interaction

The seasonal migration pattern and consequent latitudinal stratification of Pacific hake stocks by size class makes it difficult to compare food habit studies conducted at different times of the year and at different locations on the Pacific coast. Nonetheless, examining only the role of pink shrimp in the diet, we find first mention of Pacific hake preying on this species by Gotshall (1969a, b). Analyzing Pacific hake stomachs collected off California between 1966 and 1969, Gotshall found high incidences (54% frequency of occurrence) of pink shrimp during late summer and early fall, particularly in Pacific hake collected over shrimp beds. The study was an attempt to use Pacific hake as biological samplers to estimate pink shrimp abundance, focusing sampling effort on known pink shrimp beds, and, as such, the sampling design was quite different from other studies.

Outram and Haegle (1972) reported that 3% of the Pacific hake stomachs collected off the coast of British Columbia contained pink shrimp. Pink shrimp were found in 5.7% of the Pacific hake stomachs collected during the summers of 1965 and 1966 off Washington and Oregon (Alton and Nelson 1970). Livingston and Alton (1982) found that pandalid shrimp constituted 0.3% by weight of the contents of the 1,430 stomachs of Pacific hake taken off the coasts of Washington and Oregon during the

summer of 1967. From 204 stomachs collected during the 1980 NMFS West Coast Groundfish Survey off the coasts from Oregon to Vancouver Island, Livingston (1983) found pink shrimp constituted 0.7% by weight of the Pacific hake diet. Pink shrimp occurred in 1.7% of the Pacific hake stomachs collected in the study described in this paper. Thus, with the exception of Gotshall's work, studies of the food habits of Pacific hake have shown pink shrimp generally comprise well under 10% of the Pacific hake diet, and thus do not appear to be an important food source for hake. However, due to the large biomass of Pacific hake in the North Pacific, it is possible that Pacific hake may represent a significant source of mortality even for those species, including pink shrimp, that are not significant components of the Pacific hake diet (Francis 1983).

The estimated consumption of 659.3 t/season of pink shrimp compares with a commercial catch of 2,197 t of pink shrimp landed in Oregon during 1984 by 59 vessels (Saelens and Zirges 1985). It is conceivable that the magnitude of Pacific hake predation on pink shrimp may increase in the near future. Small Pacific hake, preying mainly on euphausiids, constituted the bulk of the consumers in this study. The strong 1980 year class of Pacific hake, seen as the 35-39 cm size class in these 1983 data, will have substantially greater impact on commercially valuable species upon reaching larger sizes when these valuable species comprise a larger fraction of the diet.

Francis (1983) inferred, from catch statistics of Pacific hake and pink shrimp, that increased catches of Pacific hake since the inception of the foreign and subsequent joint-venture fisheries may have contributed to the dramatic increase in the landings of pink shrimp during the late 1970s. The causal mechanism inferred is the release of predation pressure on the pink shrimp population as a result of decreased Pacific hake abundance due to fishing. This "surplus" in the pink shrimp population was harvested by the increasingly vigorous shrimp fishery.

This contention is disputed by Livingston and Bailey (1985). Their analysis focuses on pink shrimp CPUE during two time periods: 1952-65 during which Pacific hake were unexploited and 1966-77 during which a substantial joint-venture fishery occurred. They found no appreciable change in average pink shrimp CPUE between the two periods. Extending their analysis to include the most recent catch statistics, we also fail to find the existence of a significant difference between the periods 1957-65 and 1966-84 ($t = 1.05$, 26 df, $P = 0.303$).

However, if pink shrimp have constituted a fairly constant proportion of the Pacific hake diet over time, as suggested by this and previous Pacific hake food habit studies, then there may indeed be a relationship between the release of predator pressure by the Pacific hake and increased catches of pink shrimp. The regression-correlation analysis presented above has an advantage over the average pink shrimp CPUE analysis because it incorporates information about both hake and shrimp abundances. The regression-correlation results provide weak statistical support to Francis' contention that there is a relationship between Pacific hake and pink shrimp population dynamics. However, further observations are needed to obtain greater confidence in this relationship. In particular, it will be interesting to note that the impact of the strong 1980 year class Pacific hake on pink shrimp catches in the near future.

CONCLUSION

Pacific hake occupy a unique trophic position, serving not only as predators but also as prey for a variety of species carrying valuations other than those of an economic nature (endangered species and species managed under the Marine Mammal Protection Act). Euphausiids constitute the primary source of food for Pacific hake in the North Pacific. However, as Pacific hake mature, euphausiids decrease in importance and fish take on greater importance. Owing to the vast quantity of hake biomass living in the North Pacific, it has been shown that Pacific hake may consume large quantities of several commercially valuable species, even though these species comprise a fairly small percentage of the diet. It has also been demonstrated that a statistically significant relationship exists between CPUE of Pacific hake and pink shrimp. Additional years of data are required to have a clearer understanding of this relationship.

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