GEOGRAPHIC VARIATION IN THE DIET OF PACIFIC HAKE, WITH A NOTE ON CANNIBALISM

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ABSTRACT

We examined the stomach contents of Pacific hake collected from the Southern California Bight to Vancouver Island. Samples were taken during bottom trawl surveys in 1989, 1991, and 1992 and during a midwater trawl survey in 1995. We found increasing piscivory with size, and gross variation in the diet with latitude and season. Cannibalism by adults on juvenile (age 1 and young-of-the-year) Pacific hake was found in autumn 1992 south of Cape Mendocino. In summer 1995, we found adult cannibalism on juveniles (especially age 1) along the entire coast and cannibalism by age-1 on young-of-the-year Pacific hake between 33° and 36°N latitude. We discuss some of the implications of cannibalism by adjacent cohorts.

INTRODUCTION

Pacific hake (*Merluccius productus*), also known as Pacific whiting, is the largest single groundfish resource found off the U.S. Pacific coast (Dark and Wilkins 1994). Ecologically, Pacific hake is one of the most important fish species in the California Current ecosystem (Francis 1983; Livingston and Bailey 1985). Because of its large biomass, Pacific hake's predatory impact on some commercially important species can be extensive (Gotshall 1969; Francis 1983; Livingston and Bailey 1985; Rexstad and Pikitch 1986). Pacific hake preys on euphausiids, swimming crabs, pandalid shrimp, squid, schooling baitfish, and juvenile fishes, and is itself an important prey of birds, tunas, sharks, groundfish, and marine mammals (Best 1963; Livingston and Bailey 1985; Rexstad and Pikitch 1986).

Feeding habits of Pacific hake have been investigated because of their potential importance to other stocks (Livingston and Bailey 1985; Rexstad and Pikitch 1986). Quantitative assessments of the Pacific hake diet have been conducted off Vancouver Island, British Columbia (Outram and Haegele 1972; Livingston 1983; Tanasichuk et al. 1991); Washington and Oregon (Alton and Nelson 1970; Livingston 1983; Rexstad and Pikitch 1986; Brodeur et al. 1987); northern California (Gotshall 1969; Livingston 1983); and, for larvae only, southern California (Sumida and Moser 1980). The food habits of juvenile and adult Pacific hake off central and southern California have not been the object of any intensive study. However, Best (1963) gives a list of common prey from observations in California waters, and Mearns et al. (1981) present the percent of total indices of relative importance (% IRI) for prey found in Pacific hake from the Southern California Bight.

Cannibalism by Pacific hake was noted only in the studies conducted in California waters (Best 1963; Mearns et al. 1981; 7.2% IRI). On the basis of migration patterns, overlapping distributions of large and small fish (a requisite for cannibalism) would be most likely off central and southern California, in late autumn, winter, and early spring (Francis 1983).

Our objectives were to (1) quantify the diet of Pacific hake, including samples from central and southern California, (2) examine variability in the diet by latitude, predator size, and season, and (3) describe the incidence of cannibalism in our samples and discuss some of its implications for determining year-class strength.

METHODS

Study Area

This study primarily encompasses the continental shelf and upper continental slope from Point Conception, California, to British Columbia. This broad latitudinal range extends over several statistical reporting areas of the International North Pacific Fisheries Commission (INPFC). These areas—Conception (U.S.–Mexico International Boundary to 36°00'N); Monterey (36°00' to 40°30'N); Eureka (40°30' to 43°00'N); Columbia (43°00' to 47°30'N); Vancouver (47°30' to 50°30'N); and Charlotte (50°30' to 54°30'N)—will frequently be referred to by name in this paper (figure 1).

Stomachs from Pacific hake were collected in these areas during three National Marine Fisheries Service bottom trawl surveys (figure 1). In 1989, the fifth triennial groundfish survey was conducted on the continental shelf (55–366 m, or 30–200 fm deep) from Point Conception, California, to central Vancouver Island, British Columbia (34°30' to 49°35'N) between July 7 and September 29 (Weinberg et al. 1994). From October 21 to November 18, 1991, a groundfish survey was conducted on the upper continental slope (550–732 m, or 300–400 fm deep) in the Columbia and Eureka statistical areas and on the shelf and slope (183–1,280 m, or

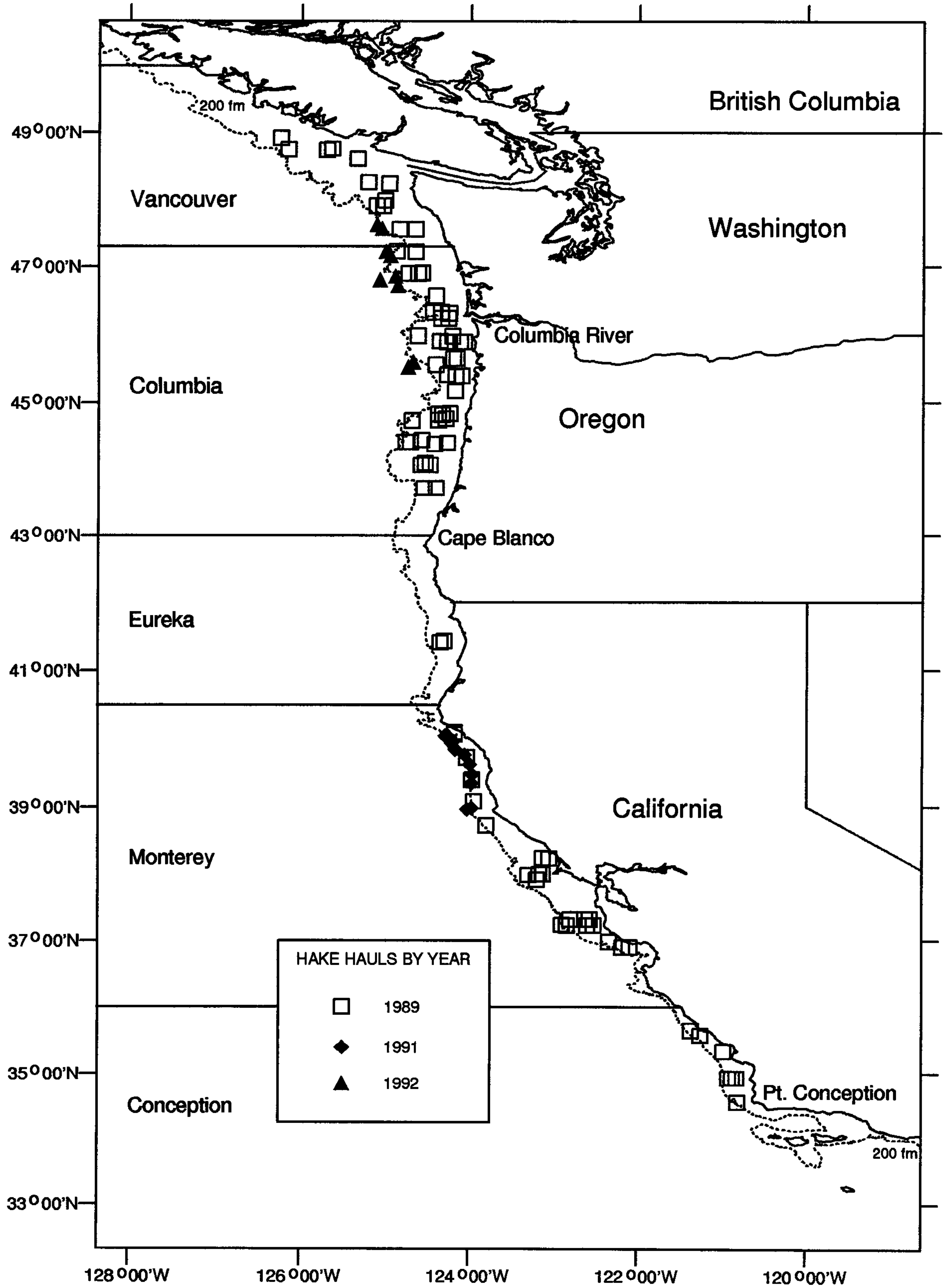

Figure 1. Haul locations of the 1989, 1991, and 1992 bottom trawl surveys where Pacific hake stomachs were collected. The 200-fm isobath is shown with a *dotted line*.

100–700 fm) in the Monterey statistical area. From October 16 to November 13, 1992, a groundfish survey was conducted on the continental shelf and slope (183–1,280 m, or 100–700 fm) in parts of the Vancouver and Columbia statistical areas.

Samples were also collected during the 1995 echo-integration trawl survey. Midwater and bottom trawls were made from July 1 to September 1, extending along the Pacific coast from the Southern California Bight to Dixon Entrance, Alaska (32°30' to 54°30'N; Wilson and Guttormsen 1997). Although these samples were collected as part of a forthcoming detailed study of euphausiid predation by Pacific hake relative to euphausiid abundance, the cannibalism observed in these samples warranted inclusion in this study.

Sample Collection

The buccal cavities of individual fish were examined for signs of regurgitation or net-feeding before the stomachs were removed. Fish with everted stomachs or partially digested prey in the mouth or gills were discarded. Fish with completely undigested prey in the mouth or protruding from the esophagus were discarded. After opening the body cavity, we discarded fish if the stomach appeared partially everted or flaccid (evidence of recent regurgitation). If a sample was discarded because of evidence of regurgitation or net-feeding, we replaced it with an acceptable sample that contained food.

Stomachs that met these collection criteria, including empty or near-empty stomachs, were placed in a cloth bag with a specimen tag indicating the species, sex, and fork length (FL) of the fish, and also the vessel, survey, haul, and specimen numbers. A maximum of 15 stomachs, from fish representative of the size composition caught, were collected per haul in 1989, 1991, and 1992. In 1995, a maximum of 15 stomachs were collected per 10-cm size-interval per haul. Stomach samples were preserved in 10% formalin. In the laboratory, samples were rinsed in water for 24 hours, then stored in 70% ethanol.

Stomach Content Analysis

In the laboratory, stomach samples were rinsed with water, and the contents were removed, blotted, and weighed to the nearest one-hundredth of a gram (one-tenth of a gram for the 1989 samples). Prey were identified to the lowest practical taxon. Two procedures were used to determine the prey composition of the stomach contents. For the samples collected in 1991, 1992, and 1995, the weight and number of prey in every taxon were recorded. For the samples collected in 1989, only the fish and crab prey were counted and weighed, and the contribution of the remaining taxa to the stomach contents was estimated as a percentage of the total volume of the contents. Whenever possible, the standard length (SL) of fish prey was measured and recorded to the nearest millimeter. Some of the stomach contents were identified as offal (discarded parts from commercial fish-processing operations); these were treated as a single prey type.

Data Analysis

To examine the diet variation by latitude and survey, we calculated the diet composition, by weight, for broad prey categories in each INPFC area covered during the 1989, 1991, and 1992 surveys. To examine the diet variation by predator size, we combined the data from the Vancouver and Columbia areas (North of Cape Blanco) and the Eureka, Monterey, and Conception areas (South of Cape Blanco). We chose to combine the areas in this fashion because of the diet similarities between the Vancouver and Columbia areas, and because of the regional physical and biological processes (U.S. GLOBEC 1994). The diet data were aggregated into broad prey categories for each 10-cm predator-length group, and the diet composition was presented by weight. The percent frequency of occurrence of cannibalism was calculated for each sampled haul in the 1995 survey.

RESULTS

A total of 1,334 Pacific hake stomachs were examined from the bottom trawl surveys (table 1). Of the 1,096 stomachs collected in the summer of 1989, 100 (9%) were empty. Seven (5%) of the 138 stomachs collected in the autumn of 1991 were empty, and 26 (26%) of the 100 stomachs collected farther north in the autumn of 1992 were empty.

The diet, by weight, of the Pacific hake sampled in the summer of 1989 was generally dominated by fishes, but euphausiids, mostly *Euphausia pacifica* and *Thysanoessa*

TABLE 1
Size Ranges of Pacific Hake and Number of Stomachs Sampled from Bottom Trawls by Year, Season, and Location

				No. examined	
Year	Season	INPFC area	Size range (cm)	Non-empty	Empty
1989	Summer	Vancouver	25–70	155	19
		Columbia	34–75	539	32
		Eureka	42–51	23	7
		Monterey	23–70	203	36
		Conception	10–58	76	6
1991	Autumn	Monterey	18–60	131	7
1992	Autumn	Vancouver	42–51	26	4
		Columbia	35–59	48	22
1995	Summer	Charlotte	44–56	75	8
		Vancouver	18–73	422	72
		Columbia	21–76	532	36
		Eureka	20–65	122	29
		Monterey	23–73	162	52
		Conception	3–56	108	12

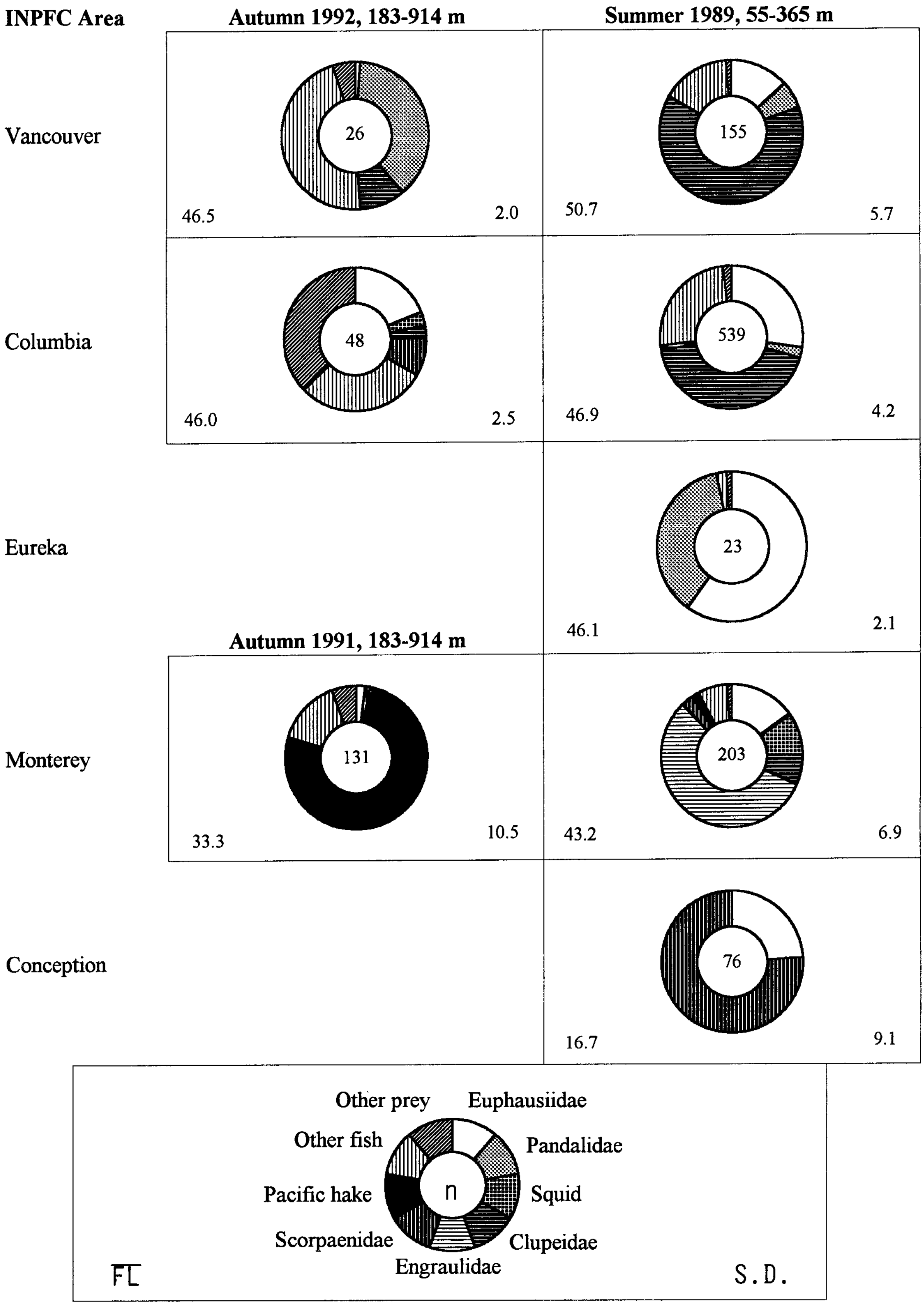

Figure 2. Diet composition (by weight) of Pacific hake by survey and INPFC area. The number of non-empty stomachs is shown in the center of each ring. Mean of the fork lengths is shown on the lower left of each box, standard deviation on the lower right.

spinifera, consistently contributed to the diet in all areas (figure 2). In the Conception INPFC area, shortbelly (*Sebastes jordani*) and stripetail (*S. saxicola*) rockfishes (Scorpaenidae) were important prey. Shortbelly and stripetail rockfishes were also eaten in the Monterey INPFC area, but northern anchovy (*Engraulis mordax*; Engraulidae) dominated the diet. In the Eureka INPFC area, euphausiids and pink shrimp (*Pandalus jordani*; Pandalidae) constituted nearly the entire diet. Pacific herring (*Clupea pallasi*, Clupeidae) was the most important diet component by weight in the Columbia and Vancouver INPFC areas. The "Other fish" category comprised mostly smelts (Osmeridae), including eulachon (*Thaleichthys pacificus*) and whitebait smelt (*Allosmerus elongatus*), contributing 21% of the Pacific hake diet in the Columbia INPFC area and 10% in the Vancouver area.

A broad size range of Pacific hake co-occurred in the Monterey INPFC area in autumn 1991, and a high level of cannibalism was found (figure 2). Although two incidents of cannibalism were found in that area in summer 1989, the diet of Pacific hake in autumn 1991 differed considerably from the diet in summer 1989. We found the same pattern of diet differences when restricting the analysis to comparable bottom depths (183–365 m) in each survey.

The diet of Pacific hake in autumn 1992 appeared different from that in summer 1989 in the Columbia and Vancouver INPFC areas (figure 2). In the Columbia area, sergestid shrimp made up most of the "Other prey" category, contributing 32% to the diet by weight; and the bathypelagic lightfishes (Gonostomatidae) and lanternfishes (Myctophidae) accounted for almost all of the "Other fish" by weight. Pacific saury (*Cololabis saira*), which are included in the "Other fish" category, and pink shrimp were very important in the Vancouver area.

Diet Variation with Predator Size

In the summer of 1989, euphausiids decreased in importance with increasing length of Pacific hake both north and south of Cape Blanco, and fishes increased (figure 3). As noted earlier, the fishes, by weight, were primarily Pacific herring north of Cape Blanco, and were mostly northern anchovy south of Cape Blanco. A similar pattern of increasing fish and decreasing euphausiid biomass in the diet was observed south of Cape Blanco in the Monterey area in autumn 1991. Cannibalism by larger Pacific hake was a main contributor to this pattern. The length frequency of the Pacific hake sampled north of Cape Blanco in autumn 1992 was too narrow to examine diet variability across a broad predator size range.

Cannibalism

In autumn 1991 a broad size range of Pacific hake co-occurred south of Cape Blanco in the Monterey INPFC area, and a high level of cannibalism was found (figure 2). Only larger Pacific hake (FL >40 cm) were cannibalistic (figure 3), and the frequency of occurrence of cannibalism was 39% for these larger fish (table 2). Many of the Pacific hake caught in the trawls were small juveniles, with modes at 18–19 and 23–29 cm FL, similar in length to the Pacific hake that were cannibalized. On the basis of growth rates of juvenile Pacific hake (Best 1963; Woodbury et al. 1995) the cannibalized hake are young-of-the-year (YOY) and small age-1 individuals. We found only two occurrences of cannibalism by large Pacific hake in the Monterey INPFC area during the summer of 1989.

TABLE 2
Percent Frequency of Occurrence (% FO) and Percent Weight (% W) in the Diet of Cannibalized Pacific Hake for Two Predator Size Groups in Surveys Where Cannibalism Was Found

Year	Season	Latitudinal range (N)	Predator size (cm FL)	Cannibalism % FO	Cannibalism % W
1989	Summer	34°30'–49°35'	>40	<1	<1
			≤40	0	0
1991	Autumn	36°00'–40°30'	>40	39	84
			≤40	0	0
1995	Summer	32°30'–54°30'	>40	5	30
			≤40	4	3

Cannibalism was found in many locations during the summer 1995 echo-integration trawl survey (figure 4), and two types of interaction were typical (figure 5). The first common interaction was cannibalism by adult Pacific hake on fish with lengths typical of age-1 individuals. There was also a single occurrence of an adult cannibalizing three YOY Pacific hake (figure 4; 44°00'N latitude). Cannibalism by large Pacific hake (FL >40 cm) was found over a wide latitudinal range (figure 4); contributed 30% to the diet by weight; and occurred with a frequency of 5%. Although rates of cannibalism by smaller Pacific hake (FL ≤40 cm) were lower (table 2; 3% W and 4% FO) than those of larger individuals, the most common interaction among these smaller fish was between juvenile Pacific hake (23–32 cm FL; mostly age-1) and YOY individuals (30–70 mm SL; figure 5). In the Conception INPFC area, cannibalism by age-1 Pacific hake on YOY hake accounted for 14% of the diet by weight and occurred with a frequency of 18%. Cannibalism by age-1 Pacific hake was not found north of the Conception area. The number of YOY in the stomachs of age-1 Pacific hake ranged from one to five.

DISCUSSION

Although there is a considerable literature describing the food habits of Pacific hake, comparisons among the studies are difficult because of the many variables involved (year, season, area, and fish size; table 3). In our

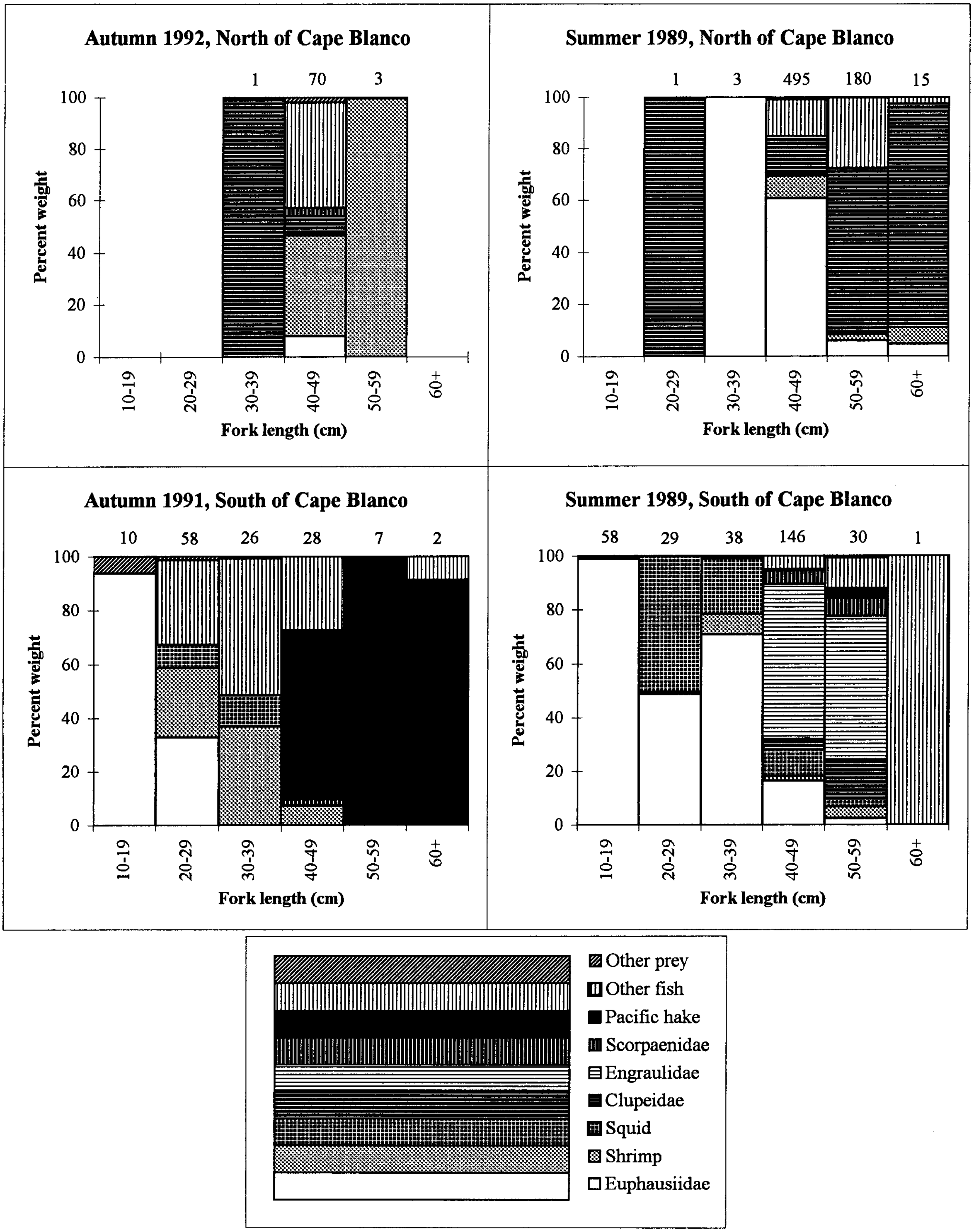

Figure 3. Diet composition (by weight) of Pacific hake length-groups from north of Cape Blanco (Vancouver and Columbia INPFC areas) in 1992 and 1989, and south of Cape Blanco in 1991 (Monterey INPFC area) and 1989 (Eureka, Monterey, and Conception INPFC areas).

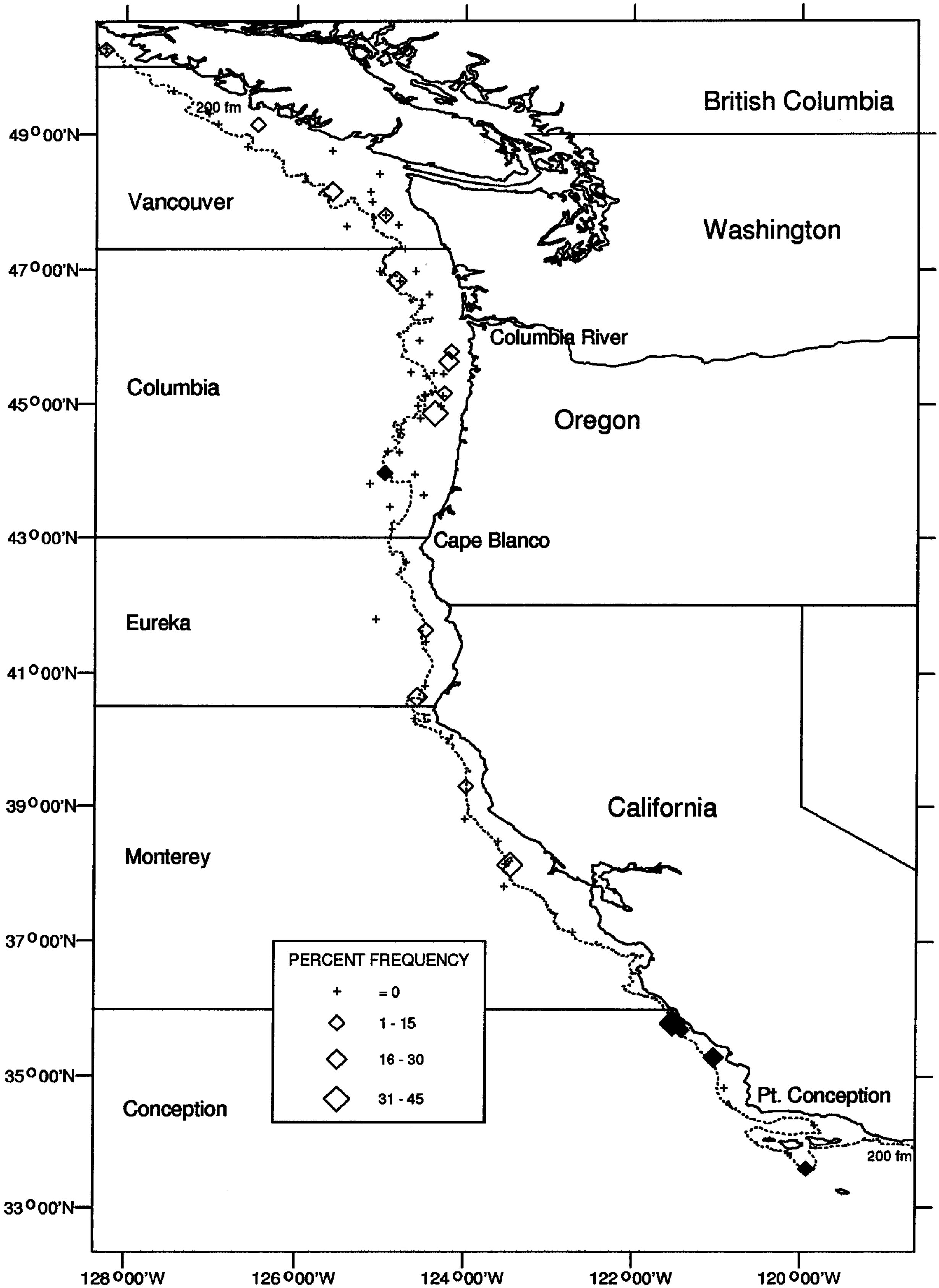

Figure 4. The percent frequency of occurrence of cannibalism by Pacific hake at each haul location where Pacific hake stomachs were collected in 1995. The *black diamonds* indicate cannibalism of YOY Pacific hake. The 200-fm isobath is shown with a *dotted line*.

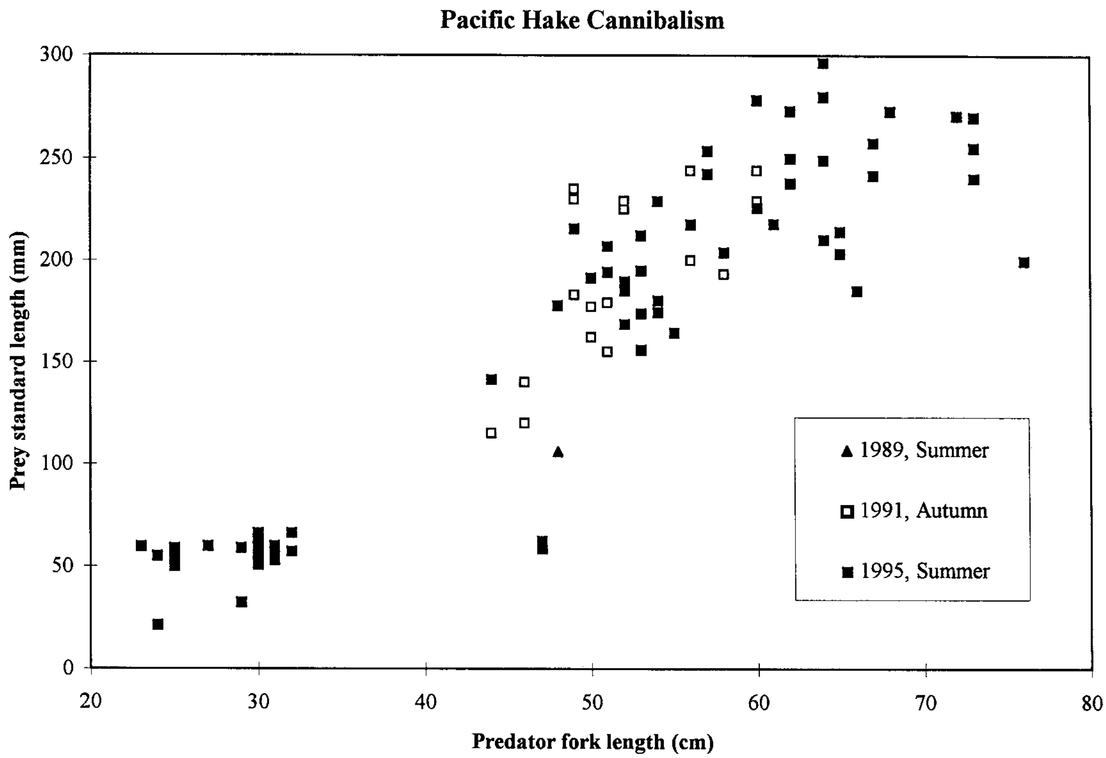

Figure 5. Scatterplot of prey size versus predator size in Pacific hake cannibalism from 1989, 1991, and 1995.

study, inferences about diet changes were limited because, in most cases, our samples were unique with respect to two or more of the following: year, season, area, depth, and fish size. Although we were able to cover a wide range of latitudes, water depths, and fish sizes in this study, stomach samples were not collected from Pacific hake feeding in water shallower than 55 m. In several years, adult hake have been seen gorging themselves on fishes schooling against the shoreline (De Witt 1952; Hobson and Howard 1989). This potentially important component in the feeding habits of Pacific hake remains poorly documented.

Pacific hake's reliance on euphausiids as a major food source in spring and summer is well known (Alton and Nelson 1970; Outram and Haegele 1972; Livingston 1983; Brodeur et al. 1987; Tanasichuk et al. 1991), as is their increasing piscivory with size (Livingston 1983; Livingston and Bailey 1985; Rexstad and Pikitch 1986; Tanasichuk et al. 1991). However, tremendous differences in diet composition can be found among these studies even when they cover the same geographic area. Although low sample sizes and differences in gear (purse seine, bottom trawl, or midwater trawl), sampling depth, and fish size may contribute to these differences, interannual variability may be the strongest influence. Interannual variability in the species composition of euphausiids in the diet can be dramatic, especially in strong El Niño years (Brodeur et al. 1987). The volumetric and gravimetric proportion of fish in the diet of Pacific hake can vary widely among years (Brodeur et al. 1987; Tanasichuk et al. 1991), and fish species that dominate the sampled diet in some years can be absent in other years (Livingston 1983; Brodeur et al. 1987).

Apparent latitudinal differences in the diet may be confounded by the size of the Pacific hake sampled (Livingston 1983; Livingston and Bailey 1985; Rexstad and Pikitch 1986). The average size of Pacific hake generally increases with latitude (figure 2) because of seasonal and size-dependent migrations (Francis 1983). However, latitudinal differences in diet composition were apparent for predator-length categories that occurred both north and south of Cape Blanco (figure 3; 40–49 cm FL and 50–59 cm FL). Pacific herring constituted a large proportion of the diet, by weight or volume, north of Cape Blanco in several other studies (Livingston 1983; Rexstad and Pikitch 1986; Tanasichuk et al. 1991), and sometimes occurs in the Pacific hake diet south of Cape Blanco (Gotshall 1969). Northern anchovy occurs in the diet of Pacific hake off California (Best 1963; Gotshall 1969) and dominated the weight of the diet south of Cape Blanco in this study. Although northern anchovy contributed little to the diet north of Cape Blanco in this study, it can be very important in some years (Livingston 1983; Brodeur et al. 1987).

TABLE 3
Summary of Literature on the Diet of Pacific Hake by Location

Study	Months[a]	Year	Gear type[b]	Size-range in cm[a]	Sample size
SW Vancouver Island					
Outram and Haegle 1972	Aug.	1970	MW&B	42–71	1,196
Tanasichuk et al. 1991[c]	Aug.–Sept.	1983	MW&B	(40–65+)	1,362
	Aug.	1985	MW&B		801
	Aug.	1986	MW&B		2,244
	Aug.	1987	MW&B		1,698
	Aug.	1988	MW&B		3,629
	Aug.	1989	MW&B		2,696
	July–Nov.	1987	MW		15,551
	June–Oct.	1988	MW		20,153
SW Vancouver Island and Washington					
Livingston 1983	Aug.–Sept.	1980	MW&B	45–65	111
Washington					
Alton and Nelson 1970	May, Aug.	1965	MW&B	(46–66)	119
	June–Sept.	1966	MW&B		245
Livingston 1983	May–July	1967	MW	49–50	1,228
Washington and Oregon					
Rexstad and Pikitch 1986	Aug.–Sept.	1983	B	30–55+	347
Brodeur et al. 1987	(May–Sept.)	1981	PS	(31–63)	28
		1982	PS		58
		1983	PS		10
		1984	PS		60
Oregon					
Livingston 1983	Apr.–July	1967	MW	49–50	202
	Apr.–May	1980	B	35–65	53
Northern California					
Gotshall 1969	July, Oct.–Dec.	1964	MW&B	10–82	212
	Mar.–Sept.	1965	MW&B	40–76	238
Livingston 1983	Oct.	1980	B	10–20	40
Southern California					
Best 1963	Unk	Unk	Unk	Juv–adult	100's
Sumida and Moser 1980	Mar.	1975	MW	0.3–1.1	208
Mearns et al. 1981	Unk	Unk	Unk	Unk	14

[a]Information in parentheses is for all samples combined.
[b]MW = midwater trawl; B = bottom trawl; PS = purse seine.
[c]Includes all Pacific hake examined (empty and non-empty) except those with everted stomachs.

The latitudinal pattern for pandalid shrimp, as a proportion of diet, by weight, in the summer of 1989 (figure 2), is similar to that found in other studies. Gotshall (1969) found that pandalid shrimp made up 44% of diet volume of Pacific hake in the Eureka INPFC area, whereas studies in the Columbia and Vancouver INPFC areas found pandalid shrimp to constitute 0–8% of the diet by weight (Alton and Nelson 1970; Livingston 1983; Rexstad and Pikitch 1986; Brodeur et al. 1987).

Because most surveys are conducted in summer, detailed seasonal changes in the diet of Pacific hake are not well documented. Brodeur et al. (1987) found that euphausiids were almost absent from the diet in May, but were the dominant prey, by weight, from June through September off the coasts of Oregon and Washington. The proportion of euphausiids, by volume, in the diet in the Vancouver INPFC area decreased from summer highs (June through August or September) to lower values in October and November (Tanasichuk et al. 1991). Our findings follow a similar pattern: in the summer (of 1989) euphausiids make up a higher percentage of the diet, by weight, than in the autumn (of 1991 and 1992; figure 2). This pattern remains when discrete size categories of Pacific hake are compared north and south of Cape Blanco (figure 3). However, the diet of juvenile Pacific hake (<20 cm FL) remained almost exclusively euphausiids in autumn 1991, similar to the diet observed by Livingston (1983) in October off California. Fishes are generally most important in the diet, by weight, in autumn (Gotshall 1969; Tanasichuk et al. 1991), winter (Gotshall 1969), and early spring (Gotshall 1969; Brodeur et al. 1987). Some observed seasonal changes in diet may be confounded by seasonal changes in size composition of the Pacific hake resulting from their seasonal migrations (Livingston 1983).

Cannibalism seems more common in the life history of Pacific hake than has been previously shown, and it may follow a seasonal pattern. We found a considerable degree of cannibalism south of Cape Blanco in the Monterey INPFC area in autumn 1991, but much less in summer 1989, even though a wide range of sizes were in the area. Although little can be inferred directly from this seasonal comparison from two different years, it is consistent with patterns in the importance of fishes in the diet and the degree of spatial overlap of adult and juvenile Pacific hake. Intracohort cannibalism by larvae (Sumida and Moser 1980) and larger YOY (9–12 cm TL predator; unpubl. data) occurs, but not frequently.

Interannual changes in the abundance of age-1 Pacific hake available to adults could also explain the differing amounts of cannibalism observed in 1989, 1991, and 1995. The relative abundance of age-1 Pacific hake in those years can be judged from estimates of year-class size in the Pacific hake stock assessment (Dorn 1996), which show that the 1988 year class was weak and the 1990 year class was moderately strong. The 1994 year class is just now being assessed, and indications are that it is the strongest year class of Pacific hake since 1984 (M. Dorn, pers. comm., Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115). Cannibalism rates of age-1 fish observed in our study reflect the same trends. Determining the effect of cannibalism on the population dynamics of Pacific hake will require more sampling to better quantify seasonal and interannual differences in cannibalism rates.

Smith (1995) suggested that the negative interannual autocorrelation, lagged 1 year, in Pacific hake recruitment may be evidence for adjacent-cohort cannibalism or another control (competition for food) on recruitment rate. The cannibalism on YOY Pacific hake by the preceding cohort documented in this study supports, but does not confirm, this hypothesized mechanism. Competition for food may also weaken a cohort that follows a successful one. The diet of very small (33–60 mm TL) YOY indicates an early reliance on euphausiids (55%–79% by weight; unpubl. data) as a food source, and euphausiids constitute the main diet of larger juvenile Pacific hake (Livingston 1983; figure 3 of this study). Although predatory and competitive interactions affecting juveniles may be of secondary importance in determining year-class strength (Bailey and Francis 1985), this study indicates that both processes may be occurring between age-1 and YOY Pacific hake within the critical three to five months after spawning. Quantifying the importance of these interactions between age-1 and YOY Pacific hake will require field sampling to determine the degree of their spatial overlap, analysis of their growth and bioenergetics, and a better understanding of the production and availability of their common prey.

ACKNOWLEDGMENTS

We thank Richard Wiggins for industrious laboratory assistance, and Douglas Smith for his help in preparing the manuscript. We are also grateful to many others who helped collect the stomach samples.

LITERATURE CITED

Alton, M. S., and M. O. Nelson. 1970. Food of Pacific hake, *Merluccius productus*, in Washington and northern Oregon coastal waters. *In* Pacific hake, U.S. Fish Wildl. Serv., Circ. 332, pp. 35–42.

Best, E. A. 1963. Contribution to the biology of the Pacific hake, *Merluccius productus* (Ayres). Calif. Coop. Oceanic Fish. Invest. Rep. 9:51–56.

Brodeur, R. D., H. V. Lorz, and W. G. Pearcy. 1987. Food habits and dietary variability of pelagic nekton off Oregon and Washington, 1979–1984. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 57, 32 pp.

Dark, T. A., and M. E. Wilkins. 1994. Distribution, abundance, and biological characteristics of groundfish off the coast of Washington, Oregon, and California, 1977–1986. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 117, 73 pp.

De Witt, J. W., Jr. 1952. An occurrence of the natural destruction of hake in Humboldt County. Calif. Fish Game 38:438.

Dorn, M. 1996. Appendix A. Status of the coastal Pacific whiting resource in 1996. *In* Pacific Fishery Management Council. Appendix volume I: status of the Pacific coast groundfish fishery through 1996 and recommended biological catches for 1997: stock assessment and fishery evaluation. (Document prepared for the council and its advisory entities.) Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, OR 97201.

Francis, R. C. 1983. Population and trophic dynamics of Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 40:1925–1943.

Gotshall, D. W. 1969. Stomach contents of Pacific hake and arrowtooth flounder from northern California. Calif. Fish Game 55:75–82.

Hobson, E. S., and D. F. Howard. 1989. Mass strandings of juvenile shortbelly rockfish and Pacific hake along the coast of northern California. Calif. Fish Game 75(3):169–172.

Livingston, P. A. 1983. Food habits of Pacific whiting, *Merluccius productus*, off the west coast of North America, 1967 and 1980. Fish. Bull., U.S. 81:629–636.

Livingston, P. A., and K. M. Bailey. 1985. Trophic role of the Pacific whiting, *Merluccius productus*. Mar. Fish. Rev. 47(2):16–22.

Mearns, A. J., D. R. Young, R. J. Olson, and H. A. Schafer. 1981. Trophic structure and the cesium-potassium ratio in pelagic ecosystems. Calif. Coop. Oceanic Fish. Invest. Rep. 22:99–110.

Outram, D. N., and C. Haegele. 1972. Food of Pacific hake, (*Merluccius productus*) on an offshore bank southwest of Vancouver Island, British Columbia. J. Fish. Res. Board Can. 29:1792–1795.

Rexstad, E. A., and E. K. Pikitch. 1986. Stomach contents and food consumption estimates of Pacific hake, *Merluccius productus*. Fish. Bull., U.S. 84:947–956.

Smith, P. E. 1995. Development of the population biology of the Pacific hake, *Merluccius productus*. Calif. Coop. Oceanic Fish. Invest. Rep. 36:144–152.

Sumida, B. Y., and H. G. Moser. 1980. Food and feeding of Pacific hake larvae, *Merluccius productus*, off southern California and northern Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 21:161–166.

Tanasichuk, R. W., D. M. Ware, W. Shaw, and G. A. McFarlane. 1991. Variation in diet, daily ration, and feeding periodicity of Pacific hake (*Merluccius productus*) and spiny dogfish (*Squalus acanthias*) off the lower west coast of Vancouver Island. Can. J. Fish. Aquat. Sci. 48:2118–2128.

U.S. GLOBEC. 1994. Eastern Boundary Current Program, A science plan for the California Current. U.S. GLOBEC Rep. no. 11. Univ. Calif. Davis, 134 pp.

Weinberg, K. L., M. E. Wilkins, R. R. Lauth, and P. A. Raymore Jr. 1994. The 1989 Pacific west coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, and length and age composition. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-33, 168 pp. plus appendices.

Wilson, C. D., and M. A. Guttormsen. 1997. Echo integration-trawl survey of Pacific whiting, *Merluccius productus*, off the west coasts of the United States and Canada during July–September 1995. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-74, 70 pp.

Woodbury, D., A. B. Hollowed, and J. A. Pearce. 1995. Interannual variation in growth rates and back-calculated spawn dates of juvenile Pacific hake (*Merluccius productus*). *In* Recent developments in fish otolith research, D. H. Secor, J. M. Dean, and S. E. Campana, eds. Univ. S. Carolina Press, pp. 481–496.