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by
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ABSTRACT

This report describes the food habits of some commercially important groundfish collected off the coasts of California, Oregon, Washington, and British Columbia. Generally, the groundfish reported on were sampled during three cruises - the triennial groundfish survey of 1989 and the continental slope surveys of 1991 and 1992. Some young-of-the-year Pacific hake (also known as Pacific whiting, *Merluccius productus*) were examined from 1987 and 1988 surveys. Where possible, the diet of each groundfish species was examined for possible ontogenetic, latitudinal, depth, and seasonal changes. Typically, ontogenetic shifts in the diet of the predators examined on this study were based on the ability of the larger fish to eat larger prey. Effects of latitude, depth, and season were also detected for some of these species.

The diet of age-0 Pacific hake shifted from copepods to euphausiids with increasing size (33-128 mm total length) in 1987, but not in 1988. Pacific hake became increasingly piscivorous with size, and cannibalism was an important diet component in 1991 in the Monterey INPFC (International North Pacific Fisheries Commission) statistical area. Sablefish (*Anoplopoma fimbria*) and shortspine thornyhead (*Sebastolobus alascanus*) consumed a wide variety of locally abundant prey items including large amounts of offal from fish-processing operations conducted at sea. The diet of juvenile sablefish captured over the continental shelf was similar to the diet of Pacific hake, but the diet of larger sablefish sampled from the upper continental slope was more similar to the shortspine thornyhead diet. Arrowtooth flounder (*Atheresthes stomias*) was the most piscivorous predator examined in this study, consuming mostly Pacific hake, Pacific herring (*Clupea pallasii*) and unidentified gadids. Longspine thornyhead (*S. altivelis*) consumed a variety of benthic crustaceans, and the presence of fishery offal in the diet indicated that longspine thornyhead also scavenged the slope bottom. Giant grenadier (*Albatrossia pectoralis*) consumed mostly deepwater crustaceans and fishes in this study, by weight. Pacific grenadier (*Coryphaenoides acrolepis*) stomachs contained mostly squid and a variety of crustaceans, by weight. A majority of the diet of Dover sole (*Microstomus paczjkus*) and deepsea sole (*Embassichthys bathybius*) was polychaete worms and brittlestars.

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INTRODUCTION

The National Marine Fisheries Service (NMFS) is charged with the mission of conducting scientific research programs to better understand and manage regional fishery resources. Presently, most of the major species of groundfish off the Pacific coast of the United States are fully utilized, and control of the excess harvesting capacity and allocation of the available catch are the two most severe concerns facing managers of the Pacific coast groundfish fishery (Low 1993). Both of these management concerns are exacerbated by the complex multi-species nature of the fishery.

Scientific research of species interactions in the Pacific coast groundfish community will increase our knowledge about the ecosystem and may assist managers in forecasting the consequences of various management actions. Predation (including cannibalism) may affect recruitment and population size, and competition for food resources may affect growth and mortality. Published studies on the feeding habits of Pacific coast groundfish typically describe the food habits of a few species, usually within a limited spatial range. The objective of this study was to describe the food habits of several commercially valuable or potentially valuable groundfish over wide latitudinal and depth ranges of the Pacific coast.

METHODS

Stomach samples were collected from important groundfish species that occupy the narrow continental shelf and the upper continental slope of North America. Bottom trawl surveys of the groundfish resources on the Pacific Coast continental shelf and upper continental slope are conducted by the National Marine Fisheries Service (NMFS), Alaska Fisheries Science Center (AFSC), Resource Assessment and Conservation Engineering Division. Stomachs from several important species of groundfish were collected during three of these surveys (1989, 1991, and 1992).

Young-of-the-year (YOY) Pacific hake (*Merluccius productus*) in this study were caught incidentally during the 1987 and 1988 annual juvenile rockfish (*Sebastes* spp.) surveys conducted by NMFS, Southwest Fisheries Science Center, Tiburon Laboratory.

Study Area

This study primarily encompasses the continental shelf and upper continental slope (30-700 fm, 50-1300 m) between Point Conception, California (34°30'N lat.), through Oregon, Washington, and into British Columbia (50°30'N lat.). This broad latitudinal range extends over several statistical areas established by the International North Pacific Fisheries Commission (INPFC). These areas -- Conception (United States-Mexico International Boundary to 36°00' N lat.), Monterey (36° 00' to 40° 30'N lat.), Eureka (40° 30' to 43° 00'N lat.), Columbia (43°00' to 47°30'N lat.) and Vancouver (47°30' to 50°30'N lat.) -- will hereafter be referred to by name (Fig. 1).

Stomachs from several important species of groundfish were collected in these INPFC statistical areas during three NMFS bottom-trawl surveys (Fig.1). In 1989, the fifth triennial groundfish survey was conducted on the continental shelf (30 to 200 fm, or

55 to 366 m) from Point Conception, California, to central Vancouver Island, British Columbia, Canada (34 ° 30' to 49 ° 35' N lat.), between 7 July and 29 September (Weinberg et al. 1994). In 1991, a groundfish survey was conducted on the upper continental slope (300 to 400 fm, or 550 to 732 m depths) in the Columbia and Eureka INPFC areas as well as the shelf and slope (100 to 700 fm, or 183 to 1,280 m) in the Monterey INPFC area between 21 October and 18 November (Lauth et al. 1997). In 1992, a groundfish survey was conducted on the continental shelf and slope (100 to 700 fm, or 183 to 1,280 m) in parts of the Vancouver and Columbia INPFC areas between 16 October and 13 November (Lauth et al. 1997).

Young-of-the-year Pacific hake were collected from midwater trawls in April 1987 and in May 1988. Samples were taken from about Point Sur to Point Reyes and out to 124° W long. off Point Reyes (Wyllie Echeverria 1990) (Fig. 2).

Sample Collection

Fish stomachs were collected from a core group of species during each of the three bottom-trawl surveys: sablefish (*Anoplopoma fimbria*), Pacific hake, shortspine thornyhead (*Sebastolobus alascanus*), and Dover sole (*Microstomus pacificus*). Some species were not sampled during all three of the surveys because they were not present in the survey area. Stomachs from arrowtooth flounder (*Atheresthes stomias*) were collected in 1989 and 1992. Stomachs from longspine thornyhead (*Sebastolobus altivelis*) and deepsea sole (*Embassichthys bathybius*) were collected in 1991 and 1992. Stomachs were collected from giant grenadier (*Albatrossiapectoralis*) and Pacific grenadier (*Coryphaenoides acrolepis*) in 1992 only.

The buccal cavities of individual fish were examined before removing the stomach, and fish showing signs of regurgitation (prey in the mouth or gills, or inverted or flaccid stomach) or evidence of net feeding were discarded. To minimize a bias toward sampling empty stomachs, when a fish was discarded due to regurgitation or net feeding, it was replaced with a fish whose stomach contained food. Stomachs from fish that met these collection criteria were placed in a cloth bag with a specimen tag indicating the species, sex, fork length (FL), vessel, survey, haul, and specimen numbers. When very small fish were encountered, whole specimens were chosen and placed in a cloth bag with a specimen tag indicating the cruise and haul numbers. Lengths of these small fish were recorded before the stomachs were removed and processed in the laboratory. Stomach samples and whole fish were preserved in 10% formalin, rinsed with water, and stored in 70% ethanol.

Stomach Content Analysis

In the laboratory, samples were rinsed with tapwater and the stomach's contents removed and blotted dry. The total weight of the stomach contents was recorded to the nearest one-tenth (0.1) of a gram. Individual prey were identified to the lowest practical taxon and, with a few exceptions, the weight and number of prey in each taxon were recorded. Only fish and crab prey were counted and weighed for Pacific hake collected in 1989. For each of the remaining prey taxa, the percentage of the total stomach contents volume was visually estimated. Whenever possible, standard length (SL) of fish prey and carapace width (CW) of crab prey were measured and recorded to the nearest

millimeter. Some of the stomach contents were identified as offal (discarded parts from commercial fish processing operations) and treated as a single prey type.

Data Analysis

For each predator, the diet was summarized using the percent frequency of occurrence, the percent number (when possible), and the percent weight of each prey taxon identified. The diet of YOY Pacific hake was summarized for each year, 1987 and 1988. The diet of each fish species sampled during the bottom-trawl surveys was summarized separately for 1991, 1992, for the region north of Cape Blanco (Vancouver and Columbia INPFC areas) in 1989, and for the region south of Cape Blanco (Eureka, Monterey and Conception INPFC areas) in 1989. Cape Blanco is a prominent coastal feature that approximately corresponds with a boundary separating regions of the California Current system with distinct oceanographic characteristics (U.S. GLOBEC 1994). North of Cape Blanco there are larger estuaries, greater freshwater input, and a relatively broad continental shelf, and the coastline is concave and fairly smooth. South of Cape Blanco the coastline is generally convex in shape, with large coastal promontories, and the continental shelf is narrower. Although primary productivity in both regions is seasonal, there are wind stress reversals that create strong upwelling in spring and summer north of Cape Blanco. South of Cape Blanco, the prevailing winds tend to favor upwelling in all seasons with only moderate spring and summer increases.

To examine the variation of diet with bottom depth and latitude for each species, the diet data were divided into four depth zones within each of the five INPFC areas (30-99 fm, 100-199 fm, 200-499 fm, and 500-699 fm). The diet data were then aggregated into broad prey categories for each depth zone and was presented in area-proportional (doughnut) charts.

To examine the variation of the diet with predator size, diet data from 1991, 1992, and 1989 south of Cape Blanco and 1989 north of Cape Blanco were divided into predator length groups for each species. We aggregated the diet data into broad prey categories, and produced figures that depict changes in the composition of the diet, by weight, with increasing predator size.

The amount of temporal variability in the diet that could be determined from these data was limited because in most cases the samples were unique with respect to two or more of the following characteristics; year, season, area, or bottom depth. However, we were able to compare autumn diets of shortspine thornyhead, longspine thornyhead, and Dover sole between 1991 and 1992 in the 200-499 fm depth range of the Columbia INPFC area.

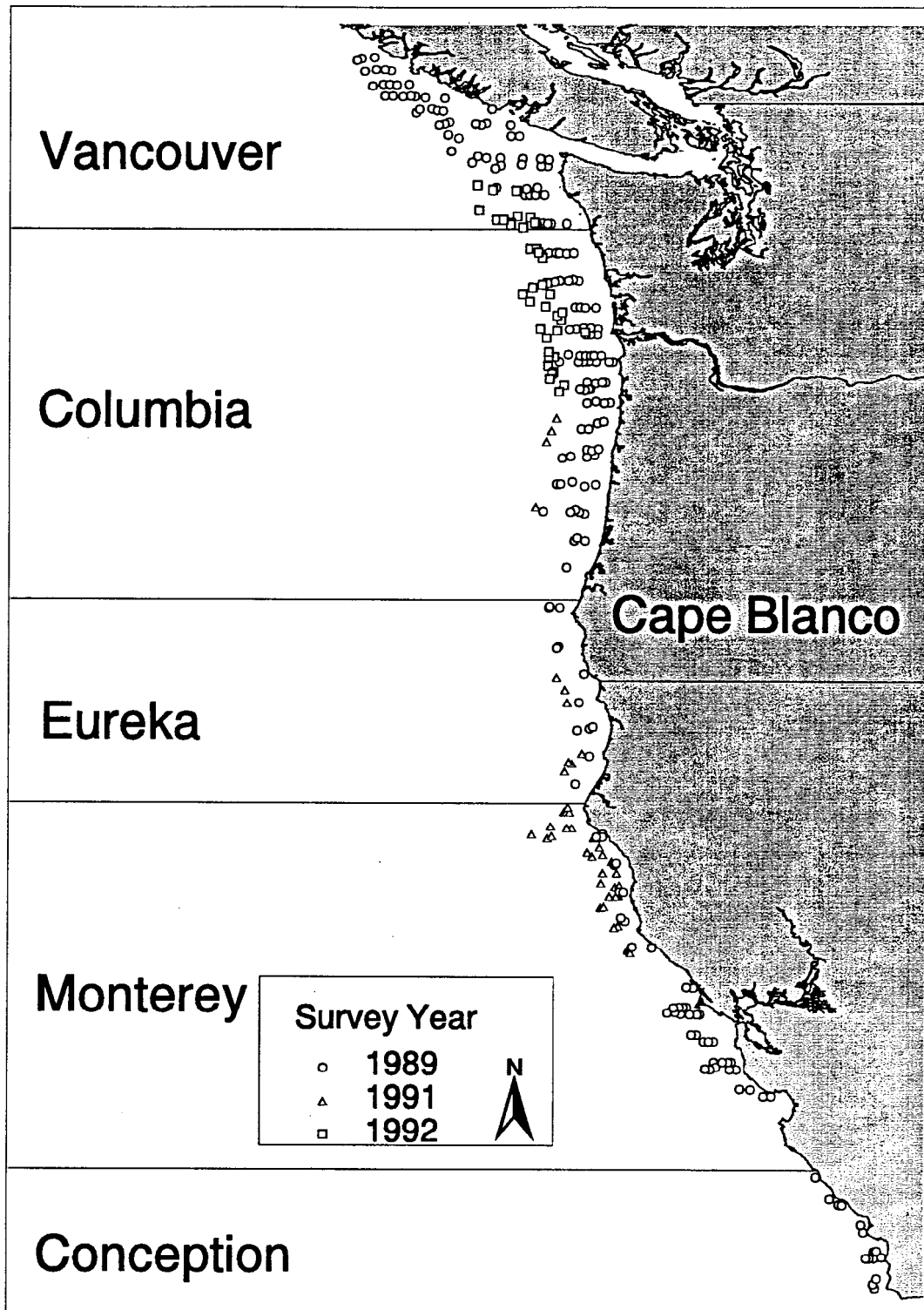


Figure 1.--Locations where stomach samples were collected during the 1989 triennial groundfish survey (circles) and the 1991 (squares) and 1992 (triangles) slope groundfish surveys.

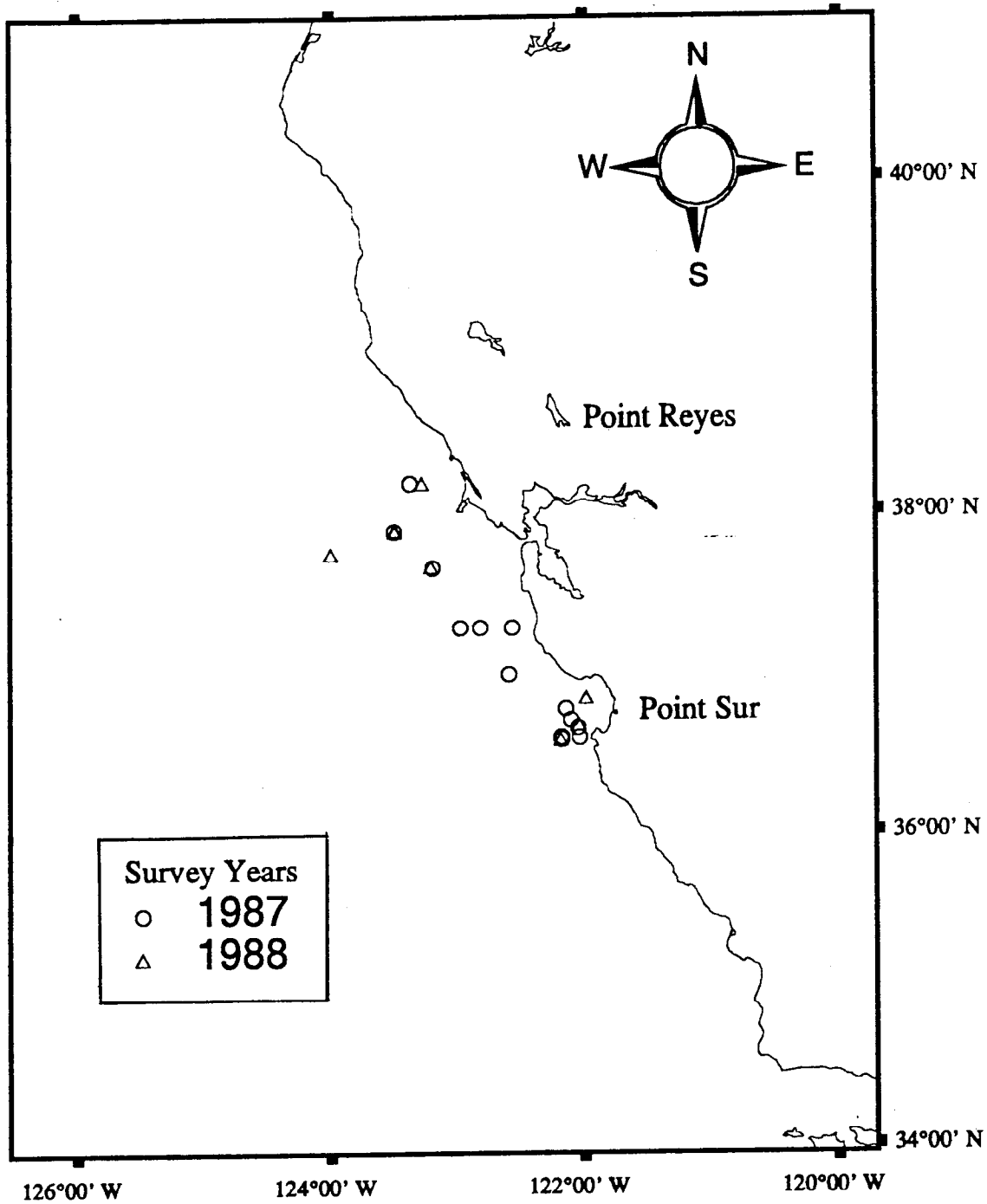


Figure 2. --Locations where young-of-the-year Pacific hake stomach samples were collected in 1987 and 1988.

YOUNG-OF-THE-YEAR PACIFIC HAKE

Age-0, or YOY, Pacific hake are an important component of the energy flow in the California Current ecosystem. They are preyed upon by albacore tuna (*Thunnus germon*), several species of rockfish (*Sebastes* sp.) (Best 1963, Livingston and Bailey 1985), and intra-cohort cannibalism has been observed among Pacific hake as small as 5.5 mm in length (Sumida and Moser 1980). Juvenile Pacific hake are preyed upon by many predatory fishes including bigmouth sole (*Hippoglossina stomata*), arrowtooth flounder, sablefish, and larger Pacific hake (Best 1963, Livingston and Bailey 1985). Marine birds that prey on juvenile hake include the sooty shearwater (*Puffinus griseus*) and the western gull (*Larus occidentalis*) (Livingston and Bailey 1985).

Little is known about the food habits of intermediate sizes of YOY Pacific hake. The larvae finish yolk absorption and begin feeding at about 3 mm SL (Sumida and Moser 1980). They feed primarily on copepod eggs, nauplii, copepodites, and adults through 10.7 mm SL (Sumida and Moser 1980). The diet of larger (10-20 cm FL) juvenile Pacific hake was found to be dominated by euphausiids (> 90% by weight) (Livingston 1983, Livingston and Bailey 1985, Fig. 3 of this study). The transition from a diet of copepods to euphausiids has not been described. The age-0 Pacific hake collected for this study during juvenile rockfish surveys cover a portion of this size range: 34 to 102 mm FL in 1987 and 33 to 128 mm FL in 1988.

RESULTS

General Diets

Stomachs from 65 YOY Pacific hake collected in 1987 off of central California were examined. Three (5%) of these stomachs were empty (Table 1). Euphausiids and calanoid copepods occurred frequently in the diet, but euphausiids dominated the stomach contents (96%) by weight because of their larger size. For all age-0 Pacific hake examined from 1987, only 3% of the stomach contents were identified as calanoid copepods by weight and the average fullness was 0.21 g/fish or 5.5% body weight.

In 1988, 43 (12%) of the 345 stomachs collected off of central California were empty (Table 2). Similar to the preceding year, euphausiids and calanoid copepods occurred most frequently in the diet and euphausiids dominated the diet by weight (74%). However, calanoid copepods contributed more to the diet by weight (19%) and the fish were less full (0.07 g/fish or 2.6% body weight), on average, than in 1987. One occurrence of cannibalism by a 128 mm FL Pacific hake was found. Because of the large relative size of this prey, compared to calanoid copepods and euphausiids, it was over 4% of the weight of the combined stomach contents.

Variation of the Diet with Predator Size

The juvenile Pacific hake samples were divided into three size groups - small (33-60 mm FL), medium (61- 90 mm FL), and large (91-128 mm FL). The diet composition, by weight, was summarized for each size group by year (Fig. 3). In 1987, a decreasing proportion of the diet was comprised of calanoid copepods as predator-length increased. In 1988, no decrease in copepod consumption was apparent with length, and the trend

appeared to be the opposite, an increasing proportion of copepods in the diet with increasing length.

DISCUSSION

Juvenile Pacific hake of the sizes examined here (33-128 mm SL) consumed primarily calanoid copepods and euphausiids. Given that the diet of larval Pacific hake (3-10.7 mm SL) consists mainly of calanoid copepods (Sumida and Moser 1980) and the diet of larger juvenile Pacific hake (10-20 cm FL) consists mainly of euphausiids (Livingston 1983; Livingston and Bailey 1985; this study, Fig. 3) this result is not surprising. However, the transition from a diet of calanoid copepods to euphausiids appears to differ between 1987 and 1988.

The contribution of calanoid copepods to the weight of the diet was greater in 1988 than in 1987 and the average fullness per fish was lower in 1988 than in 1987. Year-class strength was moderate in these two years with somewhat fewer fish in the 1988 year class, based on recruitment of age-2 Pacific hake into the fishery (Dorn and Methot 1990). Large swarms of euphausiids were encountered in the study area in 1987 (Smith and Adams 1988). It is possible that euphausiids were less available to the juvenile Pacific hake sampled in 1988, resulting in less full stomachs and a continued feeding on calanoid copepods. However, if euphausiids were less available in 1988 than 1987, it did not seem to affect their early growth because Woodbury et al. (1995) found the growth rates of Pacific hake in these two years to be nearly identical, at least up to 70 mm SL. Further investigation into the transition from calanoid copepods to euphausiids in the diet of Pacific hake is required, especially during years of differing environmental conditions.

Previously, intracohort cannibalism by Pacific hake was only known to occur in the larval stage (Sumida and Moser 1980). The incidence of cannibalism in 1988 is evidence that this behavior can occur beyond the larval stage. Intracohort cannibalism by Pacific hake requires substantial differences in size among cohort members. While differences in individual growth rates may contribute to the differences in individual size, the broad temporal distribution of spawning dates (October through March - Woodbury et al. 1995) is probably more of a factor. The potential for intracohort cannibalism may have significant implications for recruitment, especially during years when prey is scarce.

Table 1.--The percent frequency of occurrence (%F) and percent weight (%W) of the prey found in the stomachs of age-0 Pacific hake (*Merluccius productus*) caught in the spring of 1987.

Prey Name	%F	%W
Teuthoidea oegopsida (squid)	1.61	0.09
Calanoida (copepod)	41.94	3.05
Mysidae (mysid)	3.23	0.86
Gammaridea (amphipod)	1.61	0.05
Euphausiacea (euphausiid)	14.52	46.61
Euphausiidae (euphausiid)	35.48	6.99
<i>Euphausia pacifica</i> (euphausiid)	35.48	42.24
Unidentified organic material	1.61	0.12
Total prey weight:	12.92 g	
Total non-empty stomachs:	62	
Total empty stomachs:	3	

Table 2.--The percent frequency of occurrence (%F) and percent weight (%W) of the prey found in the stomachs of age-0 Pacific hake (*Merluccius productus*) caught in the spring of 1988.

Prey Name	%F	%W
Crustacea	5.63	0.53
Calanoida (copepod)	39.74	19.23
Cirripedia (barnacle)	0.33	0.05
Peracarida Mysidacea (mysid)	0.66	0.02
Hyperiidia (amphipod)	3.64	0.66
Eucarida	0.33	0.09
Euphausiidae (euphausiid)	54.97	33.76
<i>Euphausia pacifica</i> (euphausiid)	31.13	28.84
<i>Thysanoessa</i> sp. (euphausiid)	0.66	0.34
<i>Thysanoessa spinifera</i> (euphausiid)	12.58	10.87
Reptantia (crab)	0.33	0.00
Osteichthyes Teleostei (bony fish)	0.99	0.91
<i>Merluccius productus</i> (Pacific hake)	0.33	4.44
Unidentified organic material	1.99	0.21
Unidentified tube	0.33	0.05
Total prey weight:	21.86 g	
Total non-empty stomachs:	302	
Total empty stomachs:	43	

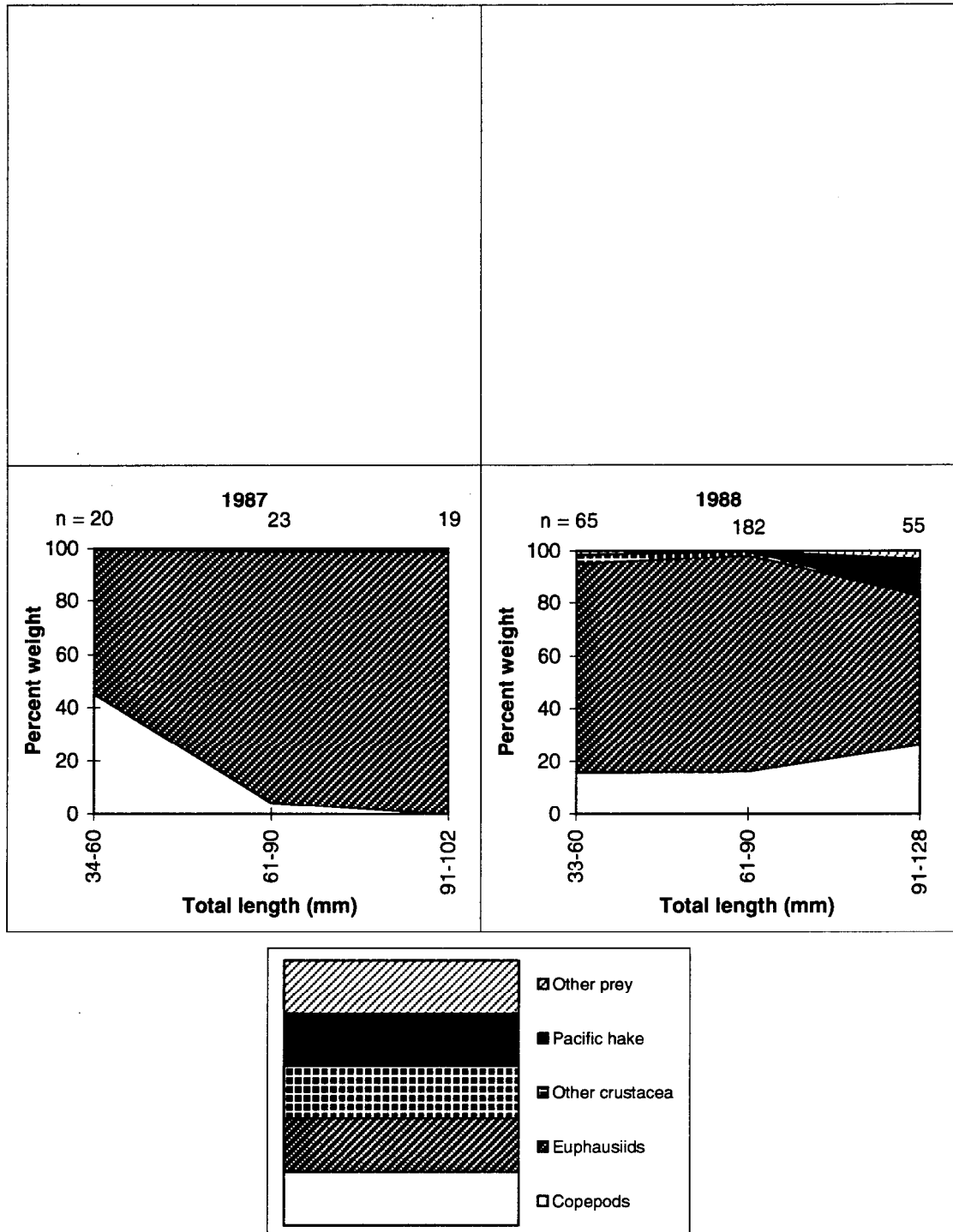


Figure 3.--Diet composition of age-0 Pacific hake (by length) from the 1987 and 1988 juvenile rockfish surveys south of Cape Blanco. The length-range shown in each figure may be different. The sample size (n) is shown above each length group.

PACIFIC HAKE

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). This resource is fully exploited with an average annual catch from 1983 to 1992 of 221,600 metric tons (t) (Dorn 1993). Commercial landings of Pacific hake from 1991 to 1993 in the U.S. were about two-thirds of the total U.S. commercial landings of groundfish from the Pacific coast (Pacific Fishery Management Council 1994).

Ecologically, Pacific hake is one of the most important fish species on the west coast of North America (Francis 1983, Livingston and Bailey 1985). It is an important prey resource for birds, tuna, sharks, groundfish, and several marine mammals (Best 1963, Livingston and Bailey 1985). Adult Pacific hake have been found in the stomachs of several large piscivorous fish: spiny dogfish (*Squalus acanthias*) (Tanasichuk et al. 1991), Pacific lancetfish (*Alepisaurus richardsoni*), northern bluefin tuna (*Thunnus thynnus*), sablefish, lingcod (*Ophiodon elongatus*), soupfin shark (*Galeorhinus zyopterus*), great white shark (*Carcharodon carcharias*), and electric ray (*Torpedo californica*) (Best 1963). Also, several marine mammals - California sea lion (*Zalophus californianus*), northern fur seal (*Callorhinus ursinus*), northern sea lion (*Eumetopias jubatus*), elephant seal (*Mirounga augustirotris*), Pacific whitesided dolphin (*Lagenorhynchus obliquidens*), and Dall porpoise (*Phocoenoides dalli*) - prey on adult Pacific hake (Best 1963, Dorn 1993). Pacific hake is also an important predator in the Pacific coast ecosystem. The diet of smaller (< 45 cm FL) Pacific hake is typically dominated by euphausiids, but larger Pacific hake feed more on fish and larger crustaceans, including commercially important species such as Pacific herring (*Clupea pallasi*), northern anchovy (*Engraulis mordax*), and pink shrimp (*Pandalus jordani*) (Francis 1983, Livingston 1983, Livingston and Bailey 1985, Rexstad and Pikitch 1986). Due to its large biomass, the impact of Pacific hake predation on these commercially important species can be extensive (Francis 1983, Gotshall 1969, Livingston and Bailey 1985).

RESULTS

General Diets

A total of 1,334 Pacific hake stomachs were examined in the laboratory. Of the 351 stomachs collected south of Cape Blanco in the summer of 1989, 49 (14%) were empty. Fifty-one (7%) of the 745 stomachs collected north of Cape Blanco in the summer of 1989 were empty. Only 7 (5%) of the 138 stomachs collected in the autumn of 1991 were empty, but 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 1989 south of Cape Blanco was dominated by fish, followed by crustaceans and cephalopods, but crustaceans occurred most frequently, especially euphausiids (Table 3). The most important fishes in the diet, by weight and frequency of occurrence, were northern anchovy, followed by Pacific herring, and rockfish (*Sebastes* spp.). The most important crustaceans by weight and frequency of occurrence were euphausiids, especially *Euphausia pacifica* and

Thysanoessa spinifera, but sergestid shrimp also occurred frequently. Gonatid squid were the most important cephalopods, including *Gonatus onyx* and *Berryteuthis magister*.

A similar pattern was found north of Cape Blanco in 1989: fish dominated the diet composition, by weight, and crustaceans, especially euphausiids, were the most frequently occurring prey (Table 4). However, the species composition of the diet was different than south of Cape Blanco and cephalopods comprised a much smaller portion of the diet by weight. The most important fishes in the diet, by weight and frequency of occurrence, were Pacific herring and the smelts (family Osmeridae) including eulachon (*Thaleichthys pacificus*) and whitebait smelt (*Allosmerus elongatus*). The most important crustaceans in the diet by weight and frequency of occurrence were euphausiids, dominated by *E. pacifica* and *T. spinifera*, and shrimp, especially the pink shrimp, contributed a larger portion to the diet than they did south of Cape Blanco.

In autumn 1991, Pacific hake stomachs were collected from the outer shelf and upper slope in the Monterey INPFC area, south of Cape Blanco. The diet, in terms of weight, was dominated by fish, but crustaceans were most numerous and occurred most frequently (Table 5). Of the crustaceans, sergestid shrimp were the most frequently occurring and contributed the most weight, while euphausiids contributed the highest number of individuals. Myctophids (lanternfishes), followed by Pacific hake, were the two most frequently occurring and numerically dominant fish in the diet and the vast majority of the fish weight in the diet was composed of Pacific hake.

North of Cape Blanco in autumn 1992, fish comprised about half the diet by weight, were few in number, and occurred infrequently (Table 6). Crustaceans comprised almost half of the diet by weight, were numerically dominant, and occurred with great frequency. The Pacific saury (*Cololabis saira*) contributed most to the weight of fish in the diet, followed by Pacific herring and bristlemouths (family Gonostomatidae), but the smaller myctophids were the most frequently occurring fish. Pandalid shrimp contributed most to the weight of crustaceans in the diet, followed closely by sergestid shrimp. Sergestid shrimp occurred with the highest frequency of all prey, followed by euphausiids which were the most numerous prey items.

Patterns in Diet Variability

In 1989, the diet of Pacific hake in the Conception INPFC area was dominated by shortbelly (*Sebastes jordani*) and stripetail (*S. saxicola*) rockfish, but in the Monterey INPFC area and northward, northern anchovy and Pacific herring generally dominated the biomass of fish eaten (Fig. 4). In the Eureka INPFC area, euphausiids and pink shrimp comprised nearly the entire diet. Euphausiids were also very important in the 100-199 fm depth zone in the Columbia and Monterey INPFC areas (Fig. 4). Although some differences in the diet of Pacific hake with depth were found, especially in the Columbia and Monterey INPFC areas, the most consistent difference with depth was the presence of myctophids (included in the "Other fish" category) in the diet of the Pacific hake caught in deeper water (100-199 fm).

In 1991, Pacific hake were sampled in the Monterey INPFC area in autumn. Pacific hake from a broad size range co-occurred in this area and a high level of cannibalism was found (Fig. 4). Although two incidents of cannibalism were found in the 30-99 fm depth zone in summer of 1989, the diet composition, by weight, was dominated by northern anchovy and euphausiids in the Monterey INPFC area.

The diet of Pacific hake in autumn 1992 appeared to be different from that in summer -1989 in the Vancouver and Columbia INPFC areas (Fig.4). In the 100-199 fm depth zone, pink shrimp, and Pacific saury (which was included in the "Other fish" category) were very important in the Vancouver INPFC area. In the Columbia INPFC area, sergestid shrimp comprised nearly all of the "Other prey" category. Gonostomatids and myctophids account for most of the "Other fish" category in the 200-499 fm depth zone in the Columbia INPFC area.

Diet Variability with Predator Size

In the summer of 1989, euphausiids decreased while fish increased in importance with increasing length of Pacific hake both north and south of Cape Blanco (Fig. 5). As noted earlier, the fishes by weight were primarily clupeids north of Cape Blanco and engraulids south of Cape Blanco. A similar pattern of increasing fish and decreasing euphausiid biomass in the diet was observed south of Cape Blanco in autumn of 1991. Cannibalism by larger Pacific hake was the main contributor to this pattern. North of Cape Blanco in 1992, the length-range of the sampled Pacific hake was too narrow to show size-related changes in the diet composition.

DISCUSSION

The reliance by Pacific hake on euphausiids as a major food source in the spring and summer is well documented (Brodeur et al. 1987, Livingston 1983, 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). Interannual variability in the species composition of the diet has been documented (Gotshall 1969, Tanasichuk 1991) and can be dramatic, especially in strong El Nino years (Brodeur et al. 1987). Due to northward summer feeding migrations and size-dependent migratory distance, the size of hake encountered tends to increase with latitude (Francis 1983, Fig. 4 of this study) and apparent latitudinal differences in the diet may be confounded with the size of the Pacific hake sampled (Livingston 1983, Livingston and Bailey 1985, Rexstad and Pikitch 1986).

Because most surveys are conducted during the summer months, seasonal changes in the diet of Pacific hake are not well documented, however stomach samples were collected year-round by Gotshall (1969) in the Eureka INPFC area. Euphausiids appear to be most important by volume in the late spring and summer (Gotshall 1969), with a peak contribution in June or July that declines over the following 3 months in the Eureka, Columbia, and Vancouver INPFC areas (Brodeur et al. 1987, Gotshall 1969, Tanasichuk et al. 1991), and less important in autumn, winter, and early spring (Gotshall 1969). Similarly, in this study the contribution of euphausiids in the diet appears to have been lower in autumn 1991 than in summer 1989 south of Cape Blanco for most sizes of Pacific hake (Fig. 5). North of Cape Blanco, this same pattern is true for 40-49 cm FL Pacific hake (the only size adequately sampled in 1992) (Fig. 5). However, the diet of juvenile Pacific hake (< 20 cm FL) was almost exclusively euphausiids in autumn 1992, similar to what Livingston (1983) found in October off California. Fish are generally most important to the weight of the diet of larger Pacific hake in autumn (Gotshall 1969, Livingston 1983, Tanasichuk et al. 1991), winter (Gotshall 1969), and early spring (Brodeur et al. 1987, Gotshall 1969). However, adult Pacific hake have been observed to

gorge themselves on fish schooling against the shoreline in June of several years (De Witt 1952, Hobson and Howard 1989).

While cannibalism has been noted previously (Best 1963, Bailey et al. 1982), it has not been quantified and the dynamics of this interaction have only been described as occurring where the large and small Pacific hake overlap in their distributions (Bailey et al. 1982). These conditions were rarely sampled during the more rigorous investigations into the feeding habits of Pacific hake (Livingston and Bailey 1985, Rexstad and Pikitch 1986). The role of cannibalism in shaping observed recruitment patterns for this species is unknown. More sampling in this area is needed to determine the degree of interannual variation in the levels of cannibalism that occur.

Table 3.--The percent frequency of occurrence (%F) and percent weight (%W) of the prey found in the stomachs of Pacific hake (*Merluccius productus*) caught south of Cape Blanco in the summer of 1989.

Prey Name	%F	%W
Gastropoda (snail)	0.33	0.00
Bivalvia (clam)	0.33	0.00
Cephalopoda (squid & octopus)	0.33	0.21
Teuthoidea oegopsida (squid)	0.66	2.18
Gonatidae (squid)	3.64	3.05
<i>Gonatus onyx</i> (Oegopsid squid)	0.33	0.05
<i>Berryteuthis magister</i> (squid)	0.99	3.65
Crustacea	0.33	0.00
Calanoida (copepod)	0.99	0.00
Cumacea (cumacean)	0.33	0.00
Gammaridea (amphipod)	0.33	0.00
Euphausiidae (euphausiid)	42.05	3.84
<i>Euphausia pacifica</i> (euphausiid)	30.46	8.14
<i>Nematobranchion boopis</i> (euphausiid)	0.33	0.00
<i>Nematoscelis</i> sp. (euphausiid)	0.66	0.00
<i>Nematoscelis dzscilis</i> (euphausiid)	0.33	0.01
<i>Thysanoessa</i> sp. (euphausiid)	0.33	0.01
<i>Thysanoessa spinifera</i> (euphausiid)	7.28	3.62
Sergestidae (sergestid shrimp)	0.33	0.00
<i>Sergestes</i> sp. (sergestid shrimp)	10.93	0.87
Car-idea (shrimp)	0.66	0.02
<i>Spirontocaris lamellicornis</i> (shrimp)	0.33	0.92
<i>Pandalus jordani</i> (shrimp)	1.66	0.78
Natantia (shrimp)	0.33	0.00
<i>Echinacea</i> sp. (sea urchin)	0.33	0.00
Osteichthyes Teleostei (bony fish)	2.98	0.56
Non-gadoid fish remains	0.03	0.00
<i>Clupea pallasii</i> (Pacific herring)	1.66	6.57
<i>Engraulis mordax</i> (northern anchovy)	9.60	53.06
Osmeridae (smelts)	0.33	0.03
<i>Mallotus villosus</i> (capelin)	0.33	0.17
<i>Idiacanthus</i> sp. (black dragonfish)	0.33	0.02
Myctophidae (lanternfish)	1.32	0.17
<i>Stenobranchius leucopsarus</i> (northern lampfish)	0.33	0.01
<i>Merluccius productus</i> (Pacific hake)	0.66	1.36

Table 3 .--Continued.

Prey Name	%F	% W
<i>Sebastes</i> sp. (rockfish)	0.33	0.29
<i>Sebastes jordani</i> (shortbelly rockfish)	0.99	3.04
<i>Sebastes saxicola</i> (stripetail rockfish)	0.66	1.87
<i>Zalemnius rosaceus</i> (pink surfperch)	0.66	1.70
<i>Icichthys lockingtoni</i> (Medusafish)	0.33	1.41
Pleuronectiformes Pleuronectoidei (flatfish)	0.33	1.40
Bothidae (left-eye flounders)	0.33	0.01
<i>Citharichthys sordidus</i> (Pacific sanddab)	0.66	0.94
Unidentified organic material	0.99	0.01
Total prey weight:	2,514.34 g	
Total non-empty stomachs:	302	
Total empty stomachs:	49	

Table 4.--The percent frequency of occurrence (%F) and percent weight (%W) of the prey found in the stomachs of Pacific hake (*Merluccius productus*) caught north of Cape Blanco in the summer of 1989.

Prey Name	%F	%W
Bivalvia (clam)	0.14	0.00
Teuthoidea (squid)	0.29	0.00
Teuthoidea oegopsida (squid)	0.43	0.02
Gonatidae (squid)	0.86	0.08
<i>Gonatus onyx</i> (Oegopsid squid)	1.73	0.24
Crustacea	0.14	0.00
Peracarida Mysidacea (mysid)	1.15	0.05
Mysidae (mysid)	0.14	0.00
Hyperiiidea (amphipod)	0.14	0.00
Hyperiididae (amphipod)	0.29	0.00
Euphausiidae (euphausiid)	55.33	5.46
<i>Euphausia</i> sp. (euphausiid)	2.02	0.21
<i>Euphausiapacifica</i> (euphausiid)	49.57	12.18
<i>Thysanoessa</i> sp. (euphausiid)	3.03	0.61
<i>Thysanoessa longipes</i> (euphausiid)	0.29	0.00
<i>Thysanoessa spinifera</i> (euphausiid)	35.73	4.97
Sergestidae (sergestid shrimp)	0.14	0.00
<i>Sergestes</i> sp. (sergestid shrimp)	4.90	0.50
Caridea (shrimp)	0.29	0.01
<i>Pasiphaea pacifica</i> (shrimp)	0.14	0.03
Hippolytidae (shrimp)	0.14	0.00
Pandalidae (shrimp)	3.03	0.25
<i>Pandalus</i> sp. (shrimp)	2.45	0.71
<i>Pandalus jordani</i> (shrimp)	4.03	2.47
Crangonidae (shrimp)	1.15	0.09
<i>Crangon</i> sp. (shrimp)	1.59	0.18
<i>Crangon communis</i> (shrimp)	0.43	0.14
Natantia (shrimp)	0.29	0.00
Galatheidae (pelagic slip crabs)	0.14	0.00
<i>Cancer</i> sp. (crab)	0.86	0.00
<i>Cancer magister</i> (Dungeness crab)	4.32	0.13
<i>Cancer oregonensis</i> (pygmy cancer crab)	1.01	0.00
Ophiuroidea Ophiurida (brittle star)	0.14	0.00
<i>Echinacea</i> sp. (sea urchin)	0.14	0.06

Table 4.--Continued.

Prey Name	%F	%W
Osteichthyes Teleostei (bony fish)	0.29	0.00
Non-gadoid fish remains	3.31	0.33
Clupeidae	0.14	0.00
<i>Clupea pallasii</i> (Pacific herring)	11.67	48.42
<i>Engraulis mordax</i> (northern anchovy)	0.86	0.76
Osmeridae (smelts)	6.63	2.34
<i>Thaleichthy pacificus</i> (eulachon)	6.05	4.25
<i>Allosmerus elongatus</i> (whitebait smelt)	2.59	11.18
Myctophidae (lanternfish)	0.58	0.09
Gadidae (gadid fish)	0.43	1.97
<i>Theragra chalcogramma</i> (walleye pollock)	0.14	0.13
Zoarcidae (eelpout)	0.14	0.01
<i>Sebastes</i> sp. (rockfish)	0.14	0.00
Pleuronectiformes Pleuronectoidei (flatfish)	0.58	0.11
Bothidae (left-eye flounders)	0.29	0.08
<i>Citharichthys sordidus</i> (Pacific sanddab)	0.29	0.39
Pleuronectidae (flatfish)	0.29	0.38
<i>Atheresthes stomias</i> (arrowtooth flounder)	0.43	0.85
<i>Pleuronectes bilineatus</i> (rock sole)	0.14	0.05
<i>Eopsetta exilis</i> (slender sole)	0.14	0.05
Unidentified organic material	0.58	0.01
Offal	0.43	0.17
Unidentified algae	0.14	0.03
Total prey weight:	6,069.11 g	
Total non-empty stomachs:	694	
Total empty stomachs:	51	

Table 5.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of Pacific hake (*Merluccius productus*) caught south of Cape Blanco in the fall of 1991.

Prey Name	%F	%N	%W
Cephalopoda (squid & octopus)	0.76	0.09	0.02
Teuthoidea (squid)	0.76	0.09	0.00
Loliginidae (squid)	0.76	0.09	0.03
Teuthoidea oegopsida (squid)	4.58	0.63	0.19
Gonatidae (squid)	2.29	0.27	0.06
<i>Gonatus onyx</i> (Oegopsid squid)	1.53	0.27	0.65
Crustacea	0.76	0.09	0.00
Calanoida (copepod)	2.29	0.27	0.00
Peracarida Mysidacea (mysid)	1.53	0.63	0.02
Hyperiid (amphipod)	0.76	0.18	0.00
Euphausiidae (euphausiid)	25.19	43.33	0.81
<i>Euphausia</i> sp. (euphausiid)	1.53	1.61	0.03
<i>Thysanoessa</i> sp. (euphausiid)	3.82	9.31	0.40
<i>Thysanoessa spinifera</i> (euphausiid)	6.87	15.22	0.76
Decapoda (shrimp & crab)	1.53	0.18	0.00
<i>Sergestes</i> sp. (sergestid shrimp)	51.91	18.35	5.11
Reptantia (crab)	0.76	0.09	0.00
Caridea (shrimp)	0.76	0.09	0.01
Pasiphaeidae (shrimp)	0.76	0.09	0.09
<i>Pasiphaea pacifica</i> (shrimp)	1.53	0.18	0.26
<i>Spirontocaris holmesi</i> (shrimp)	0.76	0.09	0.06
<i>Echinacea</i> sp. (sea urchin)	1.53	0.18	0.03
Osteichthyes Teleostei (bony fish)	2.29	0.27	0.02
Non-gadoid fish remains	3.05	0.36	0.15
Osmeridae (smelts)	0.76	0.09	0.56
<i>Bathylagus pacificus</i> (slender blacksmelt)	0.76	0.09	3.44
<i>Leuroglossus</i> sp.	0.76	0.09	0.67
<i>Leuroglossus schmidti</i> (northern smoothtongue)	1.53	0.18	0.14
Myctophidae (lanternfish)	19.08	2.78	3.44
<i>Stenobrachius leucopsarus</i> (northern lampfish)	1.53	0.18	0.50
Gadidae (gadid fish)	1.53	0.18	1.52
<i>Merluccius productus</i> (Pacific hake)	9.92	1.52	75.94
<i>Sebastolobus</i> sp. (unidentified thornyhead)	0.76	0.09	0.83
Pleuronectiformes Pleuronectoidei (flatfish)	0.76	0.18	0.10
<i>Citharichthys sordidus</i> (Pacific sanddab)	0.76	0.98	4.13
<i>Eopsetta exilis</i> (slender sole)	0.76	0.09	0.02

Table 5 .--Continued.

Prey Name	%F	%N	%W
Unidentified organic material	1.53	1.52	0.01
Offal	0.76	0.09	0.02
Total prey number:	1,117		
Total prey weight:	986.33 g		
Total non-empty stomachs:	131		
Total empty stomachs:	7		

Table 6.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of Pacific hake (*Merluccius productus*) caught north of Cape Blanco in the fall of 1992.

Prey Name	%F	%N	%W
Scyphozoa (jellyfish)	1.35	0.04	1.56
Teuthoidea (squid)	1.35	0.04	0.08
Gonatidae (squid)	5.41	0.17	1.04
<i>Gnathophausia</i> sp.	1.35	0.04	0.06
Euphausiidae (euphausiid)	36.49	44.21	3.72
<i>Euphausia pacifica</i> (euphausiid)	5.41	10.54	1.32
<i>Thysanoessa</i> sp. (euphausiid)	8.11	9.34	0.94
<i>Thysanoessa spinifera</i> (euphausiid)	5.41	12.44	1.81
Sergestidae (sergestid shrimp)	2.70	0.08	0.05
<i>Sergestes</i> sp. (sergestid shrimp)	1.35	0.04	0.04
<i>Sergestes similis</i> (Pacific sergestid)	51.35	18.35	14.71
Caridea (shrimp)	2.70	0.08	0.15
Pasiphaeidae (shrimp)	1.35	0.04	0.14
<i>Pasiphaea pacifica</i> (shrimp)	1.35	0.04	0.36
Pandalidae (shrimp)	4.05	0.17	0.85
<i>Pandalus</i> sp. (shrimp)	8.11	0.83	3.69
<i>Pandalus jordani</i> (pink shrimp)	6.76	2.44	18.98
Natantia (shrimp)	1.35	0.04	0.02
<i>Echinacea</i> sp. (sea urchin)	1.35	0.04	0.00
Non-gadoid fish remains	9.46	0.29	0.87
<i>Clupea pallasii</i> (Pacific herring)	2.70	0.08	7.07
Gonostomatidae (bristlemouth or anglemouth)	1.35	0.04	7.63
Myctophidae (lanternfish)	6.76	0.21	2.49
<i>Tarletonbeania crenularis</i> (blue lanternfish)	1.35	0.04	0.16
<i>Cololabis saira</i> (Pacific saury)	2.70	0.21	28.77
<i>Sebastolobus alascanus</i> (shortspine thornyhead)	2.70	0.12	3.22
Offal	1.35	0.04	0.26
Total prey number:	2,420		
Total prey weight:	460.71 g		
Total non-empty stomachs:	74		
Total empty stomachs:	26		

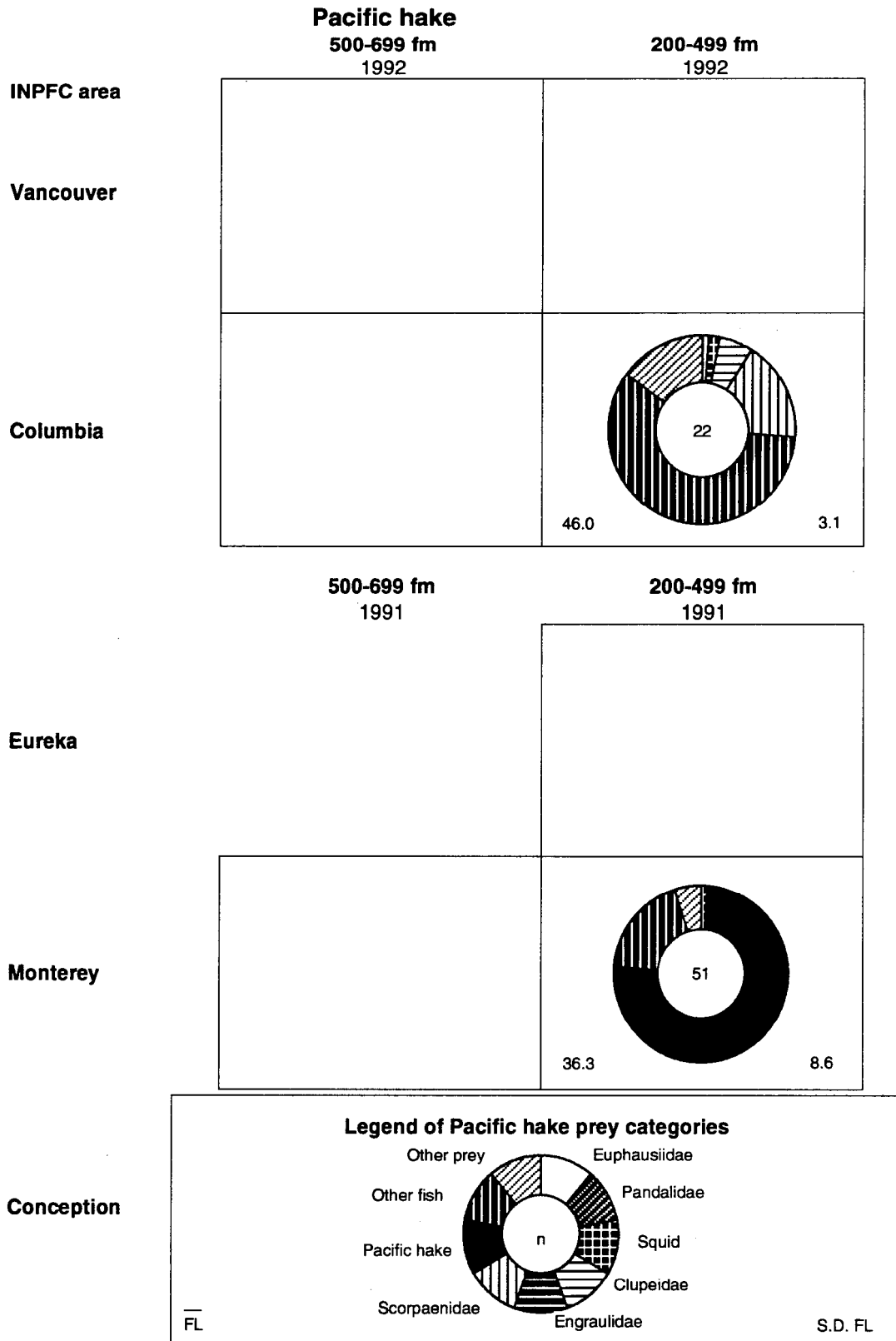


Figure 4.--Diet composition (by weight) of Pacific hake for each depth zone, INPFC area and year. The number of nonempty stomachs examined are shown in each ring. Mean and standard deviation of the fork lengths are shown in the lower left and right of each box, respectively.

Pacific hake

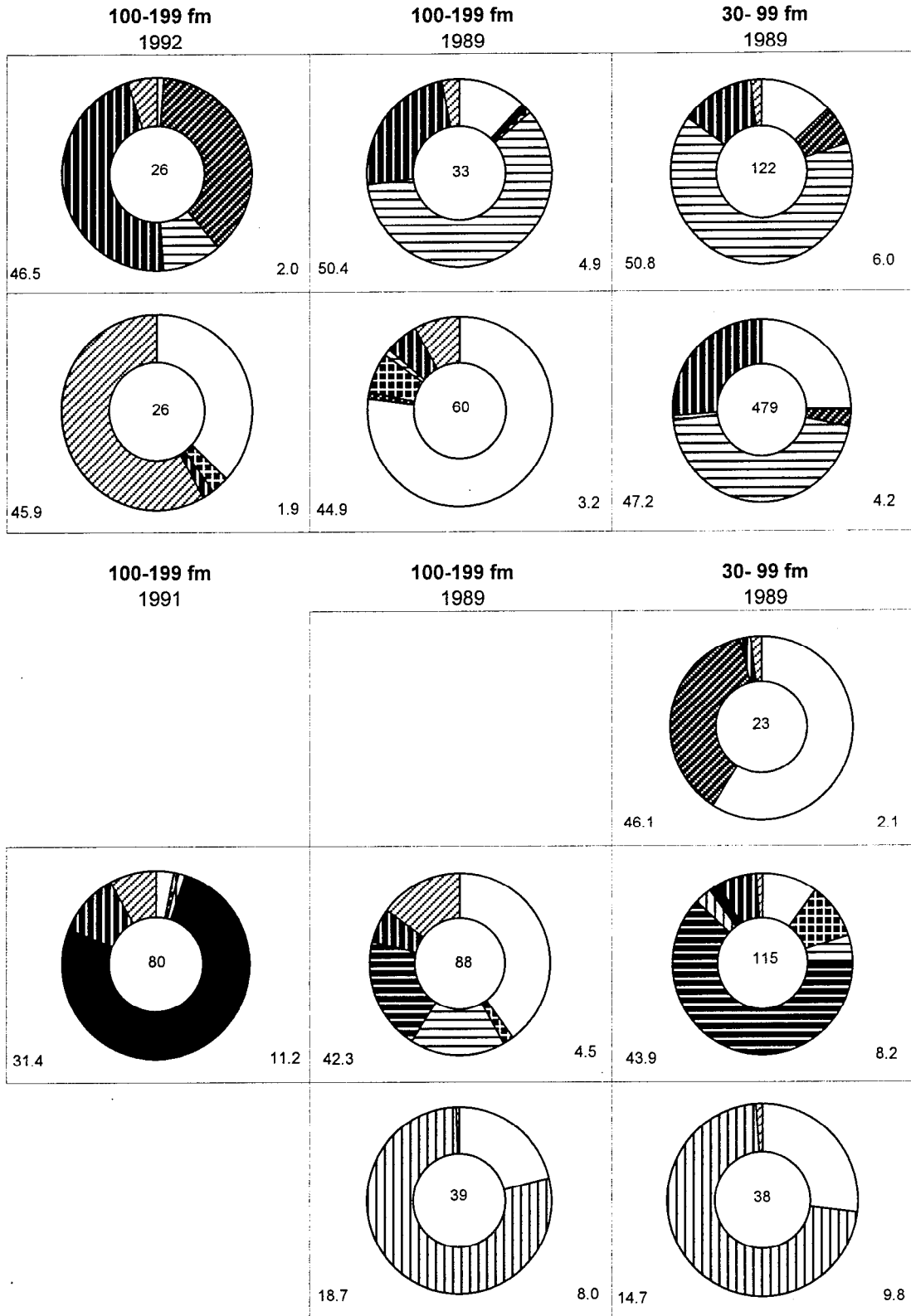


Figure 4.--Continued.

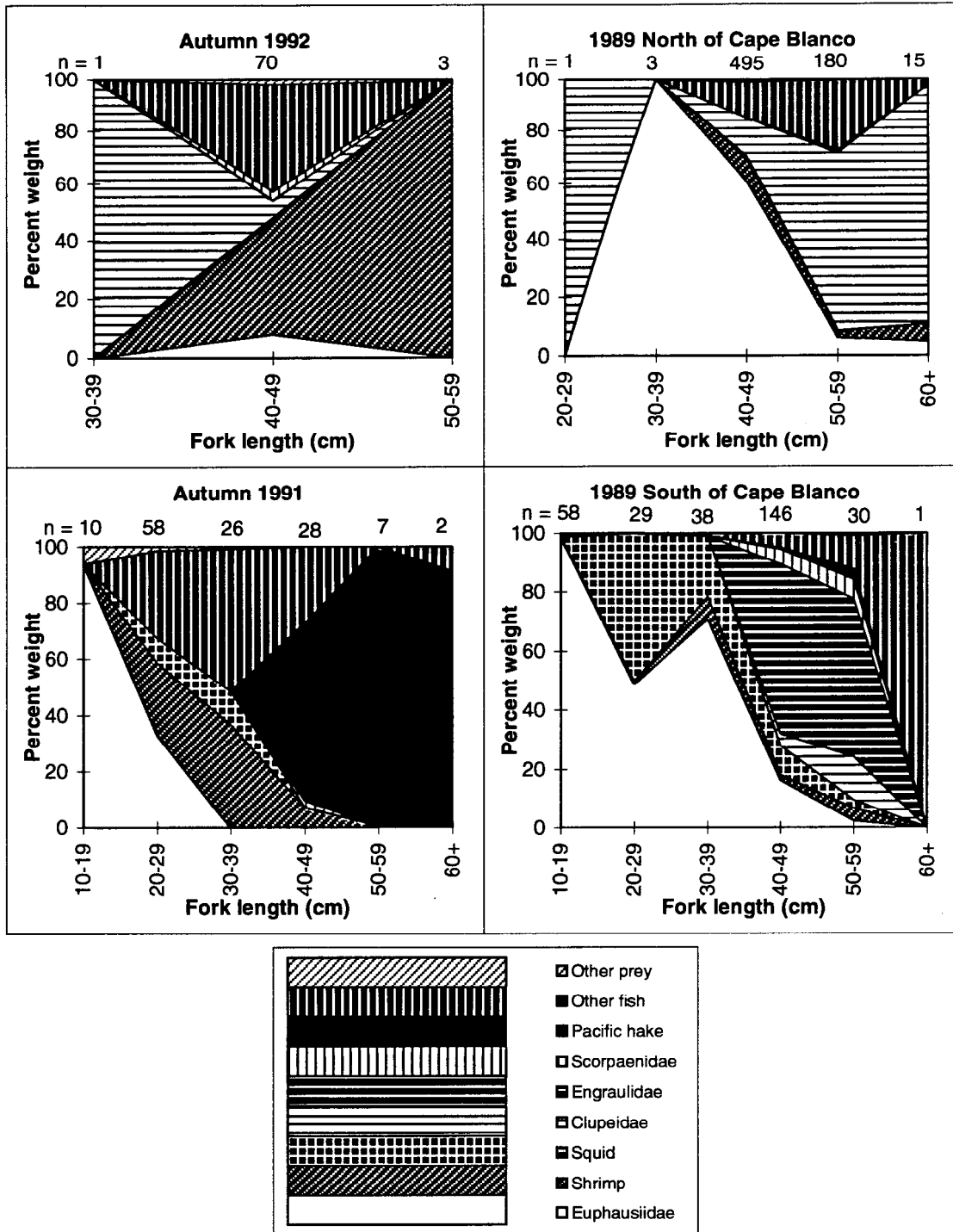


Figure 5.--Diet composition of Pacific hake (by length) from north and south of Cape Blanco in 1989, and from the 1991 and 1992 surveys. The total length-range shown in each figure may be different. The sample size (n) is shown above each length group.

SABLEFISH

Sablefish is a valuable commercial species that has a long history of exploitation, and it commands a higher price than other groundfish (Dark and Wilkins 1994). Sablefish ranked fourth in biomass and fifth in relative abundance of groundfish species in the 1989 triennial groundfish survey (Weinberg et al. 1994).

Sablefish grow rapidly as juveniles, primarily in the pelagic environment, and may reach a length of 38 cm by age 1.5 years (Methot 1993). By this age, sablefish are typically demersal and found on the continental shelf in waters less than 200 m deep (Methot 1993). Sablefish may live over 50 years and grow to a length of over 100 cm (Methot 1993). Adult sablefish inhabit the outer shelf and continental slope with older and larger sablefish inhabiting increasingly deeper waters (Cailliet et al. 1988, Methot 1993, Dark and Wilkins 1994). The sablefish range extends northwestward from Baja California along the continental shelf and slope into the Bering Sea and southwestward to Hokkaido, Japan (Hart 1973).

The food habits of sablefish have been examined from the eastern Bering Sea (Shubnikov 1963, Kulikov 1965, Sasaki 1985, Brodeur and Livingston 1988), Aleutian Islands (Sasaki 1985), Gulf of Alaska (Sasaki 1985, Yang 1993), British Columbia (Tanasichuk 1997), Washington (Grinols and Gill 1968, Brodeur et al. 1987), Oregon (Brodeur et al. 1987, Grover and Olla 1987, Laidig et al. 1997), northern California (Gotshall 1969, Laidig et al. 1997), central California (Cailliet et al. 1988, Laidig et al. 1997) and southern California (Conway 1967). In general, these studies found that sablefish are opportunistic predators that eat a variety of crustaceans, cephalopods, salps and fishes.

RESULTS

General Diets

A total of 731 sablefish stomachs were examined in the laboratory. Of the 159 stomachs collected from south of Cape Blanco in the summer of 1989, 30 (19%) were empty. Only 47 (13%) of the 355 stomachs collected from north of Cape Blanco in the summer of 1989 were empty. Sixteen (15%) of the 104 stomachs collected in the autumn of 1991 were empty, but 37 (33%) of the 113 stomachs collected farther north in the autumn of 1992 were empty.

South of Cape Blanco in 1989, the weight of the sablefish diet was dominated by fish followed by crustaceans (especially euphausiids) and fishery offal from processing vessels (Table 7). The most important fish in the diet by weight were Pacific sanddab (*Citharichthys sordidus*), shortbelly rockfish (*Sebastesjordani*), and northern anchovy, and euphausiids were the most gravimetrically important crustacean. Of all prey, euphausiids were numerically dominant and occurred most frequently. Other prey categories with a high frequency of occurrence were (unidentified) bony fish, unidentified organic material, fishery offal, and polychaetes (Table 7).

The diet of sablefish sampled north of Cape Blanco in 1989 was comprised, by weight, of fish and fishery offal followed by crustaceans (especially euphausiids) (Table 8). The fish most important to the diet were Pacific herring and unidentified clupeids,

hagfish, and flatfish. Euphausiids were numerically dominant followed by pelagic salps and gammarid amphipods. The most frequently occurring prey types were euphausiids (including *Euphausia* spp. and *Thysanoessa* spp.), fishery offal, Pacific herring, gammarid amphipods, unidentified organic material, and (unidentified) bony fish.

The diet of the sablefish collected in autumn 1991 from the upper slope (depths > 199 fm) in the Monterey and Eureka INPFC areas was dominated by fish and fishery offal by weight, number, and frequency of occurrence (Table 9). In all three measures, longspine thornyhead (*Sebastolobus altivelis*) was the largest contributor to the fish in the diet of these sablefish. Euphausiids were noticeably rare in weight, number, and frequency of occurrence.

In autumn 1992, the diet of the sablefish collected from the outer shelf and upper slope in the Columbia and Vancouver INPFC areas was comprised almost exclusively of fish and fishery offal by weight (Table 10). Longspine thornyhead and Pacific hake (*Merluccius productus*) were the greatest contributors to the weight of fish in the diet, and they had the highest frequency of occurrence. Numerically, however, euphausiids were the dominant prey type.

Patterns in Diet Variability

The sablefish sampled in the 30-99 fm depth zone of the Conception INPFC area in 1989 were much smaller on average (mean = 27.9 cm FL) than in the other areas (Fig. 6). Their diet consisted of mostly northern anchovy, by weight. In the 100-199 fm depth range, shortbelly rockfish and squid were important. In the Monterey and Eureka INPFC areas, fishery offal (mostly heads of Pacific hake) and euphausiids were most important to the weight of the diet, but Pacific sanddab, shortbelly rockfish, lithodid crabs, myctophids, and polychaetes were sometimes important. The diet also included a large proportion of fishery offal by weight in the Columbia INPFC area, where juvenile sablefish, pandalid shrimp, salps, and flatfish also contributed significantly to the weight of the diet. In the Vancouver INPFC area, clupeids and euphausiids were important diet components, by weight, across the shelf (30-199 fm), but fishery offal and hagfish were also important in the shallow zone, (30-99 fm).

In 1991, sablefish sampled in the 200-499 fm depth zone in the Monterey INPFC area ate mostly fishery offal by weight, but squid, longspine thornyhead, Pacific hake, and unidentified gadids were also part of the diet (Fig. 6). In the 500-699 fm depth zone of the Monterey INPFC area, the diet of sablefish consisted primarily of longspine thornyheads, fishery offal, squid, unidentified *Chionoecetes* sp., and tunicates. In the Eureka INPFC area, sablefish were sampled only from the 200-499 fm depth zone where their diet was dominated by fishery offal and scorpaenids (mostly longspine thornyheads).

In 1992, scorpaenids were an important part of the diet by weight in the 200-499 fm and the 500-699 fm depth zones in both the Columbia and Vancouver INPFC areas (Fig. 6). These were mostly longspine thornyheads, but some shortspine thornyheads and *Sebastes* sp. were identified in the stomachs. Fishery offal was found in the diet in the 100-199 fm and 200-499 fm depth zones. Pacific hake contributed about half the weight of the diet in the 100-199 fm and 200-499 fm depth zones of the Vancouver INPFC area, but considerably less in the 200-499 fm and 500-699 fm depth zones of the Columbia INPFC area. Pacific herring contributed a third of the weight of

the stomach contents in the 100-199 fm depth zone of the Vancouver INPFC area, but it was minimal or not identified in the other depth zones.

Diet Variability with Predator Size

Taken together, fish were very important prey in the diet of all size groups of sablefish sampled in the summer of 1989, south of Cape Blanco (Fig. 7). Fishery offal and scorpaenids (mostly shortbelly rockfish) appeared to be more important in the diet of larger sablefish than smaller sablefish, while the prey category of "Other fish" (mostly Pacific sanddab and northern anchovy) displayed the opposite pattern. North of Cape Blanco in 1989, fishery offal also appeared to be more important to the larger sablefish than the smaller ones, while the opposite pattern appeared for consumption of euphausiids. In 1991, scorpaenids (mostly longspine thornyheads) were increasingly important with size while the prey categories of other fish and fishery offal generally decreased in importance with sablefish size. In 1992, only a narrow size range of sablefish was sampled, but herring appeared to be important in the diets of only smaller (40-49 cm FL) sablefish.

DISCUSSION

The wide variety of prey in the diet of sablefish in this and other studies indicates that it is an opportunistic predator and scavenger in both pelagic and benthic habitats (Low et al. 1976). The observed sablefish diet is affected by ontogeny, geographic location, season, and interannual and daily changes in prey availability (Low et al. 1976), and these factors have been examined to various extents in other studies. In addition, Kulikov (1965, cited in Low et al. 1976) described differences in diurnal and nocturnal prey of sablefish.

The observed changes in the diet with increasing size of sablefish in this study were generally consistent with changes observed in other studies. As size increases, sablefish include an increasing amount of benthic prey in their diet and the size of prey tends to increase (Laidig et al. 1997). Off southern California, sablefish in their first year eat copepods, euphausiids, and larvaceans; age-2 sablefish eat amphipods, mysids, euphausiids, gastropods, cephalopods, and fish; sablefish over age-3 eat mostly fish (especially thornyheads) and cephalopods (Conway 1967). The diet of three size groups of sablefish were examined by Cailliet et al. (1988) in Monterey Bay. The larger sablefish occupied a wider and deeper depth range than smaller sablefish, and their diet reflected this shift in distribution from pelagic fish and cephalopods to a more diverse diet including demersal fish and crustaceans (Cailliet et al. 1988). Examining sablefish from two areas off Oregon and California, Laidig et al. (1997) found that small crustaceans and heteropods decreased and fish increased in the diet of sablefish with increasing size (from < 30 cm FL to > 60 cm FL). In addition, the species composition of the fish prey changed, with rockfish and eelpouts decreasing and thornyheads increasing in their contribution to the diet with the size of the sablefish examined (Laidig et al. 1997). Off Oregon and Washington, larval sablefish eat mostly copepods (Grover and Olla 1987) and juvenile sablefish (13-41 cm FL) caught by purse seine eat euphausiids, salps, cnidarians, and fish (Brodeur et al. 1987). Off the southwest corner of Vancouver Island, Pacific herring and other fish are eaten more often by larger (40-80 cm FL)

sablefish than smaller (< 40 cm FL) sablefish, and euphausiids and other invertebrates decrease in importance in the diet as sablefish size increases (Tanasichuk 1997). In the Gulf of Alaska, Yang (1993) found very little difference in the diets that could be attributed to change in sablefish size from 40 to 80 cm FL; however, it appeared that fishery offal decreased and walleye pollock (*Theragra chalcogramma*) increased with predator size. An increasing amount of fish in the sablefish diet with length was found in the Gulf of Alaska and the Aleutian Islands region for sablefish caught by longline, but for sablefish caught by trawl in the Aleutian Islands region and the Bering Sea, such an increase was less evident (Sasaki 1985).

Geographic variation in the diet of sablefish has been recognized on several scales. In reviewing some diet descriptions from the Bering Sea, Aleutian Islands, Gulf of Alaska, and British Columbia, Tanasichuk (1997) pointed out that the fish component of the diets reflected local species compositions. Laidig et al. (1997) found that sablefish ate more midwater prey, including heteropods and thaliacians, and less fish off central California than off Oregon. Brodeur et al. (1987) found the diet of smaller (22 cm mean FL; 13-41 cm FL range), purse-seine caught sablefish to be mostly euphausiids, fish and pteropods off central Oregon, mostly fish and secondarily cnidarians and decapod larvae off the Columbia River, and dominated by hyperiid amphipods and euphausiids off Washington. On a smaller scale, Tanasichuk (1997) found a significant location effect on the amount of Pacific herring and other fish in their diet off the southwest corner of Vancouver Island. In our study, it appears that the fish in the diet reflect the locally available species and, consequently, the latitudinal variation in the diet seems to be more pronounced on the continental shelf than on the continental slope.

Little is known about the seasonal variation in the diet of sablefish. In the Bering Sea, it is reported that the sablefish diet consists mostly of fish during the early spring, switches to shrimp, ctenophores, and some benthic organisms during the summer, and switches back to fish during autumn (Shubnikov 1963, cited in Low et al. 1976). A similar pattern in the amount of fish (primarily shortspine thornyhead, *Sebastolobus alascanus*, a benthic species) in the diet was found in the southern California Bight (September through February) (Conway 1967). The pattern in fish consumption may be related to seasonal changes in preferred habitat. Adult sablefish appear to move into shallower water during the summer, while in autumn through spring, they occupy deeper water where they spawn in the winter (Cailliet et al. 1988). We were unable to make many inferences about the seasonal feeding habits of sablefish because, although we collected stomach samples from sablefish in summer and autumn months, the depths sampled and the years sampled were different.

Interannual differences in the diet of larval sablefish have been documented and were attributed to El Nino conditions in 1983 (Grover and Olla 1987). Similarly, Brodeur et al. (1987) found interannual differences in juvenile sablefish diets, with the most difference occurring in 1983. Interannual differences in the frequency and amount of Pacific herring in the diet of sablefish was linked to the abundance of Pacific herring stocks around southwest Vancouver Island (Tanasichuk 1997). We were unable to make interannual comparisons in this study.

Although sample sizes are low in some areas, gross comparison with other studies conducted in the same area and season and on the same size of sablefish can be made. In the Conception INPFC area, we found more fish in the summer diet than found by

Conway (1967), but northern anchovy was a fairly important diet component in both studies. In the Monterey INPFC area, we found fishery offal, euphausiids, shortbelly rockfish and Pacific sanddab were important diet components in the summer (30-199 fm), and fishery offal, longspine thornyheads, squid, and *Chionoecetes* sp. crabs were important diet components in autumn (200-914 fm). The prey reported by Cailliet et al. (1988) were similar, but ranked differently in importance, perhaps because those sablefish were taken by traps and were sampled over a 1-year period. Laidig et al. (1997) collected sablefish in autumn or winter from 1987 through 1992 from a depth range similar to our autumn samples, and the prey were similar to those we found. Gotshall (1969) found pink shrimp (*Pandalus jordani*) and euphausiids in the stomachs of five sablefish from the Eureka INPFC area in summer. We found euphausiids and fishery offal dominated the diet by weight, but pink shrimp also occurred in summer in the Eureka INPFC area. The “northern area” reported on by Laidig et al. (1997) roughly corresponds to the Eureka and southern portion of the Columbia INPFC areas reported on in this study. We found the three most important prey, by weight, to be longspine thomyhead, fishery offal, and Pacific hake in the Eureka and Columbia INPFC areas. Similarly, Laidig et al. (1997) reported over 80% of the diet volume to be composed of fish in their northern area with longspine thornyheads and Pacific hake comprising the majority of fish volume in the diet. In the Vancouver INPFC area, we found euphausiids, Pacific herring, and fishery offal were important diet components in the summer (30-99 fm), which, except for the fishery offal, was similar to the diet found by Tanasichuk (1997) in summer.

The occurrence of fishery offal in the sablefish diet was a consistent difference between this study and the others. It is possible that fishery offal (mostly heads of Pacific hake) was 1) not considered a prey item, 2) identified and included as Pacific hake or unidentified fish, or 3) not present in any of the stomachs examined in other studies. Fishery offal in the diet of sablefish has also been found in the Gulf of Alaska (Yang 1993) and the eastern Bering Sea (Brodeur and Livingston 1988). Because most of the fishery offal is comprised of Pacific hake parts, and Pacific hake is already a common prey of sablefish, the at-sea fish-processing operations may not be disrupting regular food web linkages. However, the spatial distribution of sablefish may be affected by fish processing operations because sablefish may be attracted to the area by the odor plume (Lokkeborg et al. 1995) and remain in the area, feeding on the concentrations of offal.

Table 7.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of sablefish (*Anoplopoma fimbria*) caught south of Cape Blanco in the summer of 1989.

Prey Name	%F	%N	%W
Polynoidae (polychaete)	7.75	0.33	0.94
Gastropoda (snail)	1.55	0.04	0.01
Teuthoidea (squid)	4.65	0.09	5.41
Teuthoidea oegopsida (squid)	0.78	0.01	0.01
Octopoda (octopus)	3.10	0.06	1.68
Crustacea	0.78	0.03	0.00
Calanoida (copepod)	3.88	1.07	0.01
Gammaridea (amphipod)	3.88	0.49	0.03
Hyperiididae (amphipod)	3.10	0.17	0.01
Hyperiididae (amphipod)	1.55	0.03	0.00
<i>Themisto</i> sp. (amphipod)	0.78	0.01	0.00
Eucarida	1.55	0.03	0.00
Euphausiacea (euphausiid)	5.43	2.40	0.43
Euphausiidae (euphausiid)	25.58	48.30	6.48
<i>Euphausia pacifica</i> (euphausiid)	32.56	38.00	9.76
<i>Stylocheiron Zongicorne</i> (euphausiid)	0.78	0.01	0.00
<i>Stylocheiron maximum</i> (euphausiid)	0.78	0.04	0.01
<i>Thysanoessa Zongipes</i> (euphausiid)	0.78	0.01	0.01
<i>Thysanoessa spinifera</i> (euphausiid)	13.18	6.63	1.62
<i>Sergestes</i> sp. (sergestid shrimp)	3.10	0.07	0.05
Reptantia (crab)	0.78	0.01	0.00
<i>Pandalus jordani</i> (pink shrimp)	0.78	0.01	0.14
Lithodidae (king crab)	0.78	0.01	0.00
<i>Lithodes couesi</i> (couesi king crab)	0.78	0.01	1.98
<i>Cancer</i> sp. (crab)	0.78	0.38	0.01
Echiuridae (marine worm)	0.78	0.01	0.17
Echinodermata (sea star, cucumber, urchin)	0.78	0.01	0.01
Ophiuridae (brittle star)	0.78	0.01	0.00
<i>Echinacea</i> sp. (sea urchin)	3.10	0.06	0.33
Urochordata (tunicate)	1.55	0.03	0.83
Larvacea Copelata	0.78	0.01	0.00
Osteichthyes Holostei (cartilaginous fish)	0.78	0.01	0.05
Osteichthyes Teleostei (bony fish)	23.26	0.49	4.49
Clupeidae	0.78	0.01	0.62
<i>Engraulis mordax</i> (northern anchovy)	3.10	0.09	6.38
Osmeridae (smelts)	0.78	0.01	0.10

Table 7.--Continued.

Prey Name	%F	%N	%W
Myctophidae (lanternfish)	2.33	0.04	0.36
<i>Sebastes</i> sp. (rockfish)	1.55	0.03	1.93
<i>Sebastes jordani</i> (shortbelly rockfish)	3.10	0.12	15.57
<i>Peprilus simillimus</i> (Pacific butterflyfish)	0.78	0.01	3.16
Pleuronectiformes Pleuronectoidei (flatfish)	0.78	0.01	0.04
<i>Citharichthys sordidus</i> (Pacific sanddab)	3.88	0.07	18.42
Pleuronectidae (flatfish)	1.55	0.03	0.31
Unidentified organic material	15.50	0.29	0.30
Offal	15.50	0.29	17.87
Unidentified tube	0.78	0.01	0.00
Unidentified algae	1.55	0.03	0.43
Unidentified material	0.78	0.01	0.03
Total prey number:	6,913		
Total prey weight:	1,512.57 g		
Total non-empty stomachs:	129		
Total empty stomachs:	30		

Table 8.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of sablefish (*Anoplopoma fimbria*) caught north of Cape Blanco in the summer of 1989.

Prey Name	%F	%N	%W
Phaeophyta (brown algae)	0.97	0.02	0.14
Scyphozoa (jellyfish)	1.30	0.03	0.27
Annelida (worm)	0.65	0.02	0.00
Polychaeta (worm)	4.55	0.12	0.40
Polynoidae (polychaete)	0.32	0.01	0.02
Opheliidae (polychaete)	0.32	0.01	0.08
Mollusca	0.32	0.01	0.02
Gastropoda (snail)	4.22	0.18	0.02
Bivalvia (clam)	0.32	0.01	0.00
Cephalopoda (squid & octopus)	0.65	0.02	0.00
Teuthoidea (squid)	4.22	0.31	0.32
Loliginidae (squid)	0.32	0.01	0.07
<i>Loligo opalescens</i> (squid)	0.32	0.01	0.07
Teuthoidea oegopsida (squid)	0.65	0.02	0.02
Octopoda (octopus)	1.30	0.08	0.16
Octopodidae (octopus)	0.32	0.01	0.36
Crustacea	2.27	0.08	0.00
Calanoida (copepod)	0.65	0.02	0.00
Peracarida Mysidacea (mysid)	0.65	0.02	0.00
Isopoda (isopod)	1.95	0.05	0.01
Gammaridea (amphipod)	14.29	2.79	0.13
Ampeliscidae (amphipod)	0.32	0.01	0.01
Gammaridae (amphipod)	0.32	0.02	0.00
Hyperiid (amphipod)	4.22	0.32	0.01
Eucarida	1.30	0.50	0.01
Euphausiidae (euphausiid)	24.68	25.71	3.37
<i>Euphausia</i> sp. (euphausiid)	3.90	7.85	1.11
<i>Euphausia pacifica</i> (euphausiid)	23.70	12.06	2.09
<i>Nematoscelis difficilis</i> (euphausiid)	0.32	0.01	0.00
<i>Thysanoessa</i> sp. (euphausiid)	1.30	0.28	0.05
<i>Thysanoessa longipes</i> (euphausiid)	0.97	0.02	0.00
<i>Thysanoessa spinifera</i> (euphausiid)	16.23	38.22	6.80
Decapoda (shrimp & crab)	0.65	0.04	0.00
Sergestidae (sergestid shrimp)	0.32	0.01	0.00
<i>Sergestes</i> sp. (sergestid shrimp)	0.32	0.01	0.01
Reptantia (crab)	0.65	0.02	0.22

Table 8.--Continued.

Prey Name	%F	%N	%W
Caridea (shrimp)	2.92	0.08	0.23
Pandalidae (shrimp)	3.25	0.34	1.07
<i>Pandalus</i> sp. (shrimp)	2.60	0.31	1.21
<i>Pandalus jordani</i> (pink shrimp)	2.27	0.09	0.62
Crangonidae (shrimp)	1.62	0.05	0.05
<i>Crangon</i> sp. (shrimp)	0.32	0.01	0.00
<i>Argis</i> sp. (shrimp)	0.65	0.02	0.02
Natantia (shrimp)	2.92	0.07	0.01
Anomura (crab)	0.65	0.02	0.49
Galatheididae (pelagic slip crabs)	3.90	0.41	0.45
<i>Munida quadrispina</i> (pinch bug)	0.32	0.02	0.08
Decapoda brachyura (crab)	0.65	0.02	0.00
Cancriidae (crab)	0.97	0.03	0.00
<i>Cancer</i> sp. (crab)	0.65	0.06	0.01
<i>Cancer magister</i> (Dungeness crab)	1.95	0.06	0.01
<i>Cancer oregonensis</i> (pygmy cancer crab)	0.32	0.01	0.00
Sipuncula (marine worm)	1.30	0.03	0.81
Echiuroinea (marine worm)	0.32	0.01	0.09
<i>Echiurus</i> sp. (marine worm)	0.65	0.04	0.03
Ophiuroidea (basket & brittle star)	2.92	0.12	0.06
Ophiuridae (brittle star)	1.95	0.21	0.22
Echinoidea (sea urchin and sand dollar)	0.32	0.01	0.00
<i>Echinacea</i> sp. (sea urchin)	0.32	0.01	0.01
Holothuroidea (sea cucumber)	0.32	0.01	0.01
Urochordata (tunicate)	0.97	0.04	0.09
Thaliacea (pelagic salp)	9.42	6.23	2.99
<i>Eptatretus</i> sp.	0.32	0.01	3.63
<i>Eptatretus stouti</i> (Pacific hagfish)	0.65	0.02	4.41
Gnathostomata	0.32	0.01	0.00
<i>Hydrolagus colliei</i> (ratfish)	0.32	0.01	1.50
Osteichthyes Teleostei (bony fish)	11.04	0.28	0.49
Non-gadoid fish remains	6.17	0.15	1.80
Fish eggs	0.32	0.44	0.08
Clupeidae	1.30	0.06	5.74
<i>Clupea pallasii</i> (Pacific herring)	17.21	0.76	16.65
<i>Oncorhynchus</i> sp. (salmon)	0.32	0.02	0.96
Osmeridae (smelts)	0.97	0.03	0.38
<i>Thaleichthys pacificus</i> (eulachon)	0.65	0.02	0.17

Table 8.--Continued.

Prey Name	%F	%N	%W
Myctophidae (lanternfish)	0.32	0.02	0.03
<i>Tarletonbeania crenularis</i> (blue lanternfish)	0.32	0.01	0.01
Zoarcidae (eelpout)	0.32	0.02	0.24
<i>Lycodapus</i> sp. (eelpout)	0.65	0.02	0.06
<i>Lycodopsis pacifica</i> (blackbelly eelpout)	0.65	0.02	0.44
<i>Cololabis saira</i> (Pacific saury)	0.32	0.01	1.25
<i>Gasterosteus aculeatus</i> (3-spined stickleback)	0.32	0.01	0.01
Scorpaenidae (rockfish)	0.65	0.02	0.17
<i>Anoplopoma fimbria</i> (sablefish)	0.32	0.02	2.63
Agonidae (poacher)	0.65	0.02	0.32
Stichaeidae (prickleback)	0.65	0.02	0.12
Pleuronectiformes Pleuronectoidei (flatfish)	0.97	0.02	0.03
Bothidae (left-eye flounders)	0.32	0.01	0.19
<i>Citharichthys sordidus</i> (Pacific sanddab)	0.32	0.01	0.10
Pleuronectidae (flatfish)	0.65	0.02	1.34
<i>Errex zachirus</i> (rex sole)	0.65	0.02	2.10
Aves (bird part)	0.32	0.01	0.00
Unidentified organic material	11.36	0.27	0.92
Unidentified worm-like organism	0.32	0.01	0.06
Offal	22.08	0.54	29.81
Overboard material (non-fishery)	0.32	0.01	0.00
Unidentified algae	0.65	0.02	0.02
Unidentified material	0.32	0.01	0.02
Total prey number:	13,104		
Total prey weight:	4,792.42 g		
Total non-empty stomachs:	308		
Total empty stomachs:	47		

Table 9.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of sablefish (*Anoplopoma Jimbria*) caught south of Cape Blanco in the fall of 1991.

Prey Name	%F	%N	%W
Gastropoda (snail)	2.27	1.40	0.00
Bivalvia (clam)	1.14	0.70	0.00
Teuthoidea (squid)	13.64	8.39	9.63
Loliginidae (squid)	1.14	0.70	0.80
Octopoda (octopus)	1.14	0.70	0.06
Peracarida Mysidacea (mysid)	1.14	0.70	0.00
Hyperiidia (amphipod)	3.41	2.80	0.00
Hyperiididae (amphipod)	2.27	1.40	0.08
Euphausiidae (euphausiid)	1.14	0.70	0.00
<i>Sergestes</i> sp. (sergestid shrimp)	7.95	4.90	0.10
Majidae (spider crab)	2.27	1.40	2.62
<i>Chionoecetes</i> sp. (snow and Tanner crab)	4.55	3.50	3.81
Urochordata (tunicate)	1.14	0.70	3.83
<i>Eptatretus</i> sp.	1.14	0.70	0.14
Osteichthyes Teleostei (bony fish)	10.23	6.29	0.18
Non-gadoid fish remains	3.41	2.10	0.04
<i>Bathylagus pacificus</i> (slender blacksmelt)	1.14	0.70	0.26
<i>Chauliodus macouni</i> (Pacific viperfish)	1.14	0.70	1.02
<i>Saganichthys abei</i> (shining tubesnout)	1.14	0.70	0.24
Myctophidae (lanternfish)	4.55	2.80	0.32
<i>Tarletonbeania crenularis</i> (blue lanternfish)	1.14	0.70	0.09
Gadidae (gadid fish)	7.95	4.90	2.55
<i>Merluccius productus</i> (Pacific hake)	2.27	1.40	3.34
Scorpaenidae (rockfish)	2.27	1.40	0.11
<i>Sebastolobus</i> sp. (unidentified thornyhead)	3.41	2.10	1.24
<i>Sebastolobus alascanus</i> (shortspine thornyhead)	3.41	2.10	3.26
<i>Sebastolobus altivelis</i> (longspine thornyhead)	20.45	15.38	24.24
Pleuronectiformes Pleuronectoidei (flatfish)	1.14	0.70	0.13
<i>Microstomus pacificus</i> (Dover sole)	1.14	0.70	2.24
Unidentified organic material	5.68	4.20	1.98
Unidentified worm-like organism	1.14	0.70	0.42
Offal	35.23	23.08	37.22
Unidentified tube	1.14	0.70	0.00

Table 9.--Continued.

Total prey number:	143
Total prey weight:	3,352.83 g
Total non-empty stomachs:	88
Total empty stomachs:	16

Table 10.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of sablefish (*Anoplopoma fimbria*) caught north of Cape Blanco in the fall of 1992.

Prey Name	%F	%N	%W
Cnidaria	1.32	0.24	0.04
Polychaeta (worm)	2.63	0.94	0.04
Gastropoda (snail)	1.32	0.24	0.04
Bivalvia (clam)	1.32	0.24	0.03
Cephalopoda (squid & octopus)	3.95	0.71	0.04
Teuthoidea (squid)	5.26	1.18	0.87
Teuthoidea oegopsida (squid)	2.63	0.47	0.07
Octopoda (octopus)	2.63	0.47	0.08
Ampeliscidae (amphipod)	2.63	4.48	0.02
Hyperiididae (amphipod)	1.32	2.12	0.01
Euphausiacea (euphausiid)	2.63	0.94	0.00
Euphausiidae (euphausiid)	3.95	64.62	0.23
<i>Euphausia</i> sp. (euphausiid)	1.32	1.18	0.01
<i>Thysanoessa</i> sp. (euphausiid)	1.32	0.47	0.00
Decapoda (shrimp & crab)	1.32	0.47	0.30
Reptantia (crab)	1.32	0.47	0.29
<i>Eualus macrophthalma</i> (shrimp)	1.32	0.24	0.02
Pandalidae (shrimp)	1.32	0.24	0.02
<i>Hyas</i> sp. (lyre crab)	1.32	0.24	0.12
<i>Chionoecetes</i> sp. (snow and Tanner crab)	6.58	1.42	4.16
Echiuridae (marine worm)	1.32	0.24	0.09
Ophiuroidea Ophiurida (brittle star)	2.63	0.47	0.03
<i>Echinacea</i> sp. (sea urchin)	2.63	0.47	0.01
Osteichthyes Teleostei (bony fish)	17.11	3.54	3.77
Non-gadoid fish remains	7.89	1.42	0.24
<i>Clupea pallasii</i> (Pacific herring)	2.63	0.47	3.56
Osmeridae (smelts)	1.32	0.24	0.28
<i>Leuroglossus</i> sp.	1.32	0.24	0.25
<i>Merluccius productus</i> (Pacific hake)	19.74	3.77	20.19
<i>Lycodapus</i> sp. (eelpout)	1.32	-0.24	0.16
<i>Sebastes</i> sp. (rockfish)	1.32	0.24	3.53
<i>Sebastolobus alascanus</i> (shortspine thornyhead)	1.32	0.24	1.84
<i>Sebastolobus altivelis</i> (longspine thornyhead)	25.00	5.42	46.76
Offal	9.21	1.65	12.92

Table 10.--Continued.

Total prey number:	424
Total prey weight:	2,875.73 g
Total non-empty stomachs:	76
Total empty stomachs:	37

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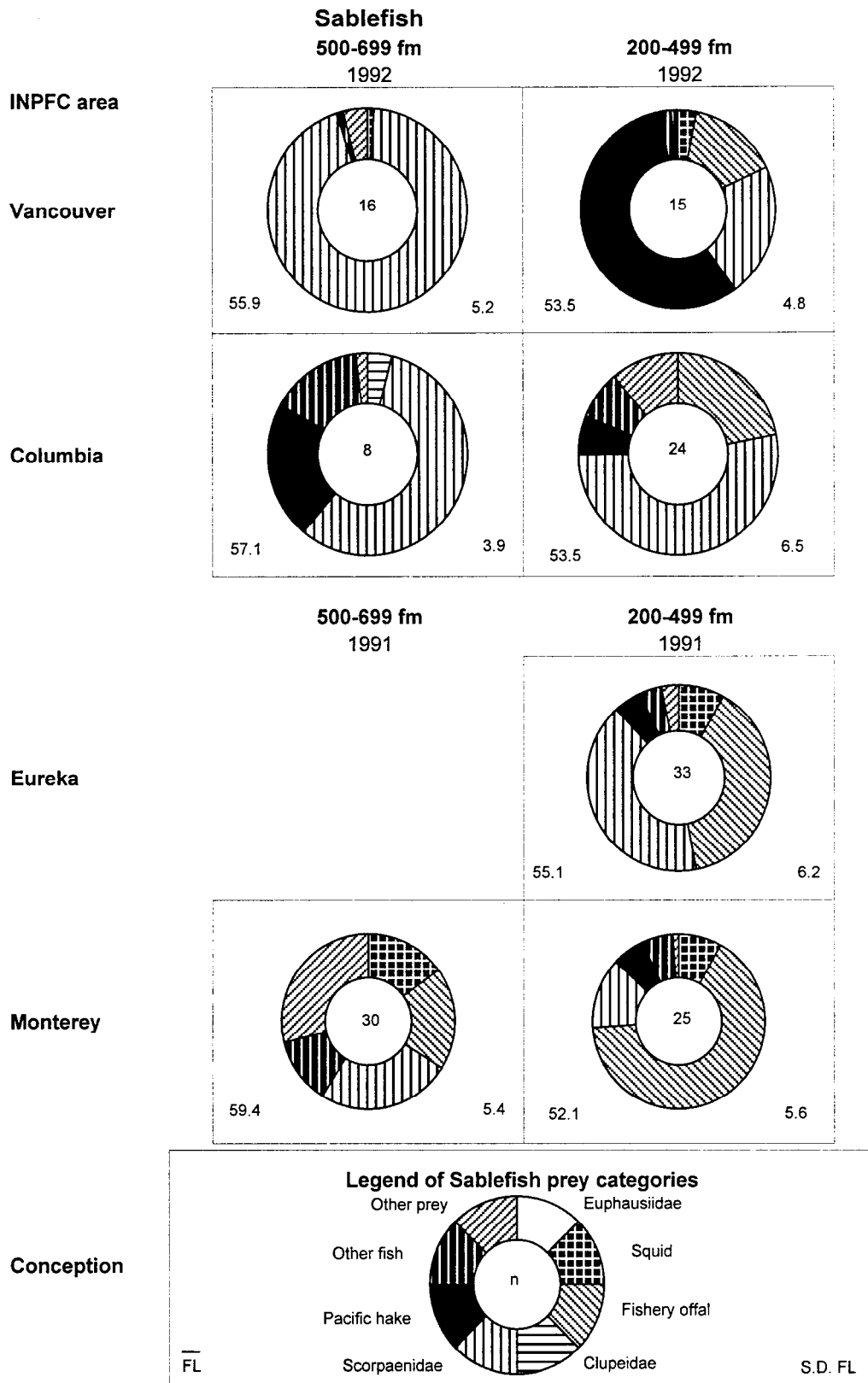


Figure 6.--Diet composition (by weight) of sablefish for each depth zone, INPFC area and year. The number of nonempty stomachs examined are shown in each ring. Mean and standard deviation of the fork lengths are shown in the lower left and right of each box, respectively.

Sablefish

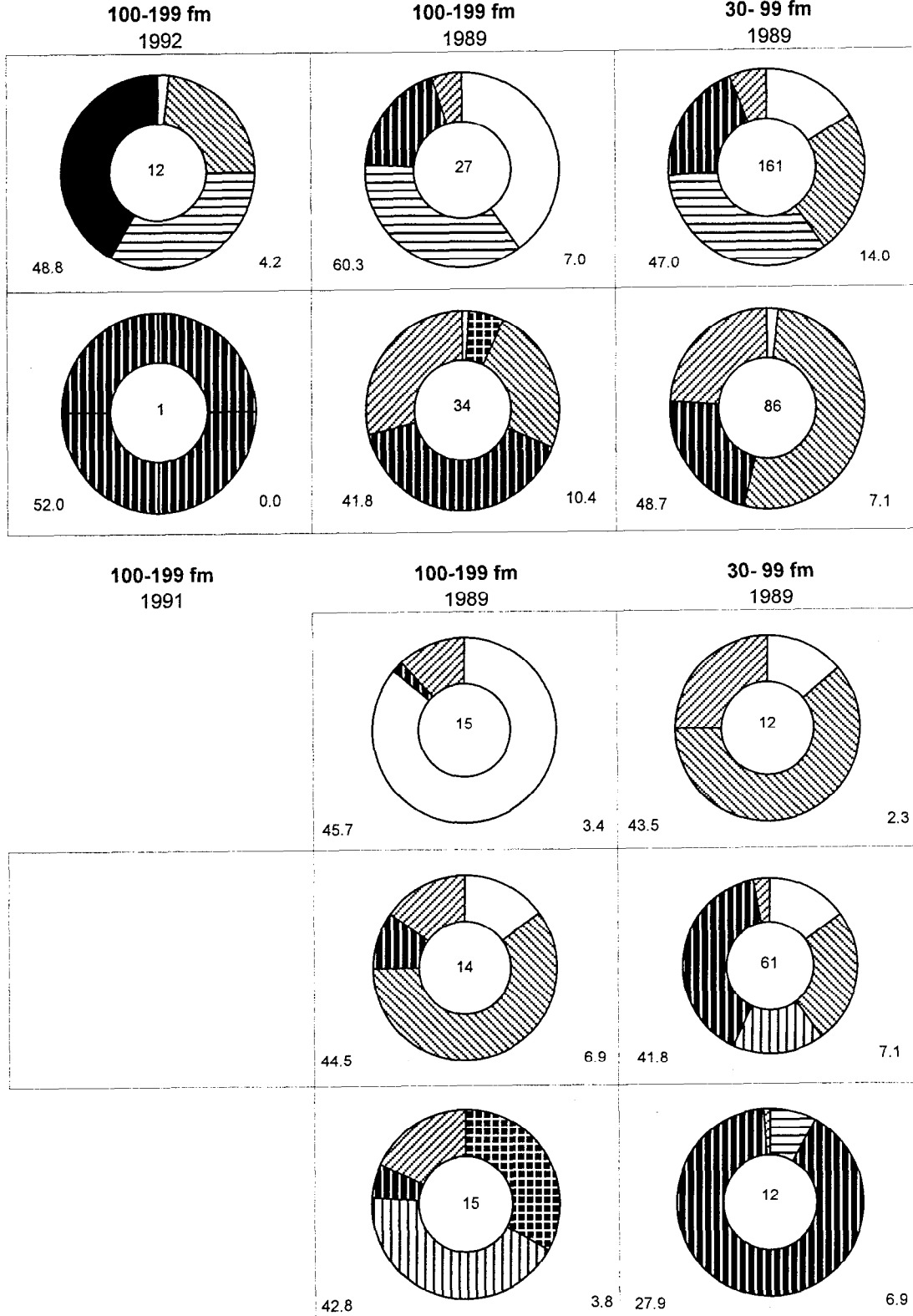


Figure 6.--Continued.

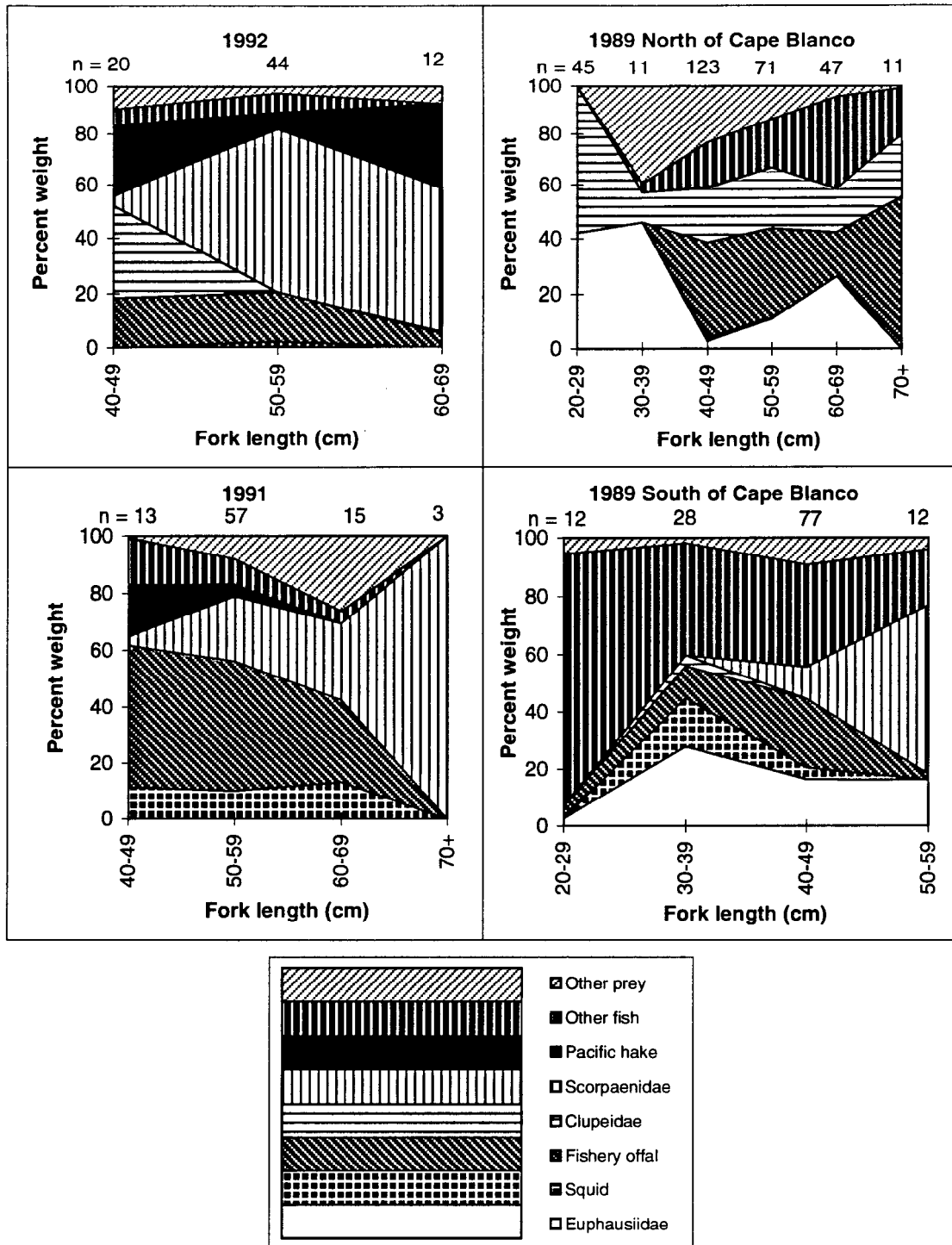


Figure 7.--Diet composition of sablefish (by length) from north and south of Cape Blanco in 1989 and from the 1991 and 1992 surveys. The total length-range shown in each figure may be different. The sample size (n) is shown above each length group.

SHORTSPINE THORNYHEAD

Shortspine thornyhead (*Sebastolobus alascanus*) is a component of the deepwater species complex managed by the Pacific Fishery Management Council (Ianelli et al. 1994). In response to developing Japanese export markets, higher prices, and the movement of the bottom trawl fishery into deeper water (Jacobson 1993), landings of shortspine thornyheads in Washington, Oregon, and California have increased from an average of 250 metric tons (t) per year in the late 1960s to 3,300 t per year in the early 1990s (Ianelli et al. 1994).

The shortspine thornyhead primarily inhabits the continental slope between 300 and 1,100 m, but they can be found as shallow as 90 m and at depths exceeding 1,500 m (Jacobson 1993). Geographically, shortspine thornyhead range from northern Baja California to the Bering Sea and to the Commander Islands of the Asiatic mainland (Jacobson 1993). In the northern portions of the range, shortspine thornyhead can be found as shallow as 25 m (Jacobson 1993). Sexual maturity is attained by 50% of the fish at 21 cm total length (TL) or about 12-13 years (Jacobson 1993). In late winter or early spring, buoyant, bilobate egg masses are spawned that range in length from 15 to 61 cm (Hart 1973, Jacobson 1993). About 14 to 15 months later, juvenile shortspine thornyhead settle out of their pelagic phase onto the continental shelf at sizes of 22 to 27 mm TL (Jacobson 1993). Shortspine thornyheads seem to move into deeper water as they grow (Ianelli et al. 1994) because larger individuals tend to be found in deeper water (Jacobson 1993). Shortspine thornyheads can grow to 75 cm TL (Hart 1973) and, based on otolith increments, may reach ages approaching 150 years (Ianelli et al. 1994). However, radiometric methods suggest that maximum ages may be between 50 and 100 years (Ianelli et al. 1994).

The stomach contents of shortspine thornyhead have been described from the Aleutian Islands (Yang 1996), Gulf of Alaska (Yang 1993), southeastern Alaska (Miller 1985), and Oregon and California (Tom Laidig, personal communication').

RESULTS

General Diets

Only 30 shortspine thornyhead stomachs were collected south of Cape Blanco in summer of 1989 and 14 (47%) of them were empty. By weight, fish (94%), especially Pacific hake, dominated the contents of the stomachs that contained food (Table 11). Forty-four (26%) of the 170 shortspine thornyhead stomachs collected north of Cape Blanco were empty. The contents of the stomachs with food in them are described in Table 12. Caridean shrimp, especially pandalids, dominated the diet by weight and number (51% and 42%, respectively). During the slope survey of autumn 1991, 216 stomachs were collected, 18 (8%) of which were empty (Table 13). Tanner crabs (*Chionoecetes* spp.) were important in the diet by weight and number (61% and 23%, respectively). During the slope survey of autumn 1992, 193 stomachs were collected

¹ National Marine Fisheries Service, Southwest Fisheries Science Center, Tiburon Laboratory, 3150 Paradise Drive, Tiburon, CA 94920. Phone: (415) 435-3149.

north of Cape Blanco and 60 (31%) of them were empty (Table 14). Fish (67%) and Tanner crabs (18%) dominated the diet by weight, but small crustaceans were more important numerically. Scorpaenids (rockfishes and thornyheads, 29%) were the most important type of fish prey by weight.

Variation of the Diet with Location

In the Conception INPFC area, Pacific hake were the dominant diet component of the shortspine thornyhead sampled, by weight, in the summer of 1989 (Fig. 8). In addition, most of the “Other fish” category was comprised of gadid fish that could not be positively identified as Pacific hake (Table 13).

The Monterey INPFC area was only sampled in the autumn of 1991, and the length of the sampled shortspine thornyheads increased with depth (Fig. 8). The diet also changed with increasing depth (and length, see below) from mostly “Other prey” (polychaetes, molluscs, and echinoderms) and fishery offal to scorpaenids, fishery offal, and some Tanner crab, then to mostly Tanner crab. Scorpaenids seemed to decrease in importance in the 200-499 fm zone going northward through the Eureka and Columbia INPFC areas.

Similar diets were observed for shortspine thornyhead sampled in the 200-499 fm zone in the Columbia INPFC area during both the 1991 and 1992 slope surveys, and thus, samples from the two years were combined in Figure 8. In the Columbia INPFC area, scorpaenids, Pacific hake and non-gadoid fish remains (included in “Other fish”) were important diet components in the 500-699 fm zone in autumn 1992. In the summer of 1989, pandalid shrimp and mud shrimp (*Axiopsis* sp., included in “Other crustacea”) were important on the continental shelf.

In the Vancouver INPFC area, “Other crustacea” were most important in the diet of shortspine thornyhead caught on the continental shelf and included crangonid shrimps, slip crabs, and decorator crabs in the 30-99 fm zone and mostly slip crabs in the 100-199 fm zone. Fishery offal was also important in the 100-199 fm zone sampled in summer 1989. Smaller shortspine thornyheads were sampled in this same depth zone in autumn 1992, and the composition of the “Other crustacea” included mysids, hyperiid amphipods, and hippolitid shrimp. In deeper water, fishery offal and Tanner crabs were important while the fraction of scorpaenids in the diet, by weight, appeared to decrease (Fig. 8).

Variation of the Diet with Predator Size

Regardless of the area, season, or year sampled, “Other crustacea” seemed to be the most important component in the diet of small (FL < 20 cm) shortspine thornyhead (Fig. 9). The importance of “Other crustacea” generally decreased with increasing size. On the continental shelf in 1989 south of Cape Blanco, predation on juvenile Pacific hake was important to the few shortspine thornyhead sampled. North of Cape Blanco in summer of 1989, pandalid shrimp appeared to increase then decrease in importance with increasing predator size. The diet of shortspine thornyheads sampled in autumn of 1991 included an increasing amount of Tanner crab, by weight, with increasing size, while the proportion of scorpaenids in the diet increased then decreased with increasing size. The opposite pattern was true for shortspine thornyheads sampled in autumn of 1992 with the

proportion of scorpaenids increasing and Tanner crabs increasing then decreasing in the diet as a function of predator size.

DISCUSSION

The results of this study were generally consistent with the results of other investigations of the stomach contents of shortspine thornyhead. Around the Aleutian Islands, fish (65%), shrimp (23%), and crab (9%) were the major components of the diet by weight (Yang 1996). In the Gulf of Alaska, shrimp (67%) comprised more of the diet than fish (17%) or crab (11%) by weight (Yang 1993). In a study conducted over a smaller area in southeastern Alaska, Miller (1985) found fish (42%), shrimp (27%) and crab (11%) were volumetrically the most important groups in the diet of shortspine thornyhead. Off Oregon and California, shortspine thornyhead eat mostly fish, shrimp, and crab (Tom Laidig, personal communication). The shortspine thornyhead appears to be an opportunistic predator that will consume a variety of locally available crustaceans and fish that are on or near the bottom. Yang (1993) suggests that the large terminal mouth and the presence of relatively few stout gill-rakers are consistent with this epibenthic feeding strategy.

The presence in the diet of offal from fish processing activities indicates that shortspine thornyhead are also scavengers. The offal found in the stomachs of this species were primarily heads of Pacific hake. It is possible that the biological identity of undigested parts of fishery offal could be identified (i.e., Pacific hake, gadidae, or fish remains), but that evidence of it being processed by the fishery would be lacking. If this were the case, the amount of fishery offal in the diet would be underestimated.

Changes in the diet that occurred as a function of predator size were generally in agreement with other studies. Yang (1996) found a decrease in the proportion of small crustaceans and an increase in the proportion of fish and larger crustaceans in the diet with increasing size of Aleutian Islands shortspine thornyheads. Similarly, in an area of southeastern Alaska, the diet was found to shift from mainly smaller shrimp and amphipods to mainly larger shrimp (pandalids) and fish (Miller 1985). Laidig also found a shift in the diet from mainly shrimp to mainly fish and crab in Oregon and northern California.

The observed changes in diet with size may also be a function of prey availability with depth because, on average, larger shortspine thornyhead are found in deeper water than smaller individuals (Jacobson 1993). Miller (1985) concluded that the observed change in diet with size was probably not related to depth, but samples were collected over a relatively narrow depth range (183-330 m, or 100-180 fm) when compared to the depth range inhabited by this species. Larger sample sizes than were taken in this study would be required to differentiate between the influence of bottom depth and predator size on the diet of shortspine thornyhead.

Table 11 .--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of shortspine thornyhead (*Sebastolobus alascanus*) caught south of Cape Blanco in the summer of 1989.

Prey	%F	%N	%W
Polynoidae (polychaete)	6.25	3.70	0.13
Terebellidae (polychaete) .	6.25	7.41	1.07
Malacostraca	6.25	3.70	0.00
Peracarida Mysidacea (mysid)	18.75	14.81	0.50
Gammaridea (amphipod)	6.25	3.70	0.03
Hyperiidea (amphipod)	6.25	3.70	0.10
<i>Euphausia pacifica</i> (euphausiid)	6.25	3.70	0.14
Caridea (shrimp)	6.25	3.70	0.20
<i>Crangon communis</i> (shrimp)	6.25	3.70	2.17
Natantia (shrimp)	12.50	7.41	1.11
Pinnotheridae (pea crab)	18.75	11.11	0.49
Non-gadoid fish remains	6.25	3.70	9.41
Gadidae (gadid fish)	12.50	7.41	17.79
<i>Merluccius productus</i> (Pacific hake)	25.00	22.22	66.85
Total prey number:	27		
Total prey weight:	40.07 g		
Total non-empty stomachs:	16		
Total empty stomachs:	14		

Table 12.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of shortspine thornyhead (*Sebastolobus alascanus*) caught north of Cape Blanco in the summer of 1989.

Prey	%F	%N	%W
Polychaeta (worm)	0.79	0.25	0.00
Aphroditidae (sea mouse)	1.59	0.50	1.20
Polynoidae (polychaete)	2.38	0.76	0.14
Gastropoda (snail)	0.79	0.25	0.08
Bivalvia (clam)	1.59	0.50	0.26
Teuthoidea (squid)	2.38	0.76	0.07
Crustacea	1.59	0.50	0.12
Copepoda	0.79	1.01	0.00
Calanoida (copepod)	0.79	0.25	0.00
Peracarida Mysidacea (mysid)	8.73	5.79	0.12
Isopoda (isopod)	1.59	0.50	0.58
Gammaridea (amphipod)	9.52	6.05	0.28
Hyperiidia (amphipod)	1.59	0.50	0.07
Euphausiidae (euphausiid)	7.94	3.78	0.06
<i>Euphausia paciJica</i> (euphausiid)	4.76	1.76	0.10
<i>Thysanoessa spinifera</i> (euphausiid)	1.59	0.50	0.05
Caridea (shrimp)	8.73	2.77	1.92
Hippolytidae (shrimp)	7.94	3.27	0.94
<i>Spirontocaris</i> sp. (shrimp)	2.38	1.26	0.44
<i>Spirontocaris holmesi</i> (shrimp)	7.94	3.53	2.64
<i>Eualus</i> sp. (shrimp)	7.94	8.31	0.42
Pandalidae (shrimp)	9.52	3.02	4.37
<i>Pandalus</i> sp. (shrimp)	10.32	4.79	16.77
<i>Pandalus jordani</i> (pink shrimp)	8.73	2.77	17.86
Crangonidae (shrimp)	14.29	5.79	1.95
<i>Crangon</i> sp. (shrimp)	1.59	0.50	0.17
<i>Crangon dulli</i> (shrimp)	3.17	1.01	1.06
<i>Crangon communis</i> (shrimp)	11.11	4.28	2.62
Natantia (shrimp)	0.79	0.25	0.00
<i>Axiopsis</i> sp. (mud shrimp)	4.76	1.76	10.63
Galatheididae (pelagic slip crabs)	20.63	22.42	10.59
<i>Munida quadrispina</i> (pinch bug)	1.59	1.01	0.20
<i>Oregonia</i> sp. (decorator crab)	1.59	0.50	0.18
<i>Cherilia longipes</i> (decorator crab)	0.79	0.76	0.25
Pinnotheridae (pea crab)	0.79	0.25	0.23
<i>Echinacea</i> sp. (sea urchin)	1.59	0.50	0.08

Table 12.--Continued.

Prey	%F	%N	%W
Osteichthyes Teleostei (bony fish)	3.17	1.01	0.33
Non-gadoid fish remains	3.17	1.01	0.58
Zoarcidae (eelpout)	1.59	0.50	3.04
<i>Lycodopsis pacifica</i> (blackbelly eelpout)	2.38	0.76	5.57
Scorpaenidae	2.38	0.76	0.18
<i>Sebastes</i> sp. (rockfish)	3.17	1.01	4.63
Agonidae (poacher)	0.79	0.25	1.28
Pleuronectidae (flatfish)	0.79	0.25	0.97
<i>Atheresthes stomias</i> (arrowtooth flounder)	1.59	0.50	0.64
<i>Errex zachirus</i> (rex sole)	2.38	0.76	0.05
Offal	1.59	0.50	5.81
Total prey number:	397		
Total prey weight:	267.43 g		
Total non-empty stomachs:	126		
Total empty stomachs:	44		

Table 13 .--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of shortspine thornyhead (*Sebastolobus alascanus*) caught south of Cape Blanco in the fall of 1991.

Prey	%F	%N	%W
Polychaeta (worm)	4.55	1.91	0.04
Aphroditidae (sea mouse)	8.08	4.47	2.07
Euphosinidae (polychaete)	1.01	0.43	0.09
Neptuneidae (snail)	0.51	0.21	0.83
Bivalvia (clam)	0.51	0.21	0.00
Teuthoidea (squid)	1.01	0.43	1.04
Octopoda (octopus)	1.52	0.64	0.16
Crustacea	1.01	1.06	0.00
Peracarida Mysidacea (mysid)	10.10	7.45	0.08
Cumacea (cumacean)	4.04	7.87	0.01
Isopoda (isopod)	3.03	1.49	0.09
Gammaridea (amphipod)	5.56	2.34	0.01
Hyperiiidea (amphipod)	0.51	0.21	0.00
Euphausiidae (euphausiid)	1.01	0.43	0.00
<i>Sergestes</i> sp. (sergestid shrimp)	1.52	0.85	0.06
Reptantia (crab)	0.51	0.21	0.03
Caridea (shrimp)	2.02	0.85	0.04
Pasiphaeidae (shrimp)	1.52	0.64	0.16
Hippolytidae (shrimp)	15.15	9.57	0.36
<i>Spirontocaris</i> sp. (shrimp)	3.03	1.70	0.10
<i>Spirontocaris holmesi</i> (shrimp)	6.57	5.96	0.49
<i>Eualus macrophthalmus</i> (shrimp)	0.51	0.21	0.01
<i>Heptacarpus decorus</i> (elegant coastal shrimp)	0.51	0.21	0.01
Pandalidae (shrimp)	0.51	0.43	0.02
<i>Pandalus</i> sp . (shrimp)	0.51	0.21	0.01
Crangonidae (shrimp)	1.52	0.64	0.02
<i>Crangon</i> sp. (shrimp)	1.52	0.85	0.15
Natantia (shrimp)	0.51	0.21	0.00
<i>Calocaris quinqueseriatus</i> (mud shrimp)	1.01	0.43	0.10
<i>Callianopsis goniophthalma</i> (mud shrimp)	1.52	0.64	0.50
Paguridae (hermit crab)	0.51	0.21	0.09
Galatheidae (pelagic slip crabs)	2.02	1.06	0.07
Majidae (spider crab)	2.53	2.34	1.51
<i>Chionoecetes</i> sp. (snow and Tanner crab)	10.61	9.79	14.17
<i>Chionoecetes tanneri</i> (grooved Tanner crab)	22.73	13.62	46.52

Table 13 .--Continued.

Prey	%F	%N	%W
Pinnotheridae (pea crab)	0.51	0.21	0.01
Ophiuroidea Ophiurida (brittle star)	2.02	0.85	0.01
<i>Echinacea</i> sp. (sea urchin)	1.52	0.64	0.00
Osteichthyes Teleostei (bony fish)	2.53	1.28	0.07
Non-gadoid fish remains	3.54	1.49	0.21
<i>BathyZagus pacificus</i> (slender blacksmelt)	0.51	0.21	0.19
Myctophidae (lanternfish)	1.52	0.64	0.10
Gadidae (gadid fish)	1.52	0.64	1.66
<i>Merluccius productus</i> (Pacific hake)	0.51	0.21	0.00
Zoarcidae (eelpout)	4.04	1.91	2.44
<i>Lychenhelys</i> sp. (eelpout)	0.51	0.43	2.81
Macrouridae (rattail)	1.52	0.64	2.80
Scorpaenidae	3.54	1.70	0.32
<i>Sebastolobus</i> sp. (unidentified thornyhead)	8.59	3.83	5.56
<i>Sebastolobus alascanus</i> (shortspine thornyhead)	1.52	0.64	0.74
<i>Sebastolobus altivelis</i> (longspine thornyhead)	4.55	1.91	6.00
Icelidae (sculpin)	0.51	0.21	0.09
Offal	6.57	2.77	8.14
Total prey number:	470		
Total prey weight:	2,490.71 g		
Total non-empty stomachs:	198		
Total empty stomachs:	18		

Table 14.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of shortspine thornyhead (*Sebastolobus alascanus*) caught north of Cape Blanco in the fall of 1992.

Prey	%F	%N	%W
Polychaeta (worm)	7.52	4.46	0.23
Euphrosinidae	3.01	1.79	0.16
Nudibranchia dendronotoidea (nudibranch)	0.75	0.45	0.02
Nuculoida (clam)	0.75	0.45	0.00
Cephalopoda (squid & octopus)	0.75	0.45	0.00
Teuthoidea (squid)	0.75	0.45	0.00
Teuthoidea oegopsida (squid)	0.75	0.45	0.71
Crustacea	2.26	1.34	0.01
Copepoda	1.50	1.79	0.00
Peracarida Mysidacea (mysid)	3.01	2.68	0.01
Mysidacea Mysida (mysid)	0.75	0.45	0.01
Cumacea (cumacean)	1.50	0.89	0.00
Isopoda (isopod)	0.75	0.45	0.08
Gammaridea (amphipod)	11.28	9.82	0.04
Gammaridae (amphipod)	0.75	0.45	0.02
Hyperiidea (amphipod)	1.50	1.34	0.01
Caridea (shrimp)	12.78	8.48	0.38
<i>Pasiphaea pacifica</i> (shrimp)	0.75	0.45	0.14
Hippolytidae (shrimp)	18.05	15.63	1.43
Pandalidae (shrimp)	2.26	2.23	0.11
Crangonidae (shrimp)	2.26	1.34	0.07
<i>Crangon</i> sp. (shrimp)	2.26	1.34	0.10
Natantia (shrimp)	3.01	1.79	0.01
Anomura (crab)	2.26	5.36	1.17
Majidae (spider crab)	0.75	0.45	0.58
<i>Chionoecetes</i> sp. (snow and Tanner crab)	5.26	3.13	10.30
<i>Chionoecetes tanneri</i> (grooved Tanner crab)	5.26	3.13	7.64
Pinnotheridae (pea crab)	0.75	0.45	0.03
Echiura (marine worm)	0.75	0.45	0.02
Ophiuroidea Ophiurida (brittle star)	2.26	1.34	0.04
Gnathostomata	0.75	0.45	0.01
Osteichthyes Teleostei (bony fish)	6.77	4.46	1.36
Non-gadoid fish remains	2.26	1.34	18.01
<i>Clupea pallasii</i> (Pacific herring)	0.75	0.45	1.23
Myctophidae (lanternfish)	0.75	0.45	0.20

Table 14.--Continued.

Prey Name	%F	%N	%W
Gadidae (gadid fish)	1.50	1.34	16.12
<i>Merluccius productus</i> (Pacific hake)	1.50	0.89	0.54
Zoarcidae (eelpout)	1.50	0.89	0.22
<i>Lycenchelys jordani</i> (shortjaw eelpout)	1.50	0.89	0.33
<i>Cololabis saira</i> (Pacific saury)	0.75	0.45	0.37
Scorpaenidae (rockfish)	12.03	7.14	25.34
<i>Sebastes</i> sp. (rockfish)	2.26	1.34	0.32
<i>Sebastolobus alascanus</i> (shortspine thornyhead)	2.26	1.34	0.62
<i>Sebastolobus altivelis</i> (longspine thornyhead)	4.51	2.68	2.53
Unidentified organic material	1.50	0.89	0.00
Offal	3.01	1.79	9.48
Total prey number:	224		
Total prey weight:	1,454.19 g		
Total non-empty stomachs:	133		
Total empty stomachs:	60		

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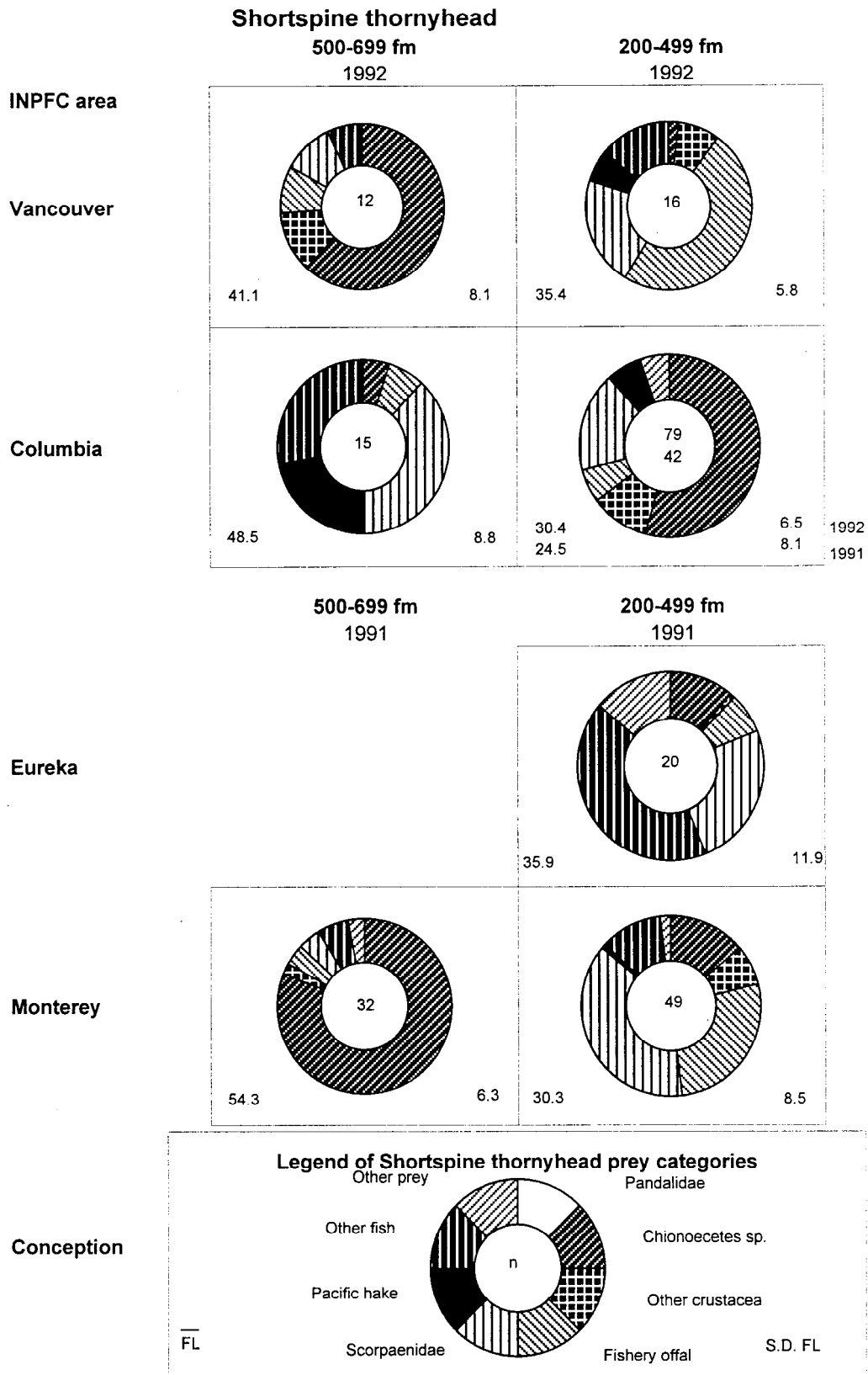


Figure 8.--Diet composition (by weight) of shortspine thornyhead for each depth zone, INPFC area and year. The number of nonempty stomachs examined are shown in each ring. Mean and standard deviation of the lengths are shown in the lower left and right of each box, respectively.

Shortspine thornyhead

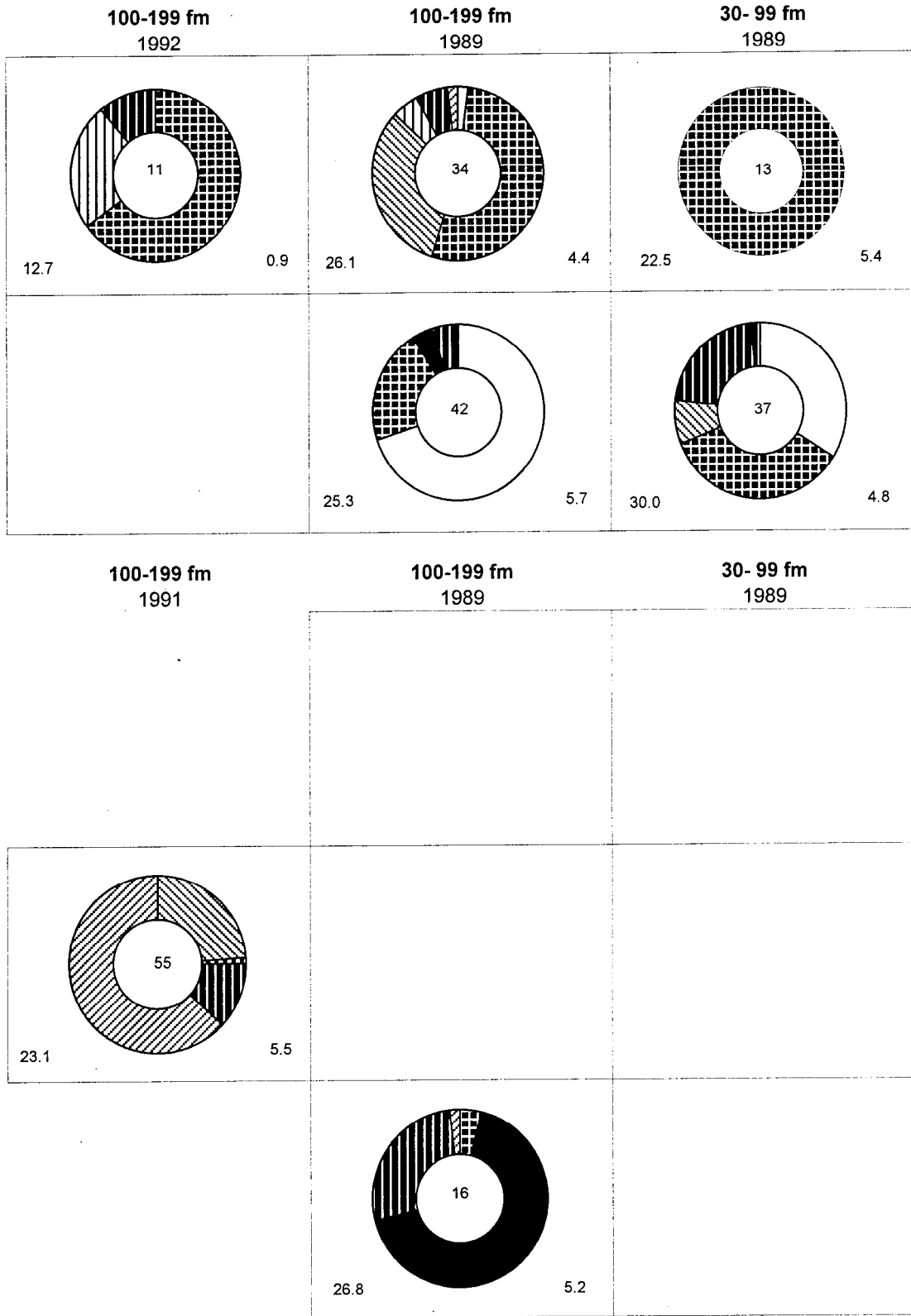


Figure 8.--Continued

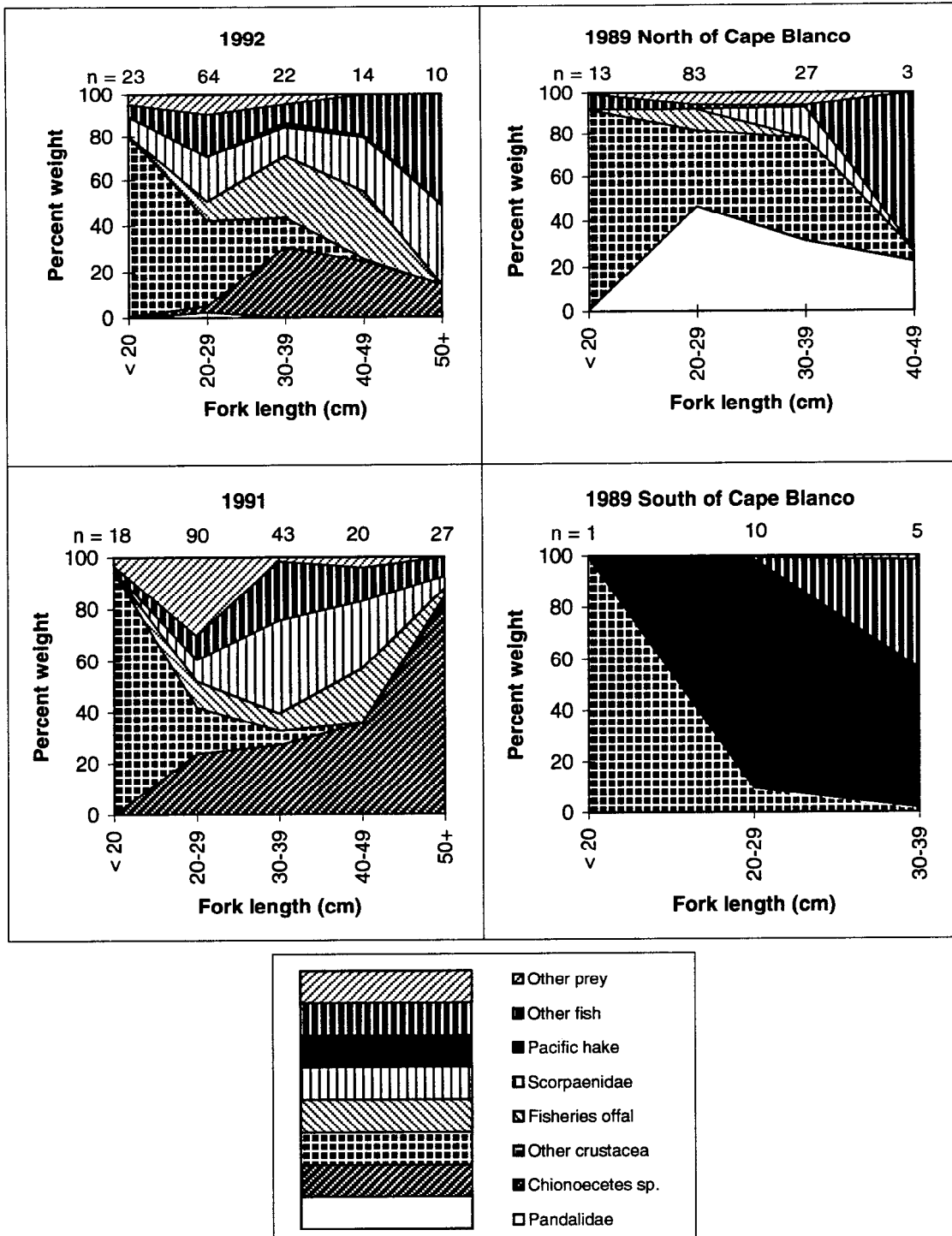


Figure 9.--Diet composition of shortspine thornyhead (by length) from north and south of Cape Blanco in 1989, and from the 1991 and 1992 surveys. The length-range shown in each figure may be different. The sample size (n) is shown above each length group.

LONGSPINE THORNYHEAD

Longspine thornyhead (*Sebastolobus altivelis*) is a component of the deepwater species complex managed by the Pacific Fishery Management Council (Ianelli et al. 1994). In response to developing Japanese export markets, higher prices, and the movement of the bottom trawl fishery into deeper water (Jacobson 1993), landings of longspine thornyheads in Washington, Oregon, and California have increased from an average of 57 t per year in the late 1960s to 5,200 t per year in the early 1990s (Ianelli et al. 1994).

The longspine thornyhead primarily inhabits the continental slope between 500 and 1,100 m but can be found from 300 m to depths exceeding 1,750 m (Hart 1973, Jacobson 1993). Geographically, longspine thornyhead ranges from southern Baja California to the Aleutian Islands (Hart 1973, Jacobson 1993). Sexual maturity is attained by 50% of the females at 19 cm TL or about 14 years (Jacobson 1993). In late winter or early spring, buoyant, bilobate egg masses are spawned (Jacobson 1993), and about 18 to 20 months later, juvenile longspine thornyhead settle out of their pelagic phase onto the continental slope at sizes of 40 to 60 mm TL (Jacobson 1993). Unlike shortspine thornyheads, there is no relationship between depth and length for longspine thornyheads (Jacobson 1993). Longspine thornyheads can grow to 35 cm TL and, based on otolith increments, may reach ages approaching 50 years (Jacobson 1993).

RESULTS

General Diets

Seventeen (9%) of the 185 longspine thornyhead stomachs collected in the autumn of 1991 were empty (Table 15). By weight, fish (26%), crab (24%), and shrimp (15%) were the most important types of prey in the diet, but cephalopods (8%), polychaetes (7%), echinoderms (7%), and fishery offal (5%) also contributed. Numerically, small, non-decapod crustaceans (33%), echinoderms (14%), and polychaete worms (12%) were the most important groups in the diet.

In 1992, 30 (21%) of the 143 longspine thornyhead stomachs collected were empty (Table 16). Fish (33%), shrimp (29%), and crab (14%) were the most important diet components, by weight, but cephalopods (9%), fishery offal (6%), and polychaetes (5%) also contributed. Numerically, the small, non-decapod crustaceans (40%) and shrimp (18%) were most important in the diet.

Overall, the diet did not seem to be dominated by a particular prey type for either year that samples were taken. However, most of the prey were benthic organisms.

Variation of the Diet with Location

The Monterey INPFC area was sampled in the autumn of 1991 (Fig. 10). In the 200-499 fm depth zone, *Chionoecetes* sp. (Tanner crab), other fish (mostly bathylagids (deepsea smelts) and unidentified fish), other prey (mostly polychaetes and fishery offal), scorpaeonids, and mudshrimp were the most important prey categories by weight. In the 500-699 fm depth zone, other prey (mostly clams, brittlestars, and fishery offal), other crustacea (mostly isopods), myctophids, and squid were the most important prey

categories by weight. In 1991, fewer longspine thornyheads were sampled from the Eureka and Columbia INPFC areas and only from the 200-499 fm depth zone. The stomach contents, by weight, were dominated by mud shrimp in the Eureka INPFC area and by *Chionoecetes* sp. in the Columbia INPFC area for the few samples that were collected.

In 1992, the Columbia and Vancouver INPFC areas were sampled (Fig. 10). In the 200-499 fm depth zone, fishery offal contributed to the large amount of “Other prey” and the diet appears considerably different from that seen in 1991. Little, if anything, can be inferred from this comparison because of the low number of samples taken in 1991. In the 500-699 fm depth zone, a variety of smaller crustacea (mostly pasiphaeid shrimp) and other fish (mostly non-gadoid remains) were important in the diet. In the Vancouver INPFC area, “Other fish” (mostly zoarcids (eelpouts) and bathylagids) contributed about half the weight to the stomach contents; squid, mud shrimp and *Chionoecetes* sp. were also important.

Variation in the Diet with Predator Size

“Other crustacea” decreased in importance in the diet with increasing size of longspine thornyhead in the areas sampled in 1991 and 1992 (Fig. 11). Squid and myctophids (lanternfishes) appeared to be more important to the diet of longspine thornyheads from the areas sampled in 1991. The “Other prey” category (includes offal and polychaete worms) was important over a wide range of sizes in 1991 and 1992, illustrating the diversity in the diet. In both years, mud shrimp, *Chionoecetes* sp., and “Other fish” became important in the diet of longspine thornyheads at lengths of 20 cm FL and larger (except for the 30-34 cm FL fish examined in 1992 when only two longspine thornyheads of that size were sampled).

DISCUSSION

There is very little information on the diet of longspine thornyhead. Off Oregon and California, longspine thornyhead eat mostly polychaete worms, shrimp, and crab (Tom Laidig, personal communication¹). The longspine thornyhead appears to be an opportunistic predator that will consume a variety of locally available crustaceans and fish that are on or near the bottom. The presence of offal from fish processing activities in the diet, primarily heads of Pacific hake, indicates that longspine thornyhead are also scavengers. It is possible that the biological identity of undigested parts of fishery offal could be identified (i.e., Pacific hake, gadidae, or fish remains), but that evidence of it being processed by the fishery would be lacking. If this occurred, the amount of fishery offal in the diet would be underestimated.

The changes in the diet that occurred as a function of predator size were generally in agreement with those found by Laidig¹. Laidig found a shift in the diet from mainly gammarid amphipods and polychaete worms to mainly crabs, shrimp, and fish. In this study, we found that small crustacea were replaced by small fish and squid, then mud shrimp, crab, and larger fish as predator size increased. The observed changes in diet with size were not likely functions of prey availability with depth because there is no relationship between depth and length for longspine thornyheads (Jacobson 1993).

Table 15.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of longspine thornyhead (*Sebastolobus altivelis*) caught south of Cape Blanco in the fall of 1991.

Prey Name	%F	%N	%W
Polychaeta (worm)	16.67	7.43	3.29
Aphroditidae (sea mouse)	0.60	0.27	0.83
Euprosinidae (polychaete)	4.76	3.45	2.46
Onuphidae (polychaete)	1.19	0.80	0.49
Gastropoda (snail)	0.60	0.27	0.03
<i>Heteropoda</i> sp. (mollusc)	1.19	1.06	0.24
Bivalvia (clam)	3.57	2.12	1.93
Cephalopoda (squid & octopus)	1.19	0.53	0.01
Teuthoidea (squid)	2.98	1.33	2.54
Teuthoidea oegopsida (squid)	5.36	2.39	4.87
Gonatidae (squid)	0.60	0.27	0.67
Crustacea	4.17	1.86	0.35
Copepoda	1.79	3.98	0.01
Calanoida (copepod)	1.19	0.53	0.01
Peracarida Mysidacea (mysid)	1.79	0.80	0.03
Mysidae (mysid)	7.74	5.84	0.53
Cumacea (cumacean)	2.98	8.22	0.10
Isopoda (isopod)	4.17	1.86	3.06
Gammaridea (amphipod)	12.50	7.96	0.35
Hyperiidia (amphipod)	1.79	0.80	0.05
Caprellidea (amphipod)	1.19	0.53	0.01
Euphausiidae (euphausiid)	2.38	1.06	0.03
Unidentified crimson shrimp	2.38	1.06	1.11
<i>Sergestes</i> sp. (sergestid shrimp)	2.98	1.59	0.96
Caridea (shrimp)	1.79	0.80	0.57
Hippolytidae (shrimp)	2.98	1.59	1.28
<i>Eualus</i> sp. (shrimp)	0.60	0.27	0.50
Crangonidae (shrimp)	0.60	0.27	0.40
<i>Crangon</i> sp. (shrimp)	0.60	0.27	0.25
Natantia (shrimp)	1.79	0.80	0.02
Axiidae (mud shrimps)	1.19	0.53	0.16
<i>Calocaris investigatoris</i> (mud shrimp)	0.60	0.27	1.02
<i>Calocaris quinqueseriatus</i> (mud shrimp)	3.57	1.59	4.17
<i>Callianopsis goniophthalma</i> (mud shrimp)	1.19	0.53	4.52
Paguridae (hermit crab)	1.79	0.80	1.32

Table 15 .--Continued.

Prey Name	% F	O/ON	% W
Galatheididae (pelagic slip crab)	0.60	0.27	0.01
<i>Munida quadrispina</i> (pinch bug)	0.60	0.27	0.02
Majidae (spider crab)	1.79	0.80	0.57
<i>Chionoecetes</i> sp. (snow and Tanner crab)	2.98	1.59	2.97
<i>Chionoecetes tanneri</i> (grooved Tanner crab)	8.33	5.04	18.21
<i>Cherilia longipes</i> (decorator crab)	0.60	0.27	1.03
Asteroidea (starfish)	1.19	0.53	1.65
Ophiuroidea Ophiurida (brittle star)	14.29	13.00	2.82
<i>Echinacea</i> sp. (sea urchin)	0.60	0.27	0.24
Holothuroidea (sea cucumber)	0.60	0.27	2.24
Urochordata (tunicate)	0.60	0.27	0.04
Osteichthyes Teleostei (bony fish)	1.79	0.80	0.39
Non-gadoid fish remains	4.76	2.39	4.77
Bathylagidae (deepsea smelts)	0.60	0.27	2.94
Myctophidae (lanternfish)	7.74	3.71	10.52
Gadidae (gadid fish)	0.60	0.27	0.88
Zoarcidae (eelpout)	0.60	0.27	1.26
Scorpaenidae (rockfish)	0.60	0.27	0.24
<i>Sebastes</i> sp. (unidentified thornyhead)	1.79	0.80	4.72
Unidentified organic material	3.57	1.59	1.08
Unidentified worm-like organism	0.60	0.27	0.04
Offal	5.95	2.65	5.03
Unidentified tube	0.60	0.27	0.15
Unidentified material	0.60	0.27	0.00
Total prey number:	377		
Total prey weight:	184.44 g		
Total non-empty stomachs:	168		
Total empty stomachs:	17		

Table 16.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of longspine thornyhead (*Sebastolobus altivelis*) caught north of Cape Blanco in the fall of 1992.

Prey Name	%F	%N	%W
Polychaeta (worm)	12.39	6.28	1.69
Aphroditidae (sea mouse)	1.77	0.90	2.31
Maldanidae (polychaete)	1.77	0.90	1.21
Gastropoda (snail)	0.88	0.45	0.00
Bivalvia (clam)	0.88	0.45	0.02
Teuthoidea (squid)	7.08	3.59	2.97
Teuthoidea oegopsida (squid)	1.77	0.90	6.20
Crustacea	7.08	4.48	0.17
Ostracoda	0.88	0.45	0.00
Calanoida (copepod)	1.77	0.90	0.02
Mysidacea Mysida (mysid)	7.08	4.04	0.13
Cumacea (cumacean)	7.08	21.52	0.27
Amphipoda (amphipod)	1.77	0.90	0.03
Gammaridea (amphipod)	10.62	5.83	0.14
Hyperiidea (amphipod)	0.88	0.45	0.02
Caprellidea (amphipod)	1.77	1.35	0.02
Sergestidae (sergestid shrimp)	0.88	0.45	0.13
<i>Sergestes</i> sp. (sergestid shrimp)	3.54	1.79	0.79
Reptantia (crab)	0.88	0.45	0.36
<i>Pasiphaea pac\$ca</i> (shrimp)	2.65	1.35	7.15
Hippolytidae (shrimp)	4.42	2.69	1.71
<i>Eualus</i> sp. (shrimp)	2.65	1.35	2.36
Natantia (shrimp)	11.50	5.83	2.08
Axiidae (mud shrimps)	1.77	0.90	0.83
<i>Calocaris investigatoris</i> (mud shrimp)	5.31	3.59	13.41
Paguridae (hermit crab)	1.77	0.90	0.45
<i>Lithodes couesi</i> (couesi king crab)	0.88	0.45	0.56
Majidae (spider crab)	3.54	1.79	2.02
<i>Chionoecetes</i> sp. (snow and Tanner crabs)	2.65	1.79	2.05
<i>Chionoecetes tanneri</i> (grooved Tanner crab)	7.96	4.04	8.73
Ophiuroidae Ophiurida (brittle star)	11.50	8.97	3.36
<i>Echinacea</i> sp. (sea urchin)	0.88	0.45	0.05
Urochordata (tunicate)	0.88	0.45	0.08

Table 16.--Continued.

Prey Name	%F	%N	%W
Osteichthyes Teleostei (bony fish)	3.54	1.79	0.17
Non-gadoid fish remains	7.08	3.59	10.89
Bathylagidae (deepsea smelts)	0.88	0.45	18.39
Zoarcidae (eelpout)	0.88	0.45	2.60
Scorpaenidae (rockfish)	0.88	0.45	0.96
Unidentified organic material	4.42	2.24	0.17
Offal	0.88	0.45	5.48
Total prey number:	223		
Total prey weight:	85.26 g		
Total non-empty stomachs:	113		
Total empty stomachs:	30		

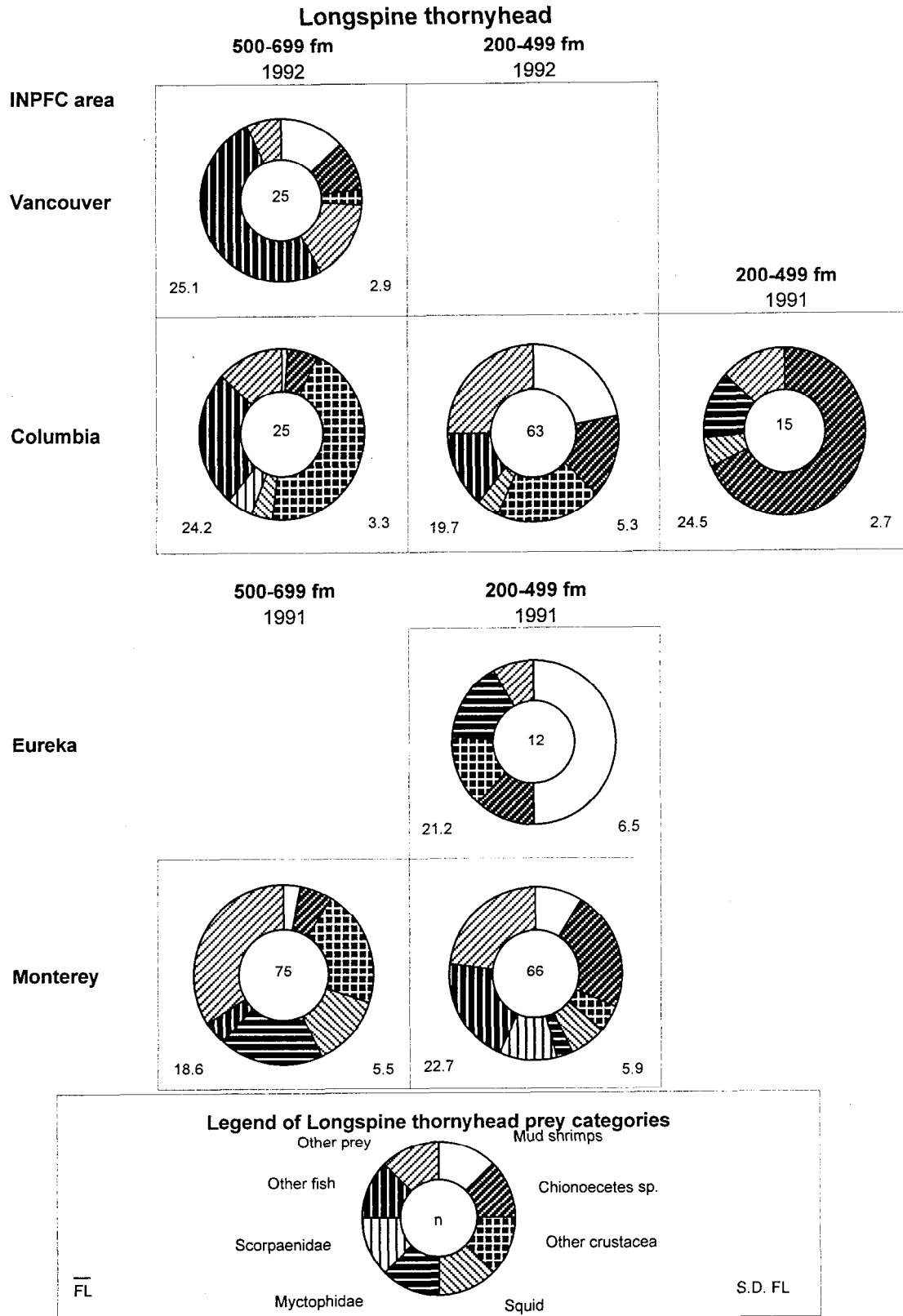


Figure 10.--Diet composition (by weight) of longspine thornyhead for each depth zone, INPFC area and year. The number of nonempty stomachs examined are shown in each ring. Mean and standard deviation of the lengths are shown in the lower left and right of each box, respectively.

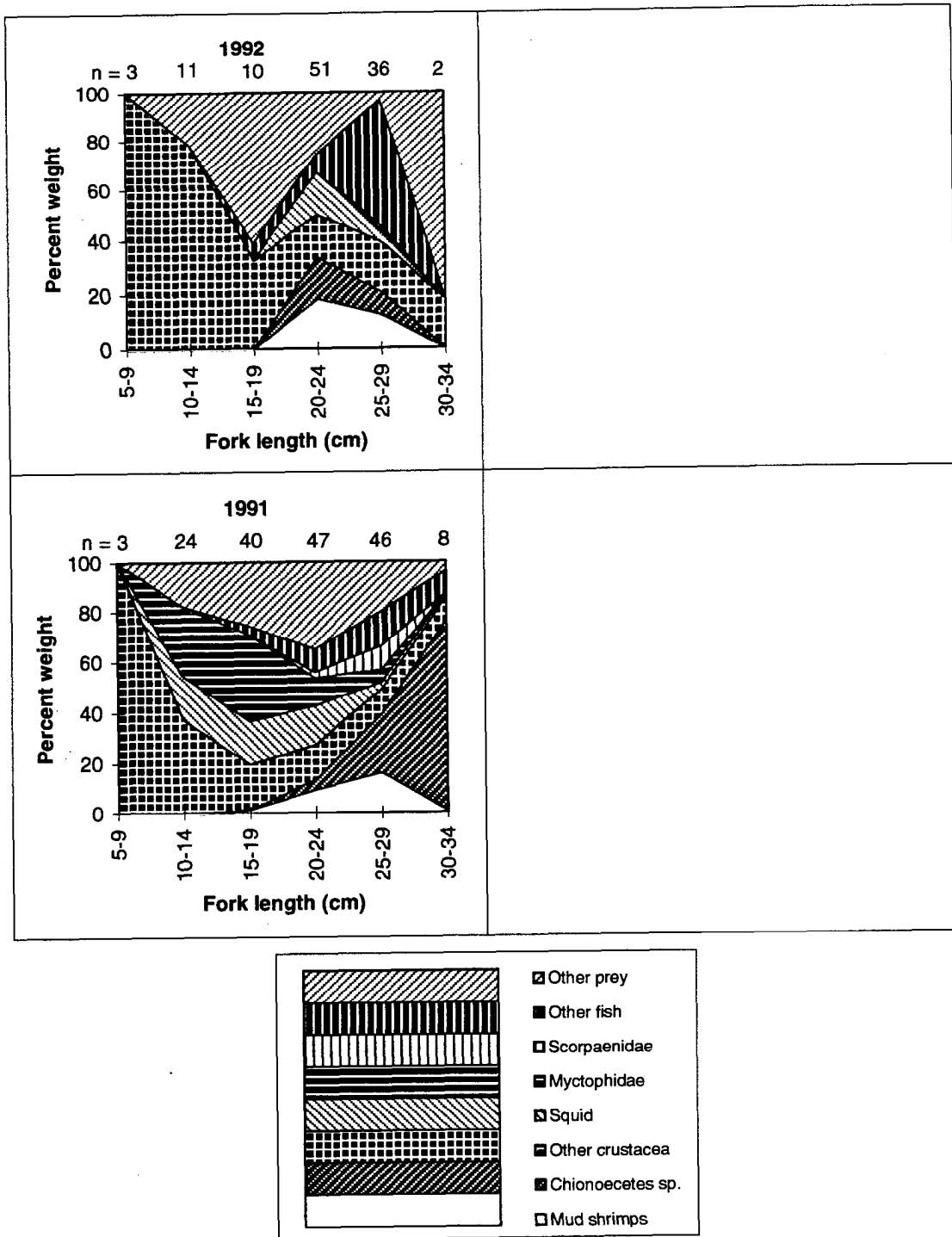


Figure 11 --Diet composition of longspine thornyhead (by length) from the 1992 survey. The length-range shown in each figure may be different. The sample size (n) is shown above each length group.

GIANT GRENADIER

Giant grenadier (*Albatrossia pectoralis*), also known as the pectoral rattail, is typically the most abundant grenadier (Family Macrouridae) by weight when trawling on the upper continental slope off Oregon (Parks et al. 1993). Giant grenadier occur along the continental slope from California through the Bering Sea to Japan and are found from depths of 200 m to 2,170 m (Iwamoto and Stein 1974). Small, presumably young, giant grenadier (TL < 50 cm) may be pelagic, but juveniles and adults are typically caught near the bottom (Novikov 1970). This species is the largest of the grenadiers and may reach a length of 150 cm TL (Iwamoto and Stein 1974).

Despite their large size and wide availability, the commercial potential of giant grenadier is limited because of their soft flesh (Matsui et al. 1990). However, large specimens are occasionally marketed in northern California (Iwamoto and Stein 1974) and Novikov (1970) considers it to be a valuable food resource because of its high biomass and the high content of vitamin-rich fats in the roe and liver.

Unlike some other deepwater fishes, the stomach contents of many giant grenadier have been described from the western Pacific Ocean (Novikov 1970, Okamura 1970), Aleutian Islands, and Bering Sea (Novikov 1970). This is due to its reduced swimbladder (Iwamoto and Stein 1974) resulting in fewer instances of stomach eversion as fish are brought to the surface (Matsui et al. 1990). However, the stomach contents of only a few giant grenadier have been examined from the eastern Pacific Ocean. Percy and Ambler (1974) describe the stomach contents of four giant grenadier caught off the Oregon coast and Hart (1973) describes the stomach contents of one specimen caught off British Columbia.

RESULTS

General Diet

Sixty-five (69%) of the 94 stomachs collected from giant grenadier north of Cape Blanco in 1992 were empty. The contents of the 29 (31%) stomachs with food in them are described in Table 17. Over 93% of the stomach contents by number, and 65% by weight, were more than half digested, making identification difficult. Squid remains (mostly beaks) had the highest frequency of occurrence followed by *Gnathophausia* sp. (a large crimson mysid) and unidentified bony fish (usually bones). Squid remains numerically dominated the diet composition, but *Gnathophausia* sp. (37%) shrimp (30%), and fish (25%) were the most important diet components by weight.

Variation of the Diet with Location

It appeared there were differences in the overall diet of giant grenadier from the Columbia and Vancouver INPFC areas (Fig. 12). A larger portion of the stomach contents, by weight, was comprised of fish, pasiphaeid shrimp, and other shrimp in the Columbia INPFC area. *Gnathophausia* sp. appeared to be more important to the weight of stomach contents in the Vancouver INPFC area.

Variation of the Diet with Predator Size

There appeared to be differences in the diet composition, by weight, with the size of the giant grenadiers examined (Fig. 13). The proportion of fish in the diet increased with size while the proportion of crustaceans (*Gnathophausia* sp., pasiphaeid, pandalid, and other shrimp) decreased.

DISCUSSION

Most of the information on the food habits of the giant grenadier is from the northwestern North Pacific Ocean (Novikov 1970, Okamura 1970). Novikov (1970) lists the stomach contents and their frequency of occurrence in over 2,000 giant grenadier from several areas - northeastern Bering Sea, Aleutian Islands, Bowers Ridge, Pacific coast of the Kamchatka Peninsula, northern Kurile Islands, and Sea of Okhotsk. Although the number of stomachs that contained food is not reported, the data indicate that the diet is quite different among these areas and consists of a mixture of benthic, bathypelagic, and pelagic prey. Squid, with a frequency of occurrence greater than 10% in all areas, appear to be the most consistently important prey type. Other prey with a frequency of occurrence greater than 10% in at least one area include shrimp, amphipods, unidentified crustaceans, *Lampanyctus* sp. (lanternfishes), liparids (snailfishes), unidentified fish, ctenophores, bryozoans, and unidentified animals. Okamura (1970) reports the volumetric composition of the stomach contents of four giant grenadier as 37% squid, 24% euphausiids, 20% fish, and 19% prawns (mysids).²

The stomach contents of very few giant grenadier have been examined from the eastern Pacific Ocean. Four giant grenadier caught off the Oregon coast had eaten cephalopods (Cranchiidae and *Japattella* sp.), brittlestars (*Ophioctenpacfxum* and *Ophiacantha* sp.), the sea cucumber *Scotoplanes* sp., and unidentified fishes (Percy and Ambler 1974). Hart (1973) reports that one of two giant grenadier caught by longline off British Columbia had two squid beaks in its stomach. Squid remains were also commonly found in the giant grenadier stomachs examined in this study but contributed little (7%) to the overall weight of the stomach contents. Crustaceans (67% by weight) were the gravimetrically dominant type of prey of giant grenadier in this study. This is similar to the results of Okamura (1970) off Japan where crustaceans (euphausiids and prawns) were the dominant type of prey by volume (43%), but dissimilar to the results of Percy and Ambler (1974) off Oregon where no crustaceans were found in the diet of giant grenadier.

Because of the low sample size (see results), differences or trends that occurred among areas or size classes should be considered preliminary until a larger number of samples can be analyzed. The differences in the composition of the stomach contents between the Vancouver and Columbia INPFC areas may indicate differences in the availability of these prey types between areas. However, the Pacific grenadier (*Coryphaenoides acrolepis*) examined in this study show the opposite pattern for fish in the diet, a higher proportion in the Vancouver INPFC area than in the Columbia INPFC area (see Fig. 13). Apparent size-related changes in the diet of giant grenadier may have contributed to the apparent areal differences. These two factors were somewhat

On page 170, Okamura (1970) uses the term "mysids" parenthetically after the term "prawns" which may indicate that shrimp and mysids were both included in this prey category, or that the prey were, *Gnathophausia*, a genus of large mysids.

confounded, so no firm conclusion about differences in diet by size or area were possible. However, increasing fish and decreasing crustaceans (*Gnathophausia* sp. and shrimp) in the diet with increasing size is consistent with patterns observed in many other fish.

The importance of *Gnathophausia* sp. as a prey item in this study (and perhaps Okamura's 1970 study, see Footnote 2) and its absence in other studies may be a result of the prey's distribution. The northern limit of *Gnathophausia* spp. in the eastern Pacific Ocean is apparently southeastern Alaska (Kathman et al. 1986). Other regional differences in the diet of giant grenadier have been found (Novikov 1970). Giant grenadier appear to opportunistically prey on the available benthic and mesopelagic fauna occurring near the continental slope.

Table 17.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of giant grenadier (*Coryphaenoides pectoralis*) caught north of Cape Blanco in the fall of 1992.

Prey Name	%F	%N	%W
Cephalopoda (squid & octopus)	3.45	1.67	0.36
Teuthoidea (squid)	75.86	68.33	7.07
Octopoda (octopus)	6.90	3.33	0.03
Crustacea	3.45	1.67	0.04
<i>Gnathophausia</i> sp. (mysid)	13.79	8.33	37.02
<i>Pasiphaeapacifica</i> (shrimp)	6.90	3.33	15.22
Pandalidae (shrimp)	3.45	1.67	1.98
Natantia (shrimp)	3.45	1.67	12.98
Ophiuroidea Ophiurida (brittle star)	3.45	1.67	0.32
Osteichthyes Teleostei (bony fish)	10.34	5.00	13.16
Non-gadoid fish remains	3.45	1.67	4.28
Bathylagidae (deepsea smelts)	3.45	1.67	7.55
Total prey number:	60		
Total prey weight:	33.41 g		
Total non-empty stomachs:	29		
Total empty stomachs:	65		

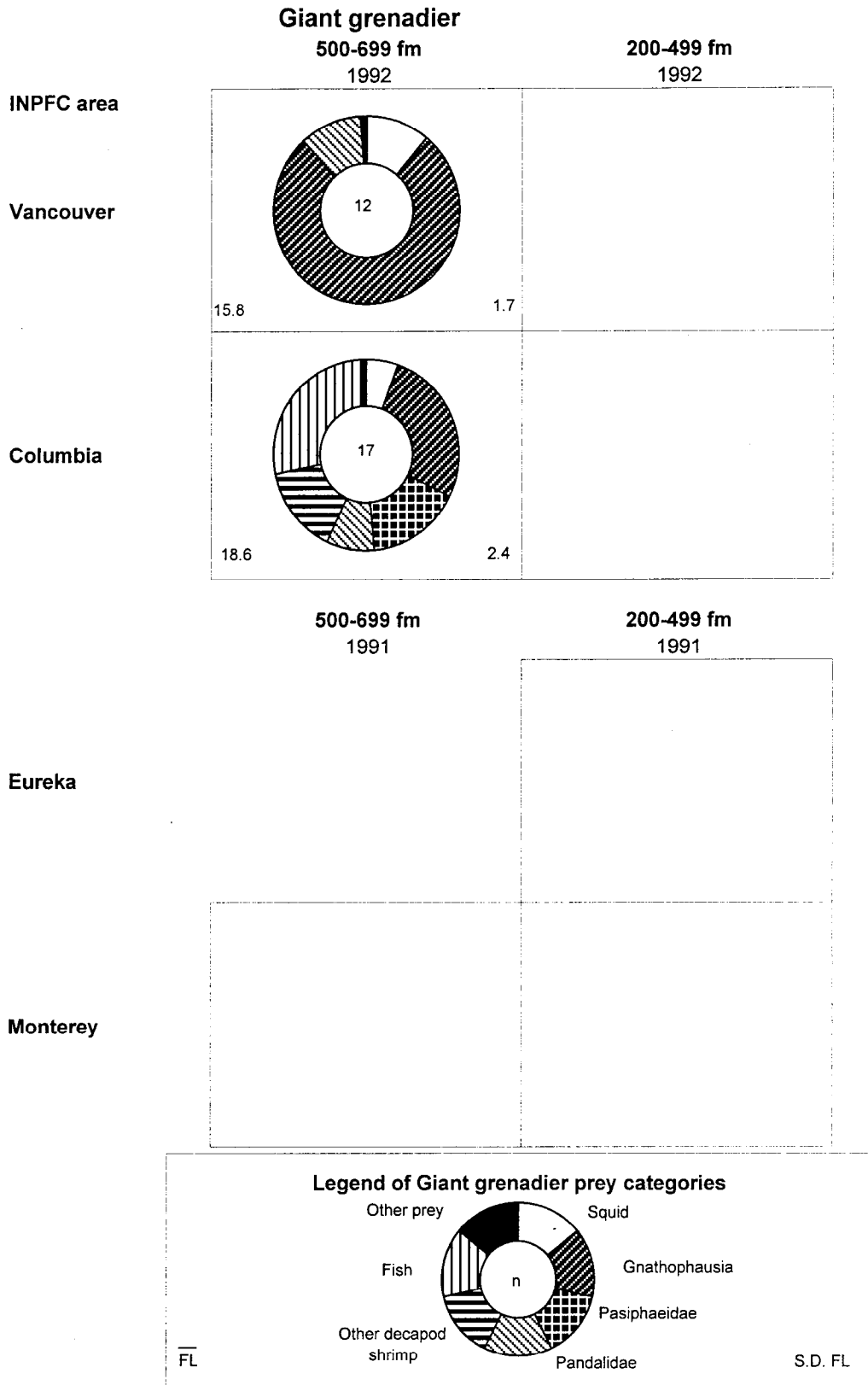


Figure 12.--Diet composition (by weight) of giant grenadier for each depth zone, INPFC area and year. The number of nonempty stomachs examined are shown in each ring. Mean and standard deviation of the lengths are shown in the lower left and right of each box, respectively.

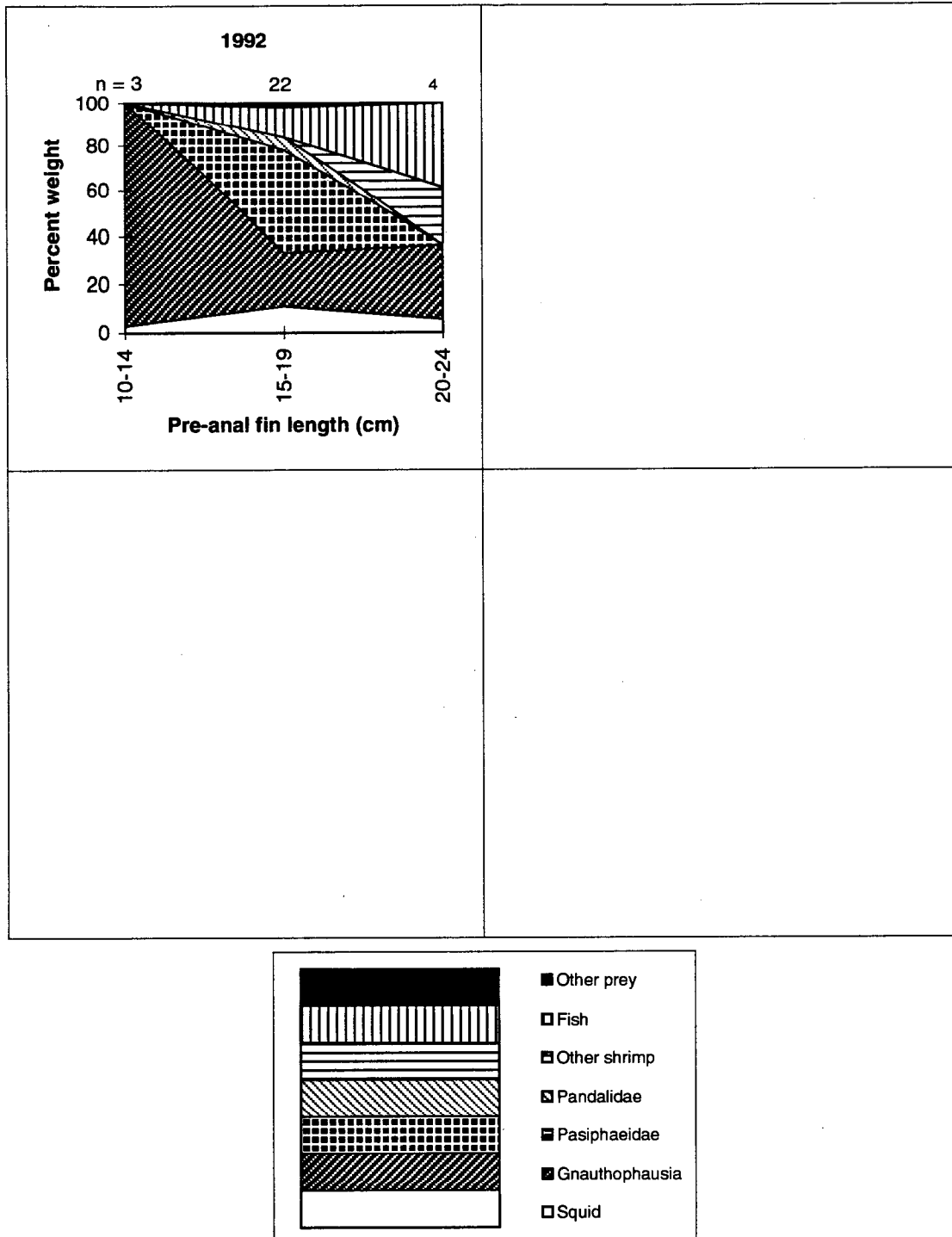


Figure 13.--Diet composition of giant grenadier (by length) from the 1992 survey. The sample size (n) is shown above each length group.

PACIFIC GRENADIER

Pacific grenadier (*Coryphaekoides acrolepis*), also known as Pacific rattail, has the best potential of the eastern North Pacific macrourids (grenadiers or rattails) for commercial use (Matsui et al. 1990). Grenadiers (Macrouridae) are the most abundant fish, by weight and number, in deep-water trawl catches off Oregon and Washington (Pearcy and Ambler 1974), and recently the commercial landings of Pacific grenadier have been rapidly increasing (Michael Hosie, personal communication³). Pacific grenadier occur along the continental slope from Baja California through the Bering Sea to Sagami Bay (near Tokyo), Japan (Hart 1973) and are found from depths of 155 m (Hart 1973) to 3,000 m (Matsui et al. 1990). Adults are typically caught near the bottom but are also frequently caught in midwater hauls and are considered by many to be bathypelagic or mesopelagic animals (Iwamoto and Stein 1974, Simenstad et al. 1977).

Obtaining accurate TL measurements is difficult because the tips of the long, thin tails are often broken off and some show signs of regeneration (Matsui et al. 1990). Consequently, length measurements are usually taken from the tip of the snout to the first anal-fin ray which is known as the pre-anal fin length (PAL). The relationship of PAL to TL is approximately $TL \text{ mm} = 2.308 \times (PAL \text{ mm}) + 122.158$ for males and $TL \text{ mm} = 2.276 \times (PAL \text{ mm}) + 115.4$ for females (Matsui et al. 1990). The largest specimen of this species measured over 95 cm TL and weighed 4 kg (Matsui et al. 1990).

Spawning appears to occur throughout the year with a peak in spring and early summer off southern California (Matsui et al. 1990). The length at maturity is approximately 23.5 cm PAL (65 cm TL) for females and 16.4 cm PAL (50 cm TL) for males (Matsui et al. 1990).

Currently, information on the food habits of Pacific grenadier is very limited. Pacific grenadier have a large gas bladder that expands, everting the stomach, when they are captured at depth and hauled to the surface. Typically, too few stomachs are found intact for meaningful analysis of their contents (e.g., Matsui et al. 1990). Pearcy and Ambler (1974) found only 3% (n = 7) of the 216 specimens that they examined still contained food in the stomachs. There is also little known about the predators of Pacific grenadier, but the holotype of this species was taken from the stomach of a northern fur seal (*Callorhinus ursinus*).

RESULTS

General Diet

The stomachs from 40 Pacific grenadier that appeared to have not regurgitated were collected north of Cape Blanco in 1992 and examined in the laboratory. Seven (17.5%) of these stomachs were empty. The contents of the remaining stomachs are shown in detail in Table 18. Most (68%) of the stomach contents by weight were more than half digested, making identification difficult. Squid or squid remains (usually beaks) occurred in the stomachs most frequently followed by polychaete worms, unidentified bony fishes (usually bones), unidentified organic material, sergestid shrimp, and

³ Oregon Department of Fish & Wildlife, P.O. Box 5430, Charleston, OR 97420, U.S.A.

amphipods. Copepods and squid dominated the numerical composition of the diet. By weight, squid and crustaceans were the most important components of the diet followed by fish, unidentified organic material, and polychaetes.

Variation of the Diet with Location

There were differences in the overall diet of Pacific grenadier from the Columbia and Vancouver INPFC areas (Fig. 14). A larger portion of the stomach contents, by weight, was comprised of fish and other shrimp in the Vancouver INPFC area. Squid, mud shrimp, and other crustacea appeared to be more important to the weight of stomach contents in the Columbia INPFC area.

Variation of the Diet with Predator Size

There appeared to be differences in the diet composition, by weight, with the size of the Pacific grenadiers examined (Fig. 15). The proportion of fish and squid in the diet increased with size while the proportion of crustaceans (other shrimp, mud shrimp, and other crustacea) and polychaetes decreased.

DISCUSSION

The stomach contents of a few Pacific grenadier have previously been reported from the eastern Pacific Ocean as well as from the Aleutian Islands. The stomach contents of seven Pacific grenadier caught off the Oregon coast included several species of cephalopods (*Gonatus fabricii*, Cranchiidae, *Japatella* sp., *Vampyroteuthis infernalis*, and unidentified squid beaks) fish remains, shrimp (*Crangon abyssorum*), crab (*Chionoecetes tanneri*, and unidentified crab), and amphipods (Pearcy and Ambler 1974). Matsui et al. (1990) report finding remains of fish, euphausiids, other crustacea, squid beaks, polychaetes, and sponge spicules in the stomach and intestines of Pacific grenadier captured off California. In the stomachs of four Pacific grenadier caught in midwater near Amchitka (an Aleutian) Island, myctophids (lanternfishes) were most important in frequency of occurrence and weight. Other prey included Pacific viperfish (*Chauliodus macouni*), tadpole snailfish (*Nectoliparis pelagicus*), mysids, isopods, euphausiids, unidentified decapod crustaceans, and cephalopods (Simenstad et al. 1977).

The results of this study were most similar to those of Pearcy and Ambler (1974) and Matsui et al. (1990). These studies were conducted in the eastern Pacific Ocean capturing Pacific grenadier near the bottom. The prey was a combination of benthic (e.g., polychaetes, crab and mudshrimp) and pelagic (e.g., squid, hyperiid amphipods, and sergestid shrimp) organisms. Carcasses of epipelagic organisms may have been eaten after they had died and sunk to the bottom or Pacific grenadier may swim into the water column to forage there (Pearcy and Ambler 1974). In addition to their stomach contents, the evidence for pelagic foraging by Pacific grenadier is their capture in midwater trawls (Simenstad et al. 1977, Iwamoto and Stein 1974). The stomachs of Pacific grenadier captured in midwater contain mostly mesopelagic prey (Simenstad et al. 1977).

Although the number of non-empty Pacific grenadier stomachs examined in this study was higher than in other studies, the sample-size was still too low to reach firm conclusions regarding area- and size-related trends. Thus, differences or trends that

occurred among areas or size classes should be considered preliminary until a larger number of samples can be analyzed.

The differences in the composition of the stomach contents between the Vancouver and Columbia INPFC areas may indicate differences in the availability of these prey types in each area. However, the giant grenadier (*Albatrossia pectoralis*) examined in this study show the opposite pattern for fish in the diet, a higher proportion in the Columbia INPFC area than in the Vancouver INPFC area (see Fig. 14).

The size-related decrease in the proportion of crustaceans and polychaetes and the increase in the proportion of fish and squid in the diet, by weight, is typical of many predatory fishes. We can not infer whether this change in diet composition is related to a change in feeding behavior (i.e., a shift from primarily benthic or pelagic foraging) because the crustaceans are a mixture of benthic and pelagic types and the fish and squid may be scavenged from the benthos or eaten in midwater. In addition, mesopelagic or vertically migrating species that occur in the diet may migrate close to the continental slope during the day and be consumed there (Pearcy and Ambler 1974).

The results of this study, combined with information from other studies, indicate that Pacific grenadier are opportunistic predators and scavengers associated with the continental slope and sometimes the mesopelagic environment. Benthic and pelagic animals are both important in their diet, but distinguishing the importance of midwater feeding relative to benthic scavenging will require further investigation.

Table 18.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of Pacific grenadier (*Coryphaenoides acrolepis*) caught north of Cape Blanco in the fall of 1992.

Prey Name	%F	%N	%W
Polychaeta (worm)	45.45	7.08	8.18
Cephalopoda (squid & octopus)	3.03	0.29	0.09
Teuthoidea (squid)	60.61	25.07	29.04
Octopoda (octopus)	6.06	1.18	0.04
Crustacea	18.18	2.95	1.35
Copepoda	6.06	1.77	0.11
Calanoida (copepod)	18.18	32.15	0.31
Mysidacea Mysida (mysid)	18.18	4.72	0.94
Cumacea (cumacean)	3.03	0.29	0.01
Isopoda (isopod)	6.06	1.47	0.12
Gammaridea (amphipod)	27.27	3.83	0.64
Hyperiidia (amphipod)	12.12	2.06	0.52
Caprellidea (amphipod)	6.06	0.59	0.07
Euphausiidae (euphausiid)	9.09	1.18	0.28
Decapoda (shrimp & crab)	3.03	0.29	0.22
<i>Sergestes</i> sp. (sergestid shrimp)	27.27	3.83	8.58
Reptantia (crab)	9.09	1.18	3.35
Caridea (shrimp)	3.03	0.29	0.09
Hippolytidae (shrimp)	9.09	1.47	5.82
Natantia (shrimp)	3.03	0.29	0.40
Axiidae (mud shrimps)	3.03	0.29	0.73
<i>Calocaris investigatoris</i> (mud shrimp)	3.03	0.29	5.21
<i>Chionoecetes</i> sp. (snow and Tanner crab)	3.03	0.29	2.10
Osteichthyes Teleostei (bony fish)	30.30	2.95	14.63
Non-gadoid fish remains	6.06	0.59	4.42
Unidentified organic material	30.30	2.95	11.81
Unidentified worm-like organism	3.03	0.59	0.94
Total prey number:	339		
Total prey weight:	35.27 g		
Total non-empty stomachs:	33		
Total empty stomachs:	7		

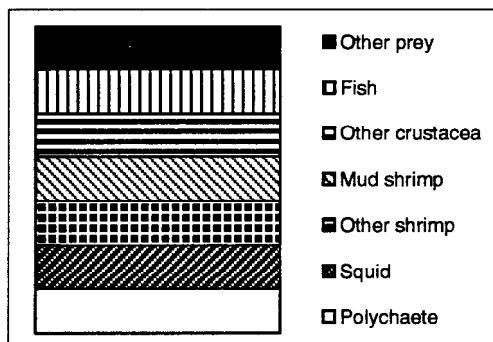
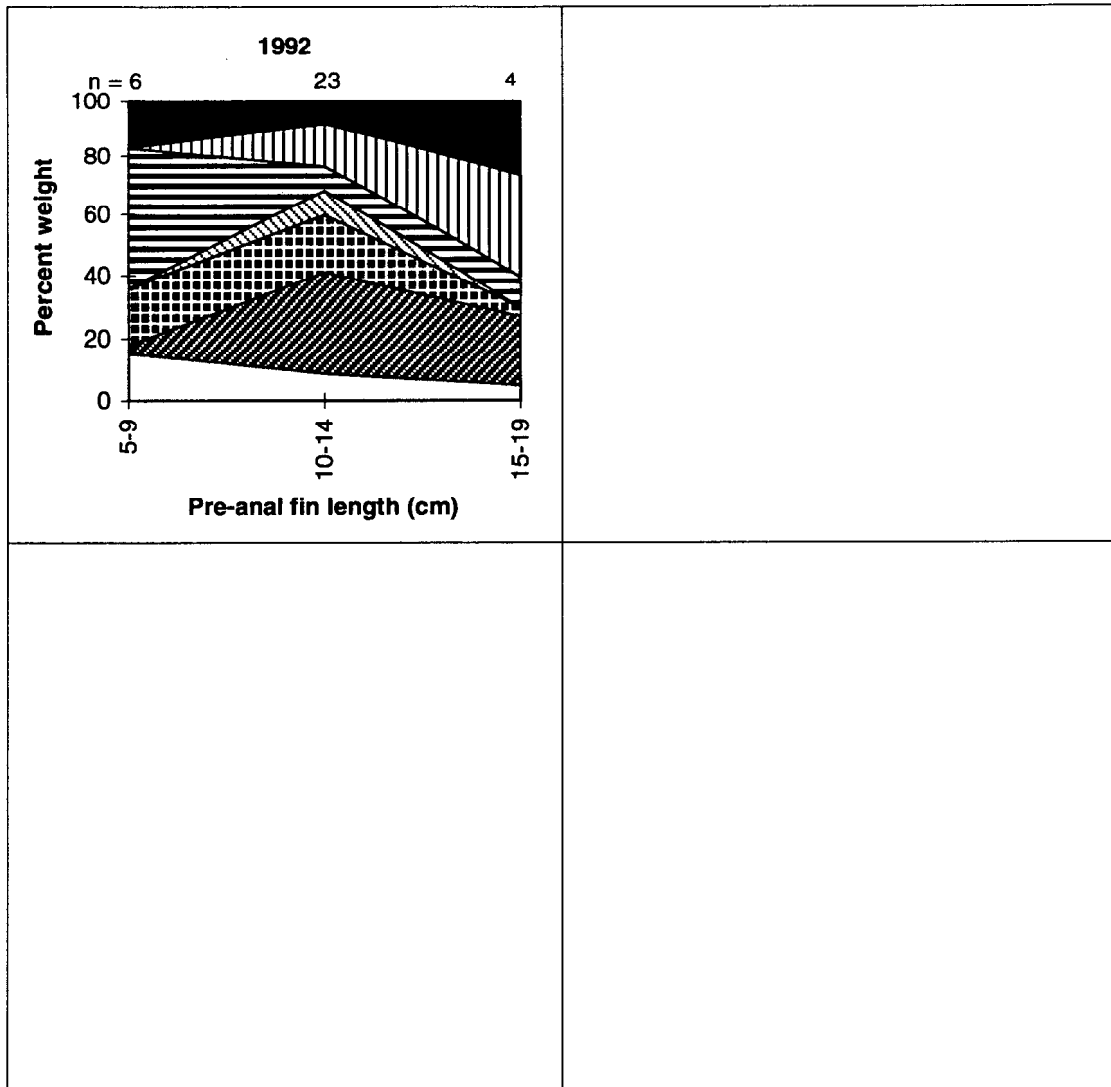


Figure 15.--Diet composition of Pacific grenadier (by length) from the 1992 survey.
The sample size (n) is shown above each length group.

DOVER SOLE

Dover sole, *Microstomus pacificus*, is a valuable commercial species with a long history of exploitation by the bottom trawl fishery (Dark and Wilkins 1994, Turnock et al. 1994). Landings, centered around the 183 m isobath, began to increase in the late 1940s after the introduction of new techniques to harden the soft flesh and produce a marketable fillet from what was previously considered a trash fish (Hagerman 1952). Coastwide landings exceeded 5,000 t per year in the 1950s and increased to a peak of 20,329 t in 1985 (Turnock et al. 1994), due in part to the expansion of the Dover sole fishery to deep water, especially off northern California (Dark and Wilkins 1994). In recent years, the fishery has continued to expand into deeper water over the continental slope (Turnock 1993, Jacobson and Hunter 1993); however, landings declined to 14,300 t in 1993 (Turnock et al. 1994).

The range of Dover sole extends from northern Baja California to the Bering Sea (Hart 1973) and occupy depths from 55 m to more than 1,500 m off the west coast of North America (Jacobson and Hunter 1993). Off Oregon, Dover sole are the most abundant fish on pure mud bottoms, but they occur in much higher densities on mud and boulder bottoms (Stein et al. 1992). Following a pelagic larval phase of 1 to 2 years, Dover sole settle onto the continental shelf as juveniles and gradually move into deeper water as they age and grow (Hart 1973, Jacobson and Hunter 1993, Turnock 1993). Superimposed on this ontogenetic increase in depth is a seasonal pattern of movement where fish migrate to deeper water in the winter to spawn and return to shallower water in the summer (Hagerman 1952, Jacobson and Hunter 1993, Turnock 1993). Sexual maturity is attained by 50% of Dover sole males and females at lengths of 32 cm and 35 cm FL, respectively (Hagerman 1952).

Dover sole are known to eat burrowing invertebrates (Hart 1973, Turnock 1993). Off northern California, Hagerman (1952) found that bivalves and scaphopods were common prey; sipunculids, polychaetes, sea urchins, brittle stars, and gastropods occurred in varying quantities; shrimp and other crustaceans were sometimes gorged upon. Percy and Hancock (1978) found a similar array of prey in the diet of Dover sole, including 11 species of polychaetes considered to be their principal prey off Oregon. Dover sole were found to select for polychaetes and brittle stars when feeding, and these prey groups were more important than molluscs and crustaceans off Oregon (Gabriel and Percy 1981).

RESULTS

General Diets

A total of 846 Dover sole stomachs were examined in the laboratory. Of the 279 stomachs examined from south of Cape Blanco in the summer of 1989, 17 (6%) were empty. Similarly, 20 (7%) of the 281 Dover sole stomachs analyzed from north of Cape Blanco in the summer of 1989 were empty. Only 4 (3%) of the 120 stomachs collected in the autumn of 1991 were empty, but 35 (29%) of the 166 stomachs collected farther north in the autumn of 1992 were empty.

South of Cape Blanco in 1989, the diet of Dover sole was gravimetrically dominated by polychaete worms (56%) and brittle stars (26%) (Table 19). These prey types were also numerically important and occurred frequently in the stomachs containing food. Gammarid amphipods and bivalves also occurred frequently and were numerically important, but because of their small size, their contribution to the weight of the diet was fairly small.

The diet of Dover sole caught north of Cape Blanco in 1989 was also gravimetrically dominated by polychaetes (42%) and brittle stars (31%) (Table 20). However, large, soft bodied prey, such as echiurans (marine worms) and holothurians (sea cucumbers), also contributed substantially to the total weight of the stomach contents (6% and 4%, respectively). Polychaete worms and brittle stars (especially brittle star legs without the central disk) occurred in the stomachs of Dover sole very frequently. Gammarid amphipods and bivalves were also numerically important and had a high frequency of occurrence, but because of their small size, their gravimetric contribution was small.

The Dover sole sampled in autumn of 1991 from the outer continental shelf and upper continental slope fed almost exclusively on polychaetes (85%) by weight (Table 21). Brittle stars (4%), amphipods (3%), and bivalves (2%) also contributed to the weight of the diet and had a high frequency of occurrence.

In autumn of 1992, the diet of Dover sole sampled from the outer continental shelf and upper continental slope north of Cape Blanco was dominated by polychaetes (49%) and brittle stars (35%) by weight (Table 22). These prey types were also numerically important and occurred very frequently in the stomachs of the Dover sole sampled. Small crustaceans - gammarid amphipods, caprellid amphipods, and cumaceans - and bivalves also had a high frequency of occurrence, but because of their small size, their contribution to the weight of the diet was fairly small. Numerically, gammarid amphipods (23% by number) were the second most important prey.

Variation in the Diet with Location

In general, polychaete worms were the dominant prey of Dover sole, by weight, throughout the study area (Fig. 16). In the summer of 1989, polychaetes were over 80% of the diet, by weight, of Dover sole sampled in the Conception INPFC area. In the Monterey INPFC area there was more variety in the diet, which included polychaetes, brittle star legs, brittle stars, crustaceans, and other prey. In the Eureka INPFC area, brittle star legs and squid (a mollusc) contributed to a diet dominated by polychaetes. In the Columbia INPFC area, sea urchins (included in other prey, Fig. 16) followed polychaetes in importance to the diet in the 30-99 fm depth zone, but in the 100-199 fm depth zone, polychaetes followed marine worms in importance, by weight. In the Vancouver INPFC area, brittle stars and polychaetes were the most important components of the diet in the summer of 1989 (Fig. 16).

In autumn of 1991, the diet of Dover sole caught in deeper water in the Monterey INPFC area was composed almost entirely (> 85%) of polychaetes, but in the Eureka INPFC area, brittle stars contributed a significant portion of the diet weight. Dover sole were sampled from the 200-499 fm depth zone in the Columbia INPFC area in both 1991 and 1992. In 1991; 14 Dover sole stomachs contained 68% polychaetes, 9% molluscs (mostly clams), 4% brittle stars, 3% crustaceans, and 16% other and unidentified prey, by

weight. In 1992, 80 Dover sole stomachs contained 50% polychaetes, 34% brittle stars, 9% crustaceans (mostly galatheids or pinch bugs), 4% marine worms, and 3% other and unidentified prey, by weight. In the 500-699 fm depth zone of the Columbia INPFC area, cumaceans and amphipods contributed to the weight of other crustaceans eaten. The stomach contents of the Dover sole caught in the 100-199 fm depth zone in the Columbia and Vancouver INPFC areas were dominated by brittle stars and polychaetes.

Diet Variation with Predator Size

In the summer of 1989, south of Cape Blanco, the composition of the diet did not appear to change very much with increasing size of the Dover sole, but the crustacea in the diet of the smallest size category (15-19 cm FL) was replaced by brittle star legs and "Other prey" in larger sizes of Dover sole (Fig. 17). North of Cape Blanco, the diet also appears to be fairly consistent for all sizes of Dover sole sampled, but brittle stars appear to increase in importance with size and marine worms were eaten by the largest fish. These increases are coupled with a decrease in other types of prey with predator size. In autumn of 1991, polychaetes were over 80% of the diet by weight for all sizes of Dover sole sampled. In autumn of 1992, it appears that a decrease in the percentage of polychaetes in the diet, by weight, was accompanied by an increase in the percentage of brittle stars and the occurrence of marine worms in the diet of Dover sole 45 cm FL and larger.

DISCUSSION

The diet of Dover sole is known from previous studies to consist primarily of benthic invertebrates (Hagerman 1952) especially polychaete worms and brittle stars (Pearcy and Hancock 1978, Gabriel and Pearcy 1981). The results of our study are in agreement with this generalization for most areas and depths examined (Fig. 16). Other studies found Dover sole consuming polychaetes and brittle stars in greater proportions than they occurred in box core samples, indicating a positive selection for these prey (Gabriel and Pearcy 1981). However, the contribution of brittle stars to the diet may be overestimated because brittle star legs may be evacuated very slowly from the stomach (Gabriel and Pearcy 1981). In addition, the brittle star legs are protected by calcareous shields (Barnes 1987) which may hinder digestion by raising the pH of the gut (Gabriel and Pearcy 1981).

Dover sole appear to select habitats with more food (Pearcy and Hancock 1978) and, although they are the most numerous fish found on mud bottoms, they occur in much higher densities on bottoms with mud and boulders (Stein et al. 1992). Mud and boulder bottoms are also occupied by very high densities of rockfishes and other species (Stein et al. 1992), and might support a higher density of brittle stars and polychaetes (food for Dover sole) than only mud bottoms because of higher nutrient (fecal) inputs from the biomass aggregated above this bottom type. Alternatively, Dover sole may prefer mud and boulder habitat because it provides better refuge than mud bottoms alone.

Seasonal differences in the feeding of Dover sole have been noted, although no conclusions could be made from the data in this study. Pearcy and Hancock (1978) found that Dover sole had fewer empty stomachs and a larger number of principal prey taxa in the summer than in the winter. This corresponds well with higher growth rates in the

summer (Demory 1972). However, the summer growth rates increase in feeding intensity and does not appear to be affected by food availability, which remains fairly constant in all seasons (Bertrand 1971).

Size-related changes in the diet composition of Dover sole in this study were seen primarily as an apparent increase in brittle stars and marine worms as predator size increased (Fig. 17). This is consistent with observations of larger Dover sole eating larger prey that were buried at increasing depths in the substrate (Gabriel and Pearcy 1981). Pearcy and Hancock (1978) found an increase in the number of polychaete species eaten with size, and found molluscs and brittle stars to be most important to intermediate sizes of Dover sole. In this study, we found the importance of molluscs in the diet to show peaks at intermediate sizes, but the size where the peak occurred was not consistent among the areas described (Fig. 17).

In general, the diet composition of Dover sole did not appear to be affected by latitude or depth (Fig. 16). However, this is probably a function of comparing prey groups at a high taxonomic level (Pearcy and Hancock 1978). Considerable variation in the species assemblage of polychaetes eaten occurs between stations (Pearcy and Hancock 1978), but only a small fraction of the polychaetes were identified down to the family level in this study. Some differences seem to occur when size groups are compared from north and south of Cape Blanco in summer of 1989 and autumns of 1991 and 1992 (Fig. 17). However, it appears that consistent differences were limited to brittle star legs being more important in the diet on the continental shelf than on the continental slope, and brittle stars being more important north of Cape Blanco than south of Cape Blanco.

Table 19.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of Dover sole (*Microstomus pacificus*) caught south of Cape Blanco in the summer of 1989.

Prey Name	%F	%N	%W
Foraminiferida (protozoan)	1.53	0.08	0.00
Hydrozoa	0.38	0.02	0.01
Polychaeta (worm)	58.02	14.56	33.55
Aphroditidae (sea mouse)	0.38	0.04	1.25
Sigalionidae (polychaete)	0.38	0.04	0.04
Euphrosinidae (polychaete)	14.12	2.83	14.16
<i>Euphrosinidae multibranchiata</i> (polychaete)	0.38	0.21	0.16
Phyllodocidae (polychaete)	4.58	0.34	0.25
Nereidae (polychaete)	0.38	0.06	0.14
Glyceridae (polychaete)	0.38	0.02	0.00
Goniadidae (polychaete)	1.15	0.06	0.08
Onuphidae (polychaete)	1.15	0.06	0.13
Lumbrineridae (polychaete)	1.15	0.11	0.01
<i>Lumbrineris</i> sp. (polychaete)	2.67	0.32	0.05
Flabelligeridae (polychaete)	2.29	0.13	0.62
Scalibregmididae (polychaete)	0.38	0.02	0.01
Opheliidae (polychaete)	0.38	0.04	0.12
<i>Travisia</i> sp. (polychaete)	0.38	0.02	0.60
<i>Sternaspis scutata</i> (polychaete)	4.96	0.51	0.66
Maldanidae (polychaete)	1.15	0.09	0.02
Oweniidae (polychaete)	0.38	0.04	0.03
Pectinariidae (polychaete)	5.34	0.41	0.46
Ampharetidae (polychaete)	1.91	0.55	0.84
Melinna (polychaete)	0.38	0.02	0.04
Terebellidae (polychaete)	4.58	0.41	2.70
Gastropoda (snail)	7.25	0.73	0.08
Aplacophora	1.53	0.08	0.00
Bivalvia (clam)	25.57	5.12	1.27
Scaphopoda	1.53	0.11	0.05
Teuthoidea (squid)	0.38	0.02	1.52
Ostracoda	1.15	0.06	0.00
Myodocopa (ostracoda)	0.38	0.04	0.00
Cirripedia Apygophora (barnacle)	0.38	0.02	0.00
Cumacea (cumacean)	14.89	1.47	0.11
Tanaidacea (peracaridan)	2.29	0.38	0.02

Table 19.--Continued.

Prey Name	%F	%N	%W
Gammaridea (amphipod)	46.56	15.84	0.43
Ampeliscidae (amphipod)	0.76	0.04	0.01
Caprellidea (amphipod)	1.91	0.38	0.03
Euphausiacea (euphausiid)	5.73	1.45	2.00
Caridea (shrimp)	0.76	0.04	0.05
Anomura (crab)	0.38	0.02	0.00
Ophiuroidea Ophiurida (brittle star)	29.01	7.16	5.73
Brittle star legs	44.66	40.83	18.45
<i>Ophiura</i> sp. (brittle star)	1.15	0.19	1.47
<i>Echinacea</i> sp. (sea urchin)	0.76	0.04	0.01
Holothuroidea (sea cucumber)	0.38	0.02	0.10
Ascidiacea (sea squirt)	3.44	0.24	0.12
Osteichthyes Teleostei (bony fish)	1.15	0.45	0.00
Unidentified organic material	24.43	1.21	11.47
Unidentified worm-like organism	6.87	0.83	0.64
Unidentified tube	10.31	1.98	0.43
Unidentified algae	2.67	0.30	0.05
Total prey number:	5308		
Total prey weight:	166.25 g		
Total non-empty stomachs:	262		
Total empty stomachs:	17		

Table 20.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of Dover sole (*Microstomus pacificus*) caught north of Cape Blanco in the summer of 1989.

Prey Name	%F	%N	%W
Phaeophyta (brown algae)	0.38	0.02	0.02
Foraminiferida (protozoan)	0.77	0.11	0.00
Foraminiferida Textulariina (foraminifera)	0.38	0.02	0.00
Nematoda (worm)	0.38	0.02	0.29
Acanthocephala (parasitic worm)	0.38	0.04	0.72
Polychaeta (worm)	73.18	22.47	17.46
Aphroditidae (sea mouse)	0.38	0.02	0.41
Euphrosinidae (polychaete)	1.53	0.31	0.21
Phyllodocidae (polychaete)	1.92	0.15	0.37
Nereidae (polychaete)	0.77	0.07	0.12
Sphaerodoridae (polychaete)	0.38	0.02	0.01
Glyceridae (polychaete)	1.15	0.15	0.44
Goniadidae (polychaete)	3.83	0.31	0.32
Onuphidae (polychaete)	1.15	0.22	0.57
Eunicidae (polychaete)	0.77	0.04	0.18
Lumbrineridae (polychaete)	5.75	1.03	0.87
<i>Lumbrineris</i> sp. (polychaete)	1.15	0.13	0.00
Paraonidae (polychaete)	0.38	0.02	0.00
Flabelligeridae (polychaete)	1.15	0.11	0.09
Scalibregmidae (polychaete)	0.38	0.02	0.01
Opheliidae (polychaete)	5.36	0.41	5.50
<i>Travisia</i> sp. (polychaete)	4.21	0.35	10.44
<i>Sternaspis scutata</i> (polychaete)	13.41	1.44	1.26
Maldanidae (polychaete)	4.60	0.33	1.50
Oweniidae (polychaete)	0.77	0.04	0.08
Sabellaridae (polychaete)	0.38	0.07	0.23
Pectinariidae (polychaete)	6.13	0.61	0.25
Ampharetidae (polychaete)	3.07	0.26	0.85
Terebellidae (polychaete)	1.53	0.13	0.38
Gastropoda (snail)	4.98	0.37	1.37
Nudibranchia dendronotoidea (nudibranch)	0.77	0.04	0.49
Bivalvia (clam)	28.35	4.19	1.94
Nuculoida (clam)	6.13	1.40	0.82
Scaphopoda	1.92	0.20	0.03
Crustacea	0.38	0.02	0.00
Ostracoda	2.30	0.94	0.02

Table 20.--Continued.

Prey Name	%F	%N	%W
Copepoda	1.53	0.11	0.00
Calanoida (copepod)	0.38	0.02	0.00
Cirripedia (barnacle)	0.38	0.11	1.61
Cumacea (cumacean)	13.03	1.70	0.18
Isopoda (isopod)	0.38	0.02	0.09
Gammaridea (amphipod)	40.23	8.60	0.31
Ampeliscidae (amphipod)	2.30	0.28	0.03
Caprellidea (amphipod)	0.77	0.04	0.00
Euphausiacea (euphausiid)	2.30	0.15	0.04
Euphausiidae (euphausiid)	0.77	0.04	0.00
<i>Euphausia pacifica</i> (euphausiid)	0.77	0.04	0.03
Decapoda (shrimp & crab)	0.38	0.02	0.01
Reptantia (crab)	0.38	0.02	0.00
Caridea (shrimp)	1.15	0.09	0.23
Pandalidae (shrimp)	1.15	0.07	0.82
Anomura (crab)	0.77	0.04	0.02
Axiidae (mud shrimps)	0.38	0.02	0.55
<i>Cancer magister</i> (Dungeness crab)	0.38	0.02	0.01
Echiura (marine worm)	1.92	0.20	5.71
Ophiuroidea Ophiurida (brittle star)	25.67	5.35	11.58
Brittle star legs	47.89	23.72	8.93
<i>Ophiura sarsi</i> (brittle star)	7.66	6.37	10.16
Echinoidea (sea urchin and sand dollar)	1.15	0.07	0.01
<i>Echinacea</i> sp. (sea urchin)	3.45	0.20	4.10
Holothuroidea (sea cucumber)	1.15	0.07	0.28
Ascidiacea (sea squirt)	1.15	0.11	0.61
Gnathostomata	0.38	0.09	0.60
Non-gadoid fish remains	0.38	0.04	0.00
Unidentified organic material	17.62	1.03	4.21
Unidentified worm-like organism	22.61	9.73	1.88
Unidentified tube	14.94	5.24	0.70
Unidentified algae	1.53	0.31	0.04
Total prey number:	4583		
Total prey weight:	457.24 g		
Total non-empty stomachs:	261		
Total empty stomachs:	20		

Table 2 1.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of Dover sole (*Microstomus pacificus*) caught in the fall of 1991.

Prey Name	%F	%N	%W
Foraminiferida Textulariina (foraminifera)	1.72	0.38	0.01
Anthozoa (anemome)	0.86	0.04	0.39
Polychaeta (worm)	92.24	33.88	58.41
Aphroditidae (sea mouse)	0.86	0.04	2.02
Euphosinidae (polychaete)	37.07	8.61	20.29
Opheliidae (polychaete)	0.86	0.04	0.00
<i>Sternaspis scutata</i> (polychaete)	11.21	1.85	2.56
Maldanidae (polychaete)	0.86	0.13	0.59
Pectinariidae (polychaete)	3.45	0.34	0.63
Mollusca	0.86	0.04	0.01
Gastropoda (snail)	3.45	0.21	0.16
Nudibranchia dendronotoidea (nudibranch)	1.72	0.08	0.05
Bivalvia (clam)	27.59	2.90	2.46
Teuthoidea (squid)	1.72	0.08	0.01
Ostracoda	14.66	8.40	0.91
Copepoda	0.86	0.04	0.00
Calanoida (copepod)	1.72	0.08	0.00
Mysidacea Mysida (mysid)	0.86	0.04	0.00
Mysidae (mysid)	1.72	0.08	0.00
Cumacea (cumacean)	18.10	2.14	0.21
Isopoda (isopod)	3.45	0.55	0.19
Gammaridea (amphipod)	68.10	23.05	2.33
Hyperiidia (amphipod)	3.45	1.72	0.12
Caprellidea (amphipod)	19.83	8.94	0.59
Sergestidae (sergestid shrimp)	0.86	0.04	0.34
Caridea (shrimp)	0.86	0.04	0.04
Natantia (shrimp)	1.72	0.08	0.16
Paguridae (hermit crab)	0.86	0.04	0.16
Majidae (spider crab)	2.59	0.13	0.06
Ophiuroidae Ophiurida (brittle star)	34.48	5.46	3.77
<i>Echinacea</i> sp. (sea urchin)	3.45	0.17	1.27
Osteichthyes Teleostei (bony fish)	0.86	0.04	0.00
Myctophidae (lanternfish)	0.86	0.04	0.22
Unidentified organic material	5.17	0.25	1.89
Unidentified worm-like organism	0.86	0.04	0.13

Table 21 .--Continued.

Total prey number:	2382
Total prey weight:	124.41 g
Total non-empty stomachs:	116
Total empty stomachs:	4

Table 22.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of Dover sole (*Microstomus pacificus*) caught north of Cape Blanco in the fall of 1992.

Prey Name	%F	%N	%W
Foraminiferida Textulariina (foraminifera)	3.82	0.95	0.02
Cnidaria	0.76	0.07	0.13
Hydrozoa Hydroida (hydroid)	0.76	0.14	0.02
Sertulariidae (hydroid)	0.76	0.07	0.52
Anthozoa (anemone)	0.76	0.07	0.31
Polychaeta (worm)	83.97	36.01	44.87
Euphrosinidae (polychaete)	1.53	0.14	2.07
Opheliidae (polychaete)	1.53	0.14	0.02
<i>Sternaspis scutata</i> (polychaete)	5.34	0.48	0.13
Maldanidae (polychaete)	7.63	0.75	1.59
Pectinariidae (polychaete)	2.29	0.27	0.06
Ampharetidae (polychaete)	1.53	0.27	0.39
Terebellidae (polychaete)	0.76	0.14	0.07
Gastropoda (snail)	3.05	0.48	0.15
Polyplacophora	0.76	0.07	0.00
Bivalvia (clam)	21.37	2.79	0.32
Scaphopoda	0.76	0.20	0.06
Teuthoidea (squid)	6.11	0.54	0.05
Crustacea	3.05	0.41	0.05
Ostracoda	1.53	0.20	0.01
Myodocopa (ostracoda)	1.53	0.14	0.00
Copepoda	0.76	0.95	0.01
Calanoida (copepod)	0.76	0.07	0.00
Mysidacea Mysida (mysid)	2.29	0.20	0.01
Cumacea (cumacean)	19.85	5.84	0.46
Tanaidacea (peracaridan)	0.76	0.07	0.00
Isopoda (isopod)	0.76	0.07	0.00
Gammaridea (amphipod)	49.62	23.37	2.20
Hyperideia (amphipod)	0.76	0.20	0.00
Caprellidea (amphipod)	20.61	3.06	0.18
Decapoda (shrimp & crab)	1.53	0.14	1.20
<i>Sergestes</i> sp. (sergestid shrimp)	2.29	0.20	0.95
Pasiphaeidae (shrimp)	0.76	0.07	0.34
Natantia (shrimp)	0.76	0.07	0.14
Anomura (crab)	0.76	0.07	0.08
<i>Munida quadrispina</i> (pinch bug)	6.11	2.11	5.35
<i>Cancer magister</i> (Dungeness crab)	0.76	0.07	0.01

Table 22.--Continued.

Prey Name	%F	%N	%W
Sipuncula (marine worm)	0.76	0.07	0.64
Echiura (marine worm)	0.76	0.07	0.00
Echiuridae (marine worm)	2.29	0.20	2.26
Ophiuroidea Ophiurida (brittle star)	54.96	18.21	34.53
<i>Echinacea</i> sp. (sea urchin)	3.05	0.27	0.26
Unidentified organic material	0.76	0.07	0.08
Unidentified worm-like organism	3.05	0.27	0.47
Total prey number:	1472		
Total prey weight:	78.83 g		
Total non-empty stomachs:	131		
Total empty stomachs:	35		

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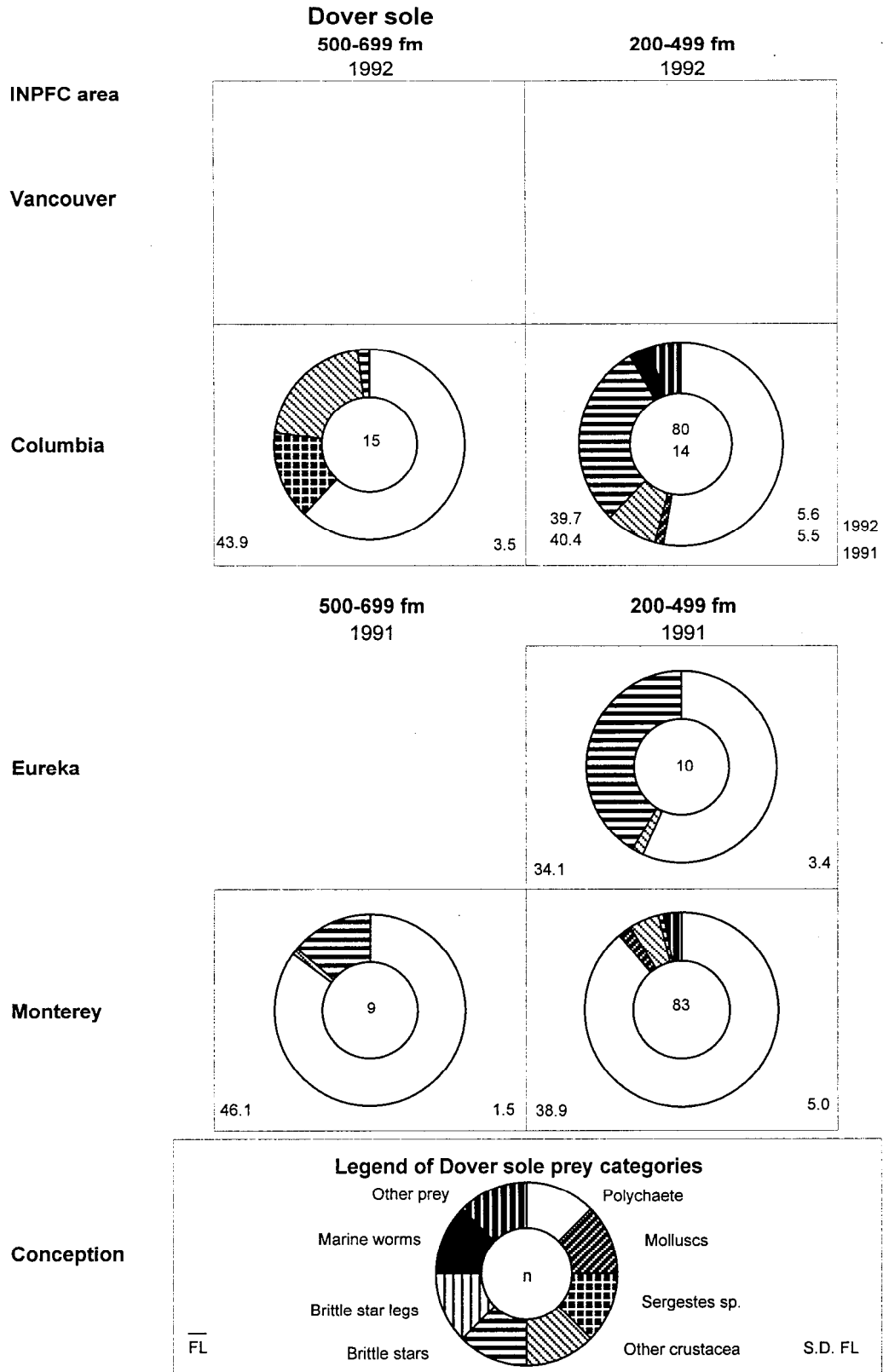


Figure 16.--Diet composition (by weight) of Dover sole for each depth zone, INPFC area and year. The number of nonempty stomachs examined are shown in each ring. Mean and standard deviation of the lengths are shown in the lower left and right of each box, respectively.

Dover sole

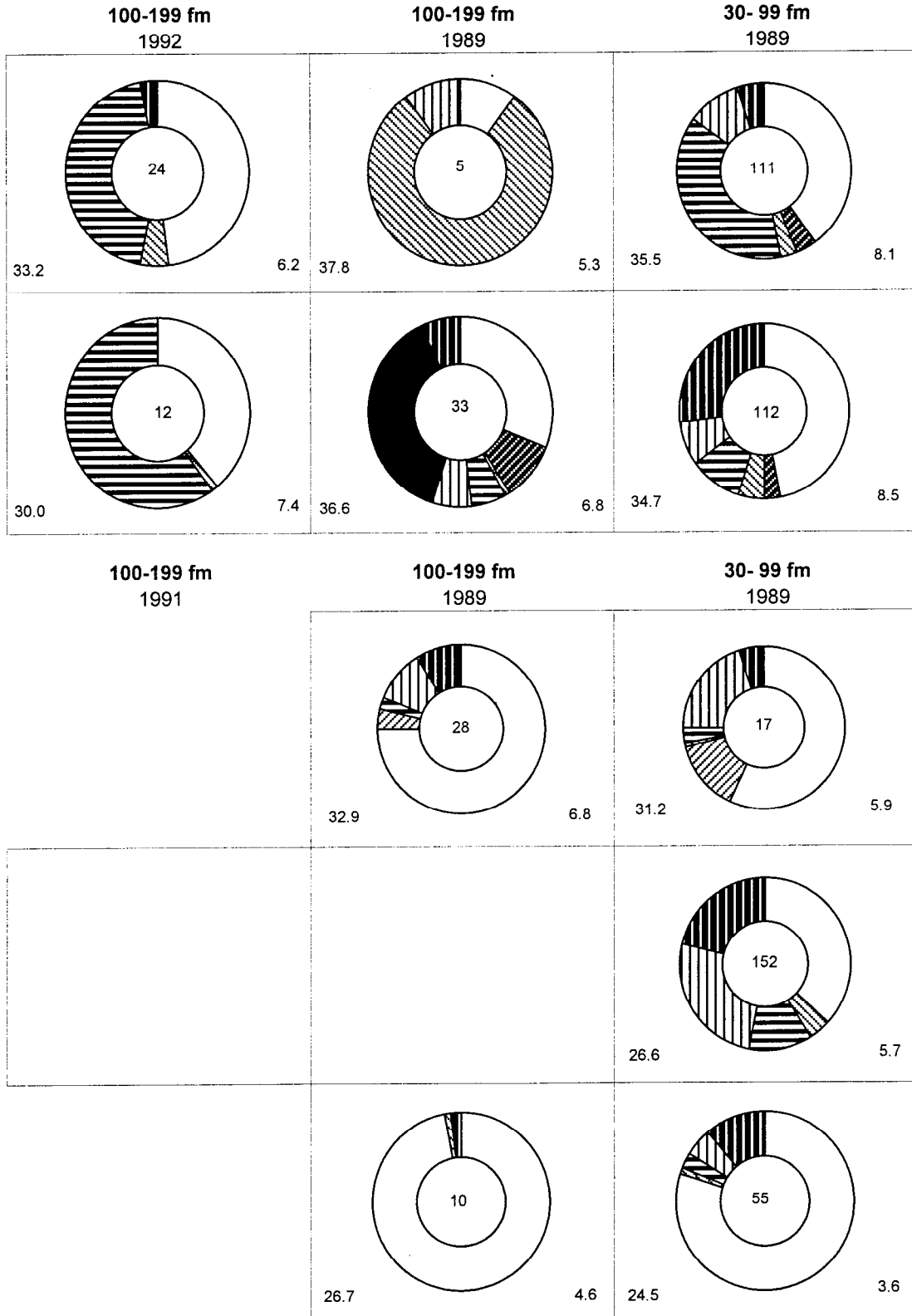


Figure 16--Continued.

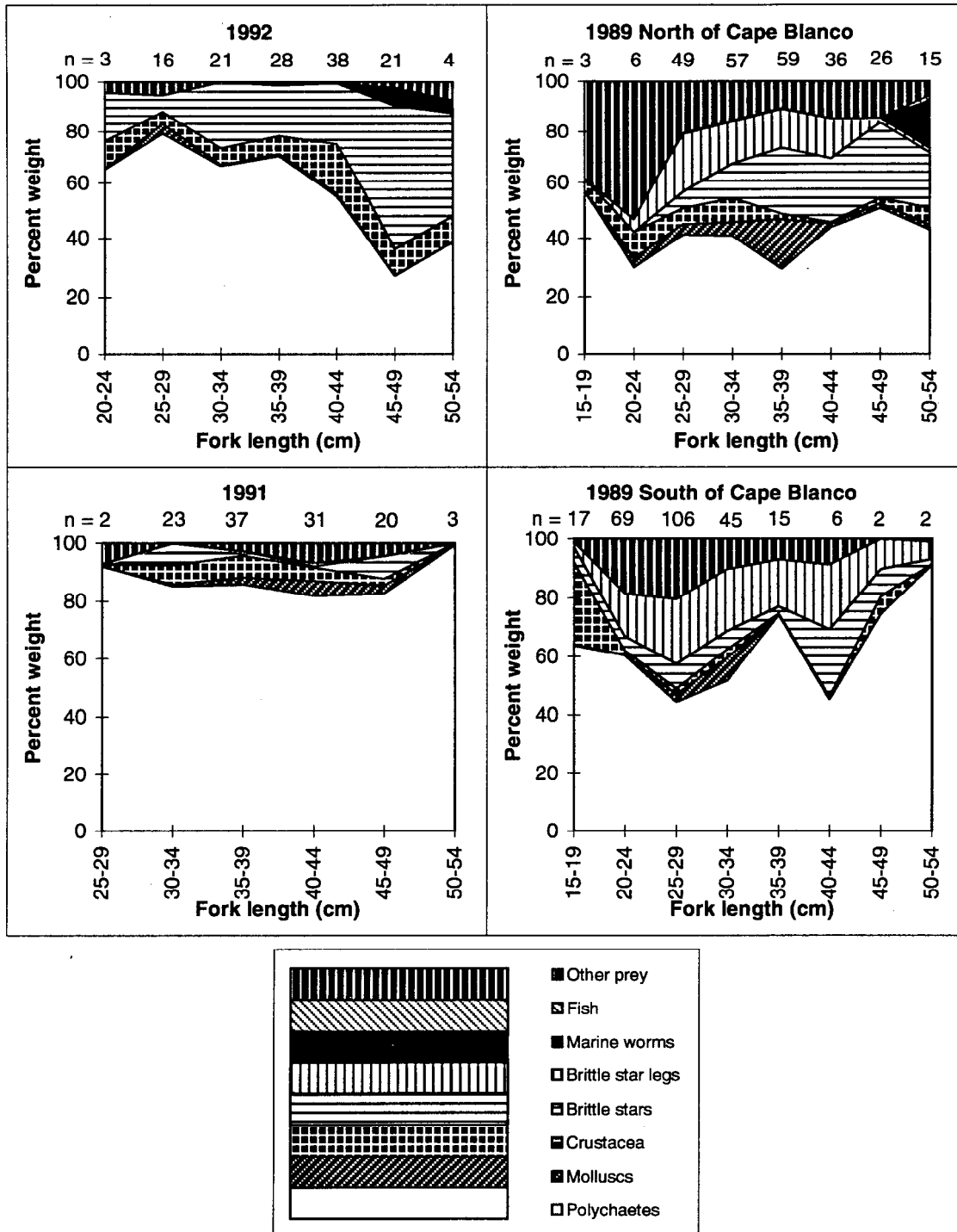


Figure 17.--Diet composition of Dover sole (by length) from north and south of Cape Blanco in 1989 and from the 1991 and 1992 surveys. The length-range shown in each figure may be different. The sample size (n) is shown above each length group.

DEEPSEA SOLE

The deepsea sole, *Embassichthys bathybius*, is a small-mouthed flatfish occurring in deep water along the western continental slope of North America. This species was first described from specimens captured off southern California in the late 1800s (Hagerman 1950) and the known northern extent of its range has increased over the years from Eureka, California (Hagerman 1950), to southeast Alaska (Hart 1973) to the Bering Sea (Matarese et al. 1989). The deepsea sole is the most deeply distributed of the flatfishes off Oregon and California (Alton 1972, Vetter et al. 1994) and possibly throughout its range. It is found mixed with Dover sole around depths of 1,000 m off central California (Vetter et al. 1994), and between depths of 732 to 870 m off Oregon (Day and Percy 1968, Alton 1972). Beyond 1,200 m, the deepsea sole is the only common flatfish, and its numbers decline with increasing depth by 1,400 m (Vetter et al. 1994). Deepsea sole may occasionally be processed in the Dover sole fishery, where they co-occur, but no fishery is directed toward its harvest.

Little is known about the life history of the deepsea sole. It can grow to 47 cm in length (Hart 1973). It spawns in winter through spring, releasing relatively large eggs, 3.0 mm in diameter, and may have a pelagic phase lasting several month (Richardson 1981). There does not appear to be any ontogenetic shift in its depth distribution, as is found for Dover sole, based on the similarity of the length distribution throughout its depth range (Vetter et al. 1994). Deepsea sole is thought to feed on polychaetes and other benthic invertebrates similar to other small-mouthed flatfish, like the Dover sole (Vetter et al. 1994).

RESULTS

General Diets

The stomach contents were examined from 171 deepsea sole sampled during the slope surveys in 1991 and 1992. In 1991, 10 (16%) of the 62 stomachs collected were empty (Table 23). Polychaete worms dominated the diet by frequency of occurrence, numerical composition, and gravimetric composition. Small crustaceans, especially mysids and amphipods, were commonly encountered in the stomachs, but because of their small size, they contributed little to the prey weight in the stomachs. Anemones and brittle stars were the second and third most important prey in terms of weight. In 1992, 30 (28%) of the 109 stomachs collected were empty (Table 24). Polychaete worms occurred about as frequently and were as important numerically in the deepsea sole diet in the 1992 survey as in the 1991 survey, but they contributed less to the weight-composition of the diet in 1992. A higher percentage of the weight of the diet was composed of brittle stars in the 1992 survey than the 1991 survey.

Variation in the Diet with Location

Polychaete worms were the dominant prey of deepsea sole, by weight, in most areas sampled (Fig. 18). In the autumn of 1991 in the Monterey INPFC area, polychaetes were the dominant prey, but sea anemones (coelenterates) were also important in the 200-499 fm depth zone. In the autumn of 1992 in the Columbia INPFC area, brittle stars were somewhat important, by weight, in the stomachs of deepsea sole,

and they were dominant in eight fish from the 500-699 fm depth zone. In the Vancouver INPFC area, polychaetes were the most important prey type, but unidentified hydrozoans (coelenterates) also contributed to the weight of the diet in the 200-499 fm depth zone.

Diet Variation with Predator Size

In general, opposite trends occurred in 1991 and 1992 with respect to the diet composition changes and predator size (Fig. 19). However, molluscs appear to be most important to intermediate sized deepsea sole and crustaceans appear to decrease in importance with increasing predator size during both years.

DISCUSSION

Previous descriptions of the food habits of deepsea sole suggest that it feeds on benthic invertebrates, especially polychaetes, similar to other small-mouthed flatfish (Vetter et al. 1994). The results of our study confirm this generalization of the food habits of deepsea sole, and it seems fairly invariant over the latitudes and depths examined, given the level of identification of the prey items in our study (Fig. 18). However, considerable between-station variation in the species assemblage of polychaetes consumed by Dover sole has been found (Pearcy and Hancock 1978).

Diet variation with predator size was very different in the 1991 and 1992 surveys (Fig. 19). It seems unlikely that the opposite trends in diet composition with predator size indicate that true differences exist in the availability or selection of prey types for the different sizes of deepsea sole. It seems more likely that larger deepsea sole would have a tendency to feed on larger prey that were buried deeper in the substrate than would smaller deepsea sole, similar to the trend found for Dover sole (Gabriel and Pearcy 1981). Perhaps if a larger number and a broader size-range of deepsea sole were sampled and the prey were identified to finer taxonomic categories (Pearcy and Hancock 1978), then more meaningful dietary changes with predator size could be described.

This is the first description of the diet of deepsea sole that we know of. The diet is generally similar to other small-mouthed flatfishes, but it may be unique because the depths at which all sizes of deepsea sole occur is deeper than most, except for the largest Dover sole.

Table 23.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of deepsea sole (*Embassichthys bathybius*) caught south of Cape Blanco in the autumn of 1991.

Prey Name	%F	%N	%W
Anthozoa (anemone)	7.69	2.60	6.26
Polychaeta (worm)	67.31	46.35	76.09
Sabellidae (polychaete)	5.77	3.13	1.58
Gastropoda (snail)	1.92	1.56	2.93
Crustacea	1.92	0.52	0.00
Calanoida (copepod)	1.92	0.52	0.00
Mysidacea Mysida (mysid)	11.54	5.21	0.35
Gammaridea (amphipod)	25.00	14.06	0.61
Caprellidea (amphipod)	1.92	1.56	0.00
Reptantia (crab)	1.92	0.52	0.09
Callianassidae (mud shrimp)	1.92	0.52	1.74
Ophiuroidea Ophiurida (brittle star)	19.23	14.58	4.94
Urochordata (tunicate)	1.92	3.13	1.35
Ascidiacea (sea squirt)	1.92	0.52	0.31
Unidentified organic material	17.31	4.69	2.43
Unidentified worm-like organism	1.92	0.52	1.31
Total prey number:	192		
Total prey weight:	42.31 g		
Total non-empty stomachs:	52		
Total empty stomachs:	10		

Table 24.--The percent frequency of occurrence (%F), percent number (o/ON), and percent weight (OhW) of the prey found in the stomachs of deepsea sole (*Embassichthys bathybius*) caught north of Cape Blanco in the autumn of 1992.

Prey Name	%F	%N	%W
Hydrozoa	2.53	0.99	5.01
Anthozoa (anemone)	3.80	1.49	0.91
Polychaeta (worm)	63.29	45.05	36.29
Polynoidae (polychaete)	1.27	0.50	2.20
Sabellidae (polychaete)	8.86	7.43	12.70
Nudibranchia dendronotoidea (nudibranch)	1.27	0.50	1.43
Bivalvia (clam)	1.27	0.50	0.05
Calanoida (copepod)	1.27	0.50	0.01
Mysidacea Mysida (mysid)	11.39	4.46	0.51
Gammaridea (amphipod)	17.72	12.38	0.87
Caprellidea (amphipod)	13.92	7.43	0.41
Crangonidae (shrimp)	1.27	0.50	0.03
Galatheidae (pelagic slip crabs)	2.53	0.99	1.01
Majidae (spider crab)	1.27	0.50	0.25
Ectoprocta (bryozoan)	1.27	0.50	0.57
Ophiuroidae Ophiurida (brittle star)	11.39	6.44	22.99
Urochordata (tunicate)	2.53	0.99	1.15
Unidentified organic material	21.52	8.42	12.60
Unidentified tube	1.27	0.50	1.00
Total prey number:	202		
Total prey weight:	18.97 g		
Total non-empty stomachs:	79		
Total empty stomachs:	30		

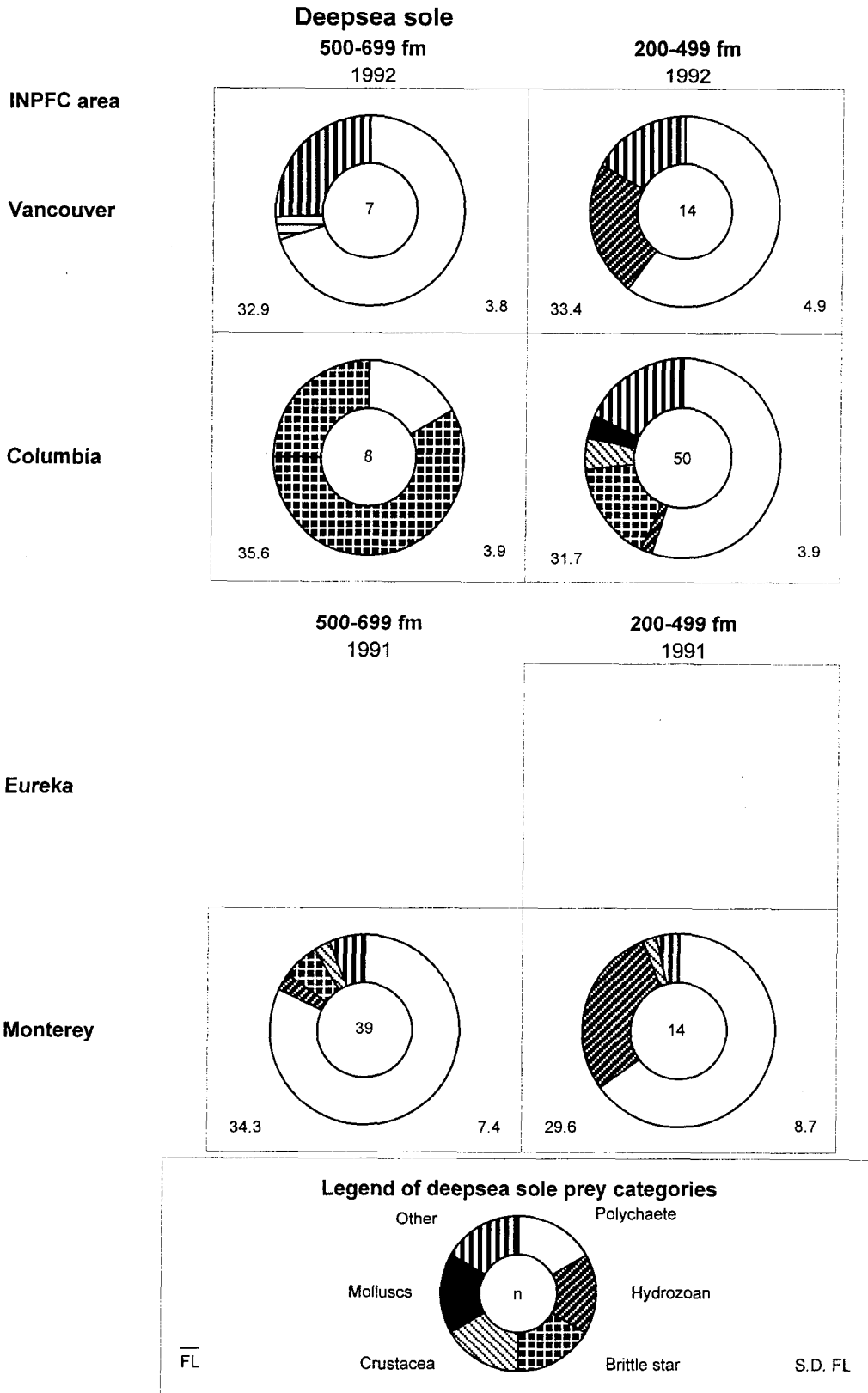


Figure 1 S.--Diet composition (by weight) of deepsea sole for each depth zone, INPFC area and year. The number of nonempty stomachs examined are shown in each ring. Mean and standard standard deviation of the lengths are shown in the lower left and right of each box, respectively.

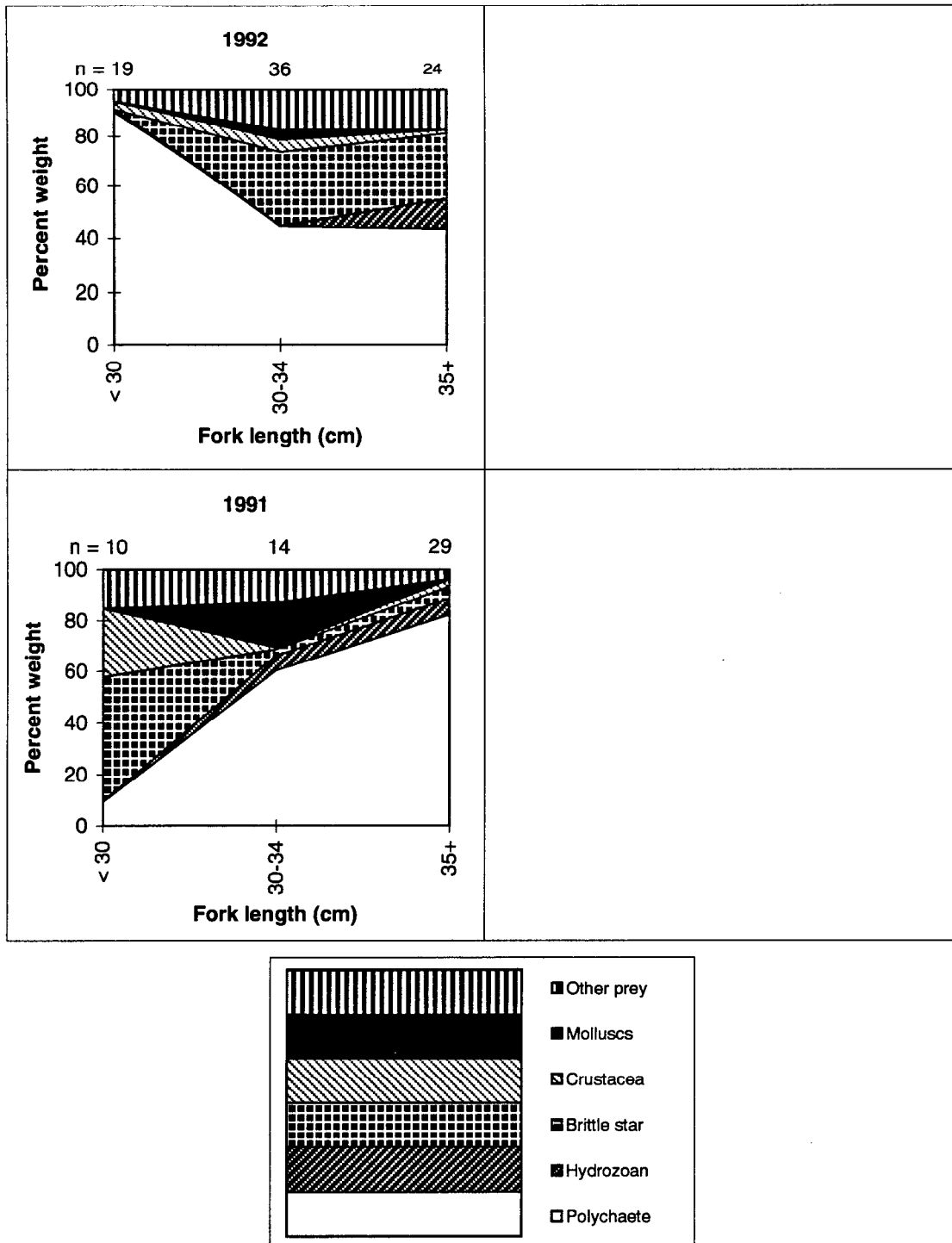


Figure 19.--Diet composition of deepsea sole (by length) from north and south of Cape Blanco in 1989, and from the 1991 and 1992 surveys. The length-range shown in each figure may be different. The sample size (n) is shown above each length group.

ARROWTOOTH FLOUNDER

Arrowtooth flounder (&here&es *stomias*) is a low-value species processed primarily by the reduction industry, but some is marketed in fillet form (Kabata and Forrester 1974, Dark and Wilkins 1994). Historically, annual landings of this species have been a few hundred metric tons for the U.S. Pacific coast (Dark and Wilkins 1994), but up to 3,180 t per year have been processed in British Columbia, Canada, for mink feed (Hart 1973). Annual U.S. landings increased in the early 1980s and were 2831 metric tons by 1987 (Dark and Wilkins 1994), and landings from areas off Washington in 1990-92 were higher than any other groundfish species except Pacific hake (Rickey 1995). However, discard rates for arrowtooth flounder are estimated to be 76% off Oregon and Washington and over 80% in the Gulf of Alaska (Rickey 1995).

Arrowtooth flounder extend from central California to the Bering Sea and inhabit depths down to 499 fm (900 m) (Hart 1973, Dark and Wilkins 1994). The biomass of this species is centered in the Gulf of Alaska with the biomass density decreasing southward, becoming very low in the Eureka and Monterey INPFC areas (Dark and Wilkins 1994). As with several other flattish species, arrowtooth flounder exhibits a tendency for larger, older fish to occupy deeper depths and perform seasonal spawning migrations into deeper waters in the winter (Alton 1972, Kabata and Forrester 1974, Dark and Wilkins 1994, Rickey 1995). Sexual maturity is attained by 50% of arrowtooth flounder at lengths of 28 cm FL for males and 37 cm FL for females (Rickey 1995).

The diet of arrowtooth flounder has been described from the eastern Bering Sea (Yang and Livingston 1986, Yang 1991, Livingston et al. 1993, Lang and Livingston 1996), Aleutian Islands (Yang 1996), Gulf of Alaska (Yang 1993) and the eastern Pacific Ocean off British Columbia (Hart 1973, Kabata and Forrester 1974) and northern California (Gotshall 1969). Arrowtooth flounder is primarily piscivorous, consuming schooling gadids and small, schooling fishes, but it also eats shrimp and euphausiids.

RESULTS

General Diets

The stomach contents of 380 arrowtooth flounder from the 1989 and 1992 surveys were examined in the laboratory. Of the 341 stomachs collected in the summer of 1989, 163 (47.8%) were empty (Table 25). Euphausiids, especially *Euphausiapaczjka* and *Thysanoessa spinifera*, occurred more frequently in the diet than any other prey types and they dominated the numerical composition of the diet. However, because of their small size relative to other prey types, they contributed very little to the gravimetric composition of the diet. Pacific herring (*Clupeapallasi*) also occurred fairly often in the stomachs that contained food, and was of little importance to the numeric composition of the diet due to the great number of euphausiids. However, Pacific herring was an important component of the diet, by weight, because of its intermediate size relative to the other prey types. Unidentified gadids and Pacific hake (*Merluccius productus*) dominated the weight of the stomach contents because of their large size (64% combined), even though they did not occur frequently. Twenty-eight (72%) of the 39 stomachs collected in autumn of 1992 were empty (Table 26). Pacific herring occurred

most frequently in the stomachs and was the dominant prey by number. However, Pacific hake was the dominant prey by weight.

Variation in the Diet with Location

In the Columbia INPFC area, flatfish (pleuronectiformes), pandalid shrimp, and “Other fish” (mostly unidentified gadids) comprised the bulk of the diet in the 30-99 fm depth zone in the summer of 1989 (Fig. 20). In the 100-199 fm depth zone, pandalid shrimp and “Other fish” dominated the diet. Pacific hake was followed by “Other fish” and clupeids as the three most important diet components, by weight, in the 30-99 fm depth zone of the Vancouver INPFC area. Euphausiids were the dominant prey of the 14 arrowtooth flounder sampled with food in their stomachs in the 100-199 fm depth zone of the Vancouver INPFC area in the summer of 1989.

Few arrowtooth flounder sampled during the 1992 autumn survey of the continental shelf and slope had prey in their stomachs (Table 26 and Fig. 20). Pacific herring was the only prey type found in four fish from the Vancouver INPFC area in the 100-199 fm depth zone. Pacific hake was the dominant prey of seven arrowtooth flounder captured in the 200-499 fm depth zone in the Columbia INPFC area.

Variation in the Diet with Predator Size

The stomach samples collected in 1989 north of Cape Blanco indicated a high degree of piscivory, even in very small arrowtooth flounder, that is highest for the largest arrowtooth flounder (Fig. 21). However, fish were less important in the smallest size categories, reaching a minimum percentage of the stomach contents weight by 30-39 cm FL, before increasing rapidly with predator size to comprise almost the entire diet. Euphausiids decreased as a component of the diet, by weight, and pandalid shrimp were important to intermediate sizes of arrowtooth flounder. Pacific herring, flatfish, and “Other fish” were important components of the diet over a broad range of size categories (10-19 to 50-59 cm FL). Pacific hake was an important prey for larger arrowtooth flounder (FL > 59 cm) in all samples that we examined.

DISCUSSION

The results of this study were generally consistent with the results of other studies on the food habits of arrowtooth flounder which found that the diet primarily consists of available schooling fishes. On the continental shelf of the eastern Bering Sea, arrowtooth flounder consume mostly walleye pollock (*Theragra chalcogramma*) (56-88%), by weight, but euphausiids (2-22%), shrimp (0-7%), and Pacific herring (0-3%) are sometimes important (Yang and Livingston 1986, Yang 1991). Walleye pollock (55%) is also the primary prey of arrowtooth flounder caught on the continental slope of the eastern Bering Sea, and Pacific herring (11%) and squid (11%) also contribute to the weight of the stomach contents when they are available (Lang and Livingston 1996). Around the Aleutian Islands, Atka mackerel (*Pleurogrammus monopterygius*) (44%) was the most important prey, by weight, followed by walleye pollock (11%), lanternfish (Myctophidae) (7%) and euphausiids (5%) (Yang 1996). In the Gulf of Alaska, walleye pollock (66%) dominate the weight of the diet followed by Pacific herring (9%) and capelin (*Mallotus villosus*) (8%) (Yang 1993). Kabata and Forrester (1974) examined the

numerical composition of the arrowtooth flounder diet off British Columbia and found euphausiids (58%) were most important followed by pandalid shrimp (18%), eulachon (*Thaleichthys pacificus*) (6%), and Pacific herring (3%). Walleye pollock and Pacific hake were both identified in the diet. Given the relative sizes of these prey types, it is likely that, by weight, fish was the most important prey category followed by pandalid shrimp and euphausiids. A similar numeric-gravimetric reversal in the order of prey importance can be seen in Table 25 where euphausiids are dominant numerically and fish are dominant gravimetrically. Hart (1973) describes the diet of arrowtooth flounder, presumably from British Columbia, as consisting of shrimp and Pacific herring. Off northern California, the diet of arrowtooth flounder includes, by volume, fish (mostly flatfish and small, schooling fish) (47%), pink shrimp (*Pandalus jordani*) (38%), and euphausiids (7%) (Gotshall 1969), and arrowtooth flounder is listed as a predator of Pacific hake (Best 1963).

The vast majority of the prey are pelagic or semi-pelagic, and we can conclude that arrowtooth flounder is primarily a pelagic predator off the coasts of Washington and Oregon, as they are in other areas (Kabata and Forrester 1974, Yang and Livingston 1986). The rare presence of benthic organisms (polychaete worm, snail, starfish, and algae) in the stomach contents may indicate that arrowtooth flounder occasionally forage on the bottom. However, these organisms may not normally be preyed upon, and might only be eaten when they are lifted up from the bottom by the trawl footrope and are available to arrowtooth flounder in the net (net feeding).

Arrowtooth flounder appears to be an opportunistic and somewhat non-selective predator of relatively large prey such as fish, shrimp, and squid (Yang and Livingston 1986, Lang and Livingston 1996, Yang 1996). The variety of fishes in the diet (Table 25) and the importance of the "Other fish" category across areas (Fig. 20), as well as the differing composition of the "Other fish" category among areas, support this conclusion. This generalization also appears to be applicable over seasonal (Gotshall 1969, Yang 1991, Lang and Livingston 1996) as well as regional scales (Yang and Livingston 1986, Yang 1996).

Increasing piscivory and decreasing euphausiid consumption with increasing size of arrowtooth flounder is well documented in northern regions (Yang and Livingston 1986, Yang 1991, Yang 1993, Lang and Livingston 1996, Yang 1996). Similarly, in this study the percentage of euphausiids, by weight, in the diet decreased with increasing size, and the percentage of fish in the diet was higher for larger arrowtooth flounder than smaller ones (Fig. 21). However, a large percentage of the diet, by weight, of the 30-39 cm FL size group was comprised of pandalid shrimp, creating a decrease then increase in the proportion of fish in the diet with increasing length. It is possible that larger sample sizes might show a consistent and gradual increase in the proportion of fish in the diet, as was found in other studies examining a similar size-range of arrowtooth flounder (Yang and Livingston 1986, Yang 1993, Yang 1996). However, pandalid shrimp may represent an abundant and appropriately sized prey type for intermediate sizes of arrowtooth flounder in this area.

Table 25.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of arrowtooth flounder (*Atheresthes stomias*) caught north of Cape Blanco in the summer of 1989.

Prey Name	%F	%N	%W
Scyphozoa (jellyfish)	0.56	0.05	0.01
Polynoidae (polychaete worm)	0.56	0.05	0.02
Gastropoda (snail)	0.56	0.05	0.01
Peracarida Mysidacea (mysid)	0.56	0.05	0.00
Gammaridea (amphipod)	0.56	0.05	0.00
Euphausiidae (euphausiid)	19.66	21.77	0.41
<i>Euphausia pacifica</i> (euphausiid)	20.22	44.73	2.02
<i>Thysanoessa longipes</i> (euphausiid)	1.12	0.21	0.00
<i>Thysanoessa spinifera</i> (euphausiid)	26.40	23.95	0.96
Caridea (shrimp)	1.69	0.21	0.03
Pasiphaeidae (shrimp)	1.12	0.16	0.10
Pandalidae (shrimp)	7.87	0.83	0.75
<i>Pandalus</i> sp. (shrimp)	2.81	0.31	0.51
<i>Pandalus jordani</i> (shrimp)	7.87	0.73	2.05
<i>Crangon communis</i> (shrimp)	1.12	0.10	0.09
<i>Argis</i> sp. (shrimp)	0.56	0.05	0.01
<i>Argis lar</i> (shrimp)	0.56	0.05	0.01
Natantia (shrimp)	1.12	0.10	0.00
Galatheididae (pelagic slip crabs)	0.56	0.05	0.01
Asteroidea (starfish)	0.56	0.05	0.00
Osteichthyes Teleostei (bony fish)	1.69	0.16	0.15
Non-gadoid fish remains	3.37	0.47	0.31
<i>Clupea pallasii</i> (Pacific herring)	18.54	2.75	19.77
Osmeridae (smelts)	2.81	0.42	0.20
<i>Thaleichthys pacificus</i> (eulachon)	5.06	0.88	0.76
<i>Chauliodus macouni</i> (Pacific viperfish)	0.56	0.05	0.37
Myctophidae (lanternfish)	1.69	0.21	0.29
Gadidae (gadid fish)	3.93	0.36	27.72
<i>Merluccius productus</i> (Pacific hake)	1.69	0.16	36.21
Scorpaenidae	1.12	0.10	0.58
<i>Sebastes</i> sp. (rockfish)	0.56	0.05	0.06
Stichaeidae (prickleback)	0.56	0.05	0.20

Table 25.--Continued.

Prey Name	%F	%N	%W
Pleuronectidae (flatfish)	2.25	0.21	0.81
<i>Atheresthes stomias</i> (arrowtooth flounder)	0.56	0.05	0.85
<i>Errex zachirus</i> (rex sole)	1.12	0.10	1.37
<i>Eopsetta exilis</i> (slender sole)	0.56	0.10	2.08
<i>Psettichthys melanostictus</i> (sand sole)	0.56	0.05	1.26
Unidentified organic material	1.69	0.16	0.02
Unidentified algae	0.56	0.05	0.01
Unidentified material	0.56	0.05	0.01
Total prey number:	1925		
Total prey weight:	2763.77 g		
Total non-empty stomachs:	178		
Total empty stomachs:	163		

Table 26.--The percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) of the prey found in the stomachs of arrowtooth flounder (*Atheresthes stomias*) caught north of Cape Blanco in the autumn of 1992.

Prey Name	%F	%N	%W
Pandalidae (shrimp)	9.09	7.69	0.07
Osteichthyes Teleostei (bony fish)	18.18	15.38	0.00
<i>Clupeapallasi</i> (Pacific herring)	36.36	46.15	13.94
<i>Merlucciusproductus</i> (Pacific hake)	27.27	23.08	83.57
<i>Atheresthes stomias</i> (arrowtooth flounder)	9.09	7.69	2.42
Total prey number:	13		
Total prey weight:	659.09 g		
Total non-empty stomachs:	11		
Total empty stomachs:	28		

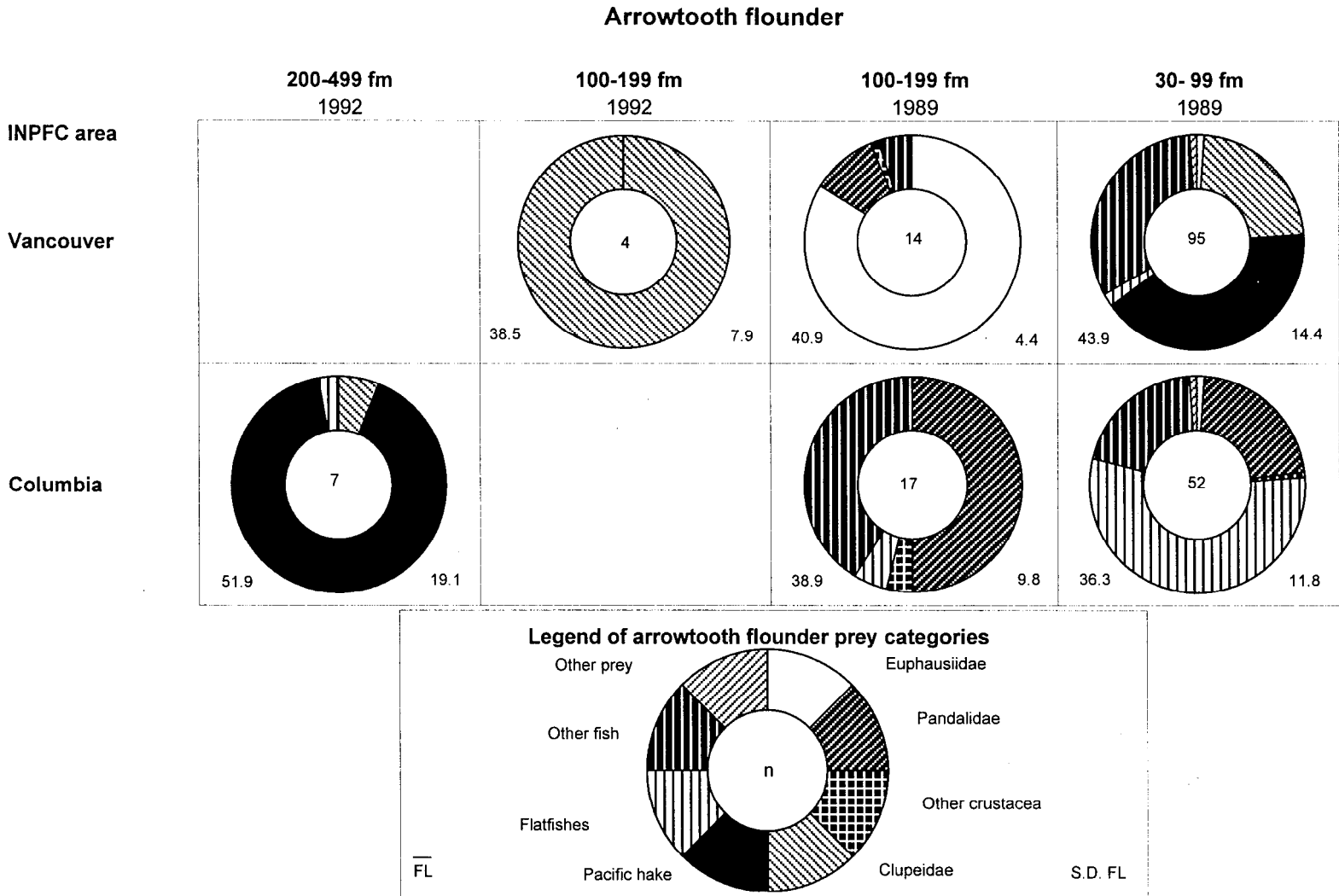


Figure 20.--Diet composition (by weight) of arrowtooth flounder for each depth zone, INPFC area and year. The number of nonempty stomachs examined are shown in each ring. Mean and standard deviation of lengths are shown in the lower left and right of each box, respectively.

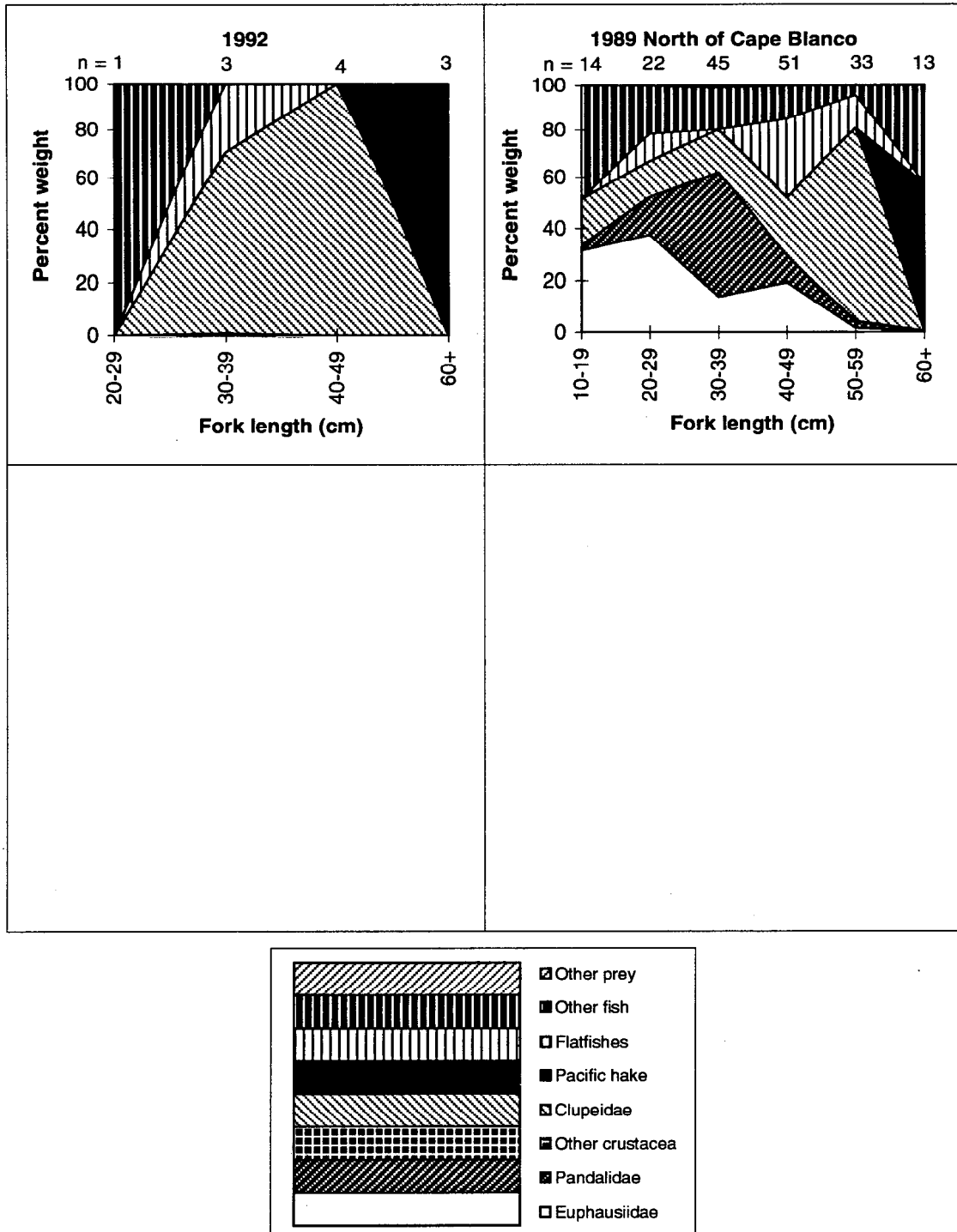


Figure 2 1 .--Diet composition of arrowtooth flounder (by length) from north of Cape Blanco in the 1989 and 1992 surveys. The length-range shown in each figure may be different. The sample size (n) is shown above each length group.

SPECIES INTERACTIONS

Species interactions can be between predator and prey or among competitors for the same prey resource. The first step in examining the potential for competition among species is to assess the similarity in their diets. Comparisons of various indices of dietary overlap or similarity indicate that those based on the quantities or proportions of prey types are generally better than those based solely on the presence or absence of prey types in the diets (Cailliet and Barry 1979). The Percent Similarity Index (PSI), also commonly known as Schoener's (1970) Index, is the simplest, and it has been independently developed several times since 1938 (Hurlbert 1978, Cailliet and Barry 1979). The PSI can be calculated in two ways:

$$\text{PSI} = 1 - \frac{1}{2} (\sum | p_{xi} - p_{yi} |)$$

or

$$= \sum [\min (p_{xi}, p_{yi})],$$

where p is the percentage (or proportion) of prey i in predators x and y . The value of this index ranges from 0 to 100 (or 0 to 1 if proportions are used) indicating, respectively, no similarity to complete similarity of the diets. The PSI performs well (Cailliet and Barry 1979, Linton et al. 1981), responds to both rare and dominant prey types, and is less sensitive to skewness in prey composition than some other indices (Cailliet and Barry 1979). However, its accuracy decreases when overlap is very low (< 7%) or very high (> 90%) (Linton et al. 1981). When overlap is very low, an index based on comparison of prey lists (presence or absence) can be a better measure (Pielou 1974).

METHODS

Predator diet data were pooled into 61 mutually exclusive prey categories, and the percentage weight composition of the 61 prey categories was calculated for each predator. The PSI was calculated for each pair of predators using all 61 prey categories including miscellaneous shrimp, miscellaneous crabs, miscellaneous crustacea, miscellaneous vertebrata, miscellaneous organic material, and miscellaneous prey. The "miscellaneous" categories were mostly composed of unidentified prey. By using the "miscellaneous" prey categories in the calculation of the PSI, an assumption was implied that the identified and unidentified components of those categories were identical in both predators. The PSI was also calculated for each pair of predators without using the "miscellaneous" prey categories, implying that the components of those categories were assumed to be completely different. When one wants to avoid biasing the PSI estimate due to improperly assuming predators contain identical prey, the second method of calculating PSI should be used to generate an estimate of minimum diet overlap. In our calculations, when the difference between the PSI with "miscellaneous" categories and the minimum estimate of PSI without "miscellaneous" categories was less than four, the mean value was presented; otherwise, the range was presented. The amount of diet overlap was categorized as low (0-24%), moderate (25-49%), high (50-74%), or very high (75- 100%) based on the mean of the two index values.

RESULTS

The percentage weight composition of the diet of each predator, based on the 61 prey categories, was presented for samples collected in the summer 1989 shelf survey south of Cape Blanco (Table 27) and north of Cape Blanco (Table 28) and the autumn slope surveys of 1991 (Table 29) and 1992 (Table 30). Using these values, the PSI was calculated with and without the 'miscellaneous' prey categories, as described above.

South of Cape Blanco in the 1989 shelf survey, moderate diet overlap was found between Pacific hake and sablefish (Table 32). This was due mainly to the consumption of euphausiids, but cephalopods (mostly squid), engraulids (anchovies), scorpaenids (rockfishes), and pleuronectiform fish also contributed (Table 27).

North of Cape Blanco in the 1989 survey of the continental shelf, moderate PSI values were found among Pacific hake, sablefish, and arrowtooth flounder, indicating moderate diet overlap (Table 31). The diet overlap among Pacific hake, sablefish, and arrowtooth flounder was due to consumption of clupeids (mostly herring), euphausiids, and some pandalid shrimp. Pleuronectiform (flat) fish also contributed to the diet overlap between arrowtooth flounder and sablefish (Table 28).

Among the predators sampled in the 1991 slope survey, moderate diet overlap was found among sablefish, shortspine thornyhead, and longspine thornyhead, and very high diet overlap was found between Dover sole and deepsea sole (Table 33). The overlap in the diets of sablefish and shortspine thornyhead was attributed mainly to predation on scorpaenids (mostly thornyheads), offal, gadids (mostly hake), and *Chionoecetes* sp. (Table 29). Sablefish and longspine thornyhead overlapped in their consumption of cephalopods, scorpaenids, offal, and *Chionoecetes* sp. Longspine and shortspine thornyhead diets had mostly *Chionoecetes* sp., scorpaenids, offal, and polychaetes in common. The very high overlap between the diets of Dover and deepsea soles was attributed to polychaete worms and ophiuroids (brittle stars) (Table 29).

In the 1992 survey, moderate diet overlaps were found between longspine and shortspine thornyheads, longspine thornyhead and Pacific grenadier, and longspine thornyhead and giant grenadier (Table 34). High diet overlap was found between sablefish and shortspine thornyhead and between Dover and deepsea soles (Table 34). The diets of longspine and shortspine thornyheads overlapped mostly in miscellaneous vertebrates (mostly unidentified fish), *Chionoecetes* sp., and offal (Table 30). Longspine thornyhead mostly consumed miscellaneous vertebrates, cephalopods, thalassinids (mudshrimp), polychaete worms, and hippolytid shrimp in common with Pacific grenadier. Longspine thornyhead and giant grenadier diets overlapped mostly in miscellaneous vertebrates, bathylagids (deepsea smelts), cephalopods, and miscellaneous shrimp. Shortspine thornyhead and sablefish consumed scorpaenids, gadids, offal, *Chionoecetes* sp., miscellaneous vertebrates, and clupeids in common. The very high diet overlap between Dover and deepsea soles consisted of polychaete worms and ophiuroids (Table 30).

DISCUSSION

These diet comparisons were made using data combined from all sizes of the predators examined over large regions. However, this is only a first step in determining

the degree of predator interaction that may be taking place. Differences in spatial and temporal distribution of the predators, available prey, and predator size have a large effect on the diet. If the diet overlap of two predators was examined only when they were captured at the same time and location, it is possible that the diets would appear more similar than would be found over a broad area. In addition, the diet of certain sizes of a predator might overlap only with certain sizes of another predator, and comparing all sizes at once may mask some of the intensity of this diet overlap. However, comparisons of the overall diets provide perspective on the diet overlap and on the potential for competition among the predator populations in a general sense.

The moderate overlap among the diets of Pacific hake, sablefish, and arrowtooth flounder north of Cape Blanco and the moderate overlap between the diets of Pacific hake and sablefish south of Cape Blanco in 1989 is consistent with the results of other food habits studies. Gotshall (1969) found pandalid shrimp and euphausiids were the most frequently occurring prey in the stomachs of all three predators off northern California. Euphausiids were the dominant prey of Pacific hake and juvenile sablefish off Oregon and Washington (Brodeur et al. 1987). Livingston (1983) recognized euphausiids as a unifying factor in the diet of Pacific hake because they attract small schooling fishes (clupeids, osmerids, and engraulids) and invertebrates that also prey on euphausiids. This phenomenon also appears to be a unifying factor among the diets of Pacific hake, sablefish, and arrowtooth flounder because euphausiids and schooling fishes that eat euphausiids, including Pacific hake and rockfish (*Sebastes* spp.), often contributed to the diet overlap among these three species. Shortspine thornyhead sampled during the three NMFS bottom-trawl surveys reported on here, also consumed Pacific herring, rockfish, and Pacific hake (Table 35).

Pacific hake is recognized as one of the most ecologically important species in the California Current ecosystem (Bailey et al. 1982, Francis 1983, Livingston and Bailey 1985). In this study, we found Pacific hake eaten by pelagic predators, arrowtooth flounder, and other Pacific hake, as well as denizens of the upper continental slope, sablefish, and shortspine thornyhead (Table 35). In addition, much of the fishery offal eaten by sablefish, shortspine thornyhead, and longspine thornyhead consisted of severed heads of Pacific hake.

In contrast to 1989, Pacific hake displayed low diet similarity to sablefish in 1991 and to sablefish and arrowtooth flounder in 1992. However, the diets of sablefish and arrowtooth flounder were almost moderate in similarity (24%, Table 34) due to predation on Pacific hake and Pacific herring. The 1991 and 1992 surveys of the upper continental slope were conducted in deeper water than the 1989 survey of the continental shelf. Smaller sablefish were absent from the samples taken from the 1991 and 1992 surveys (Fig. 7), and larger sablefish tend to lead a more demersal existence (Dark and Wilkins 1994) while Pacific hake maintain a semi-pelagic lifestyle above the continental slope.

The diet of sablefish was found to exhibit moderate or high similarity to the diet of shortspine thornyhead in 1991 and 1992 (Tables 33 and 34, respectively). The diet of longspine thornyhead moderately overlapped with the diets of sablefish and shortspine thornyhead in 1991, but with only shortspine thornyhead in 1992. The diet similarity among these three predators was based on consumption of *Chionoecetes* sp., offal and scorpaenids in 1991, and of *Chionoecetes* sp., offal, and miscellaneous vertebrates in 1992. However, the similarity between the diets of shortspine thornyhead and sablefish

was based mainly on the consumption of fishes (scorpaenids, gadids, and clupeids) and offal, while the diet overlap between shortspine and longspine thornyheads was based largely on the consumption of similar benthic invertebrates (*Chionoecetes* sp., polychaete worms, hippolytid shrimp and miscellaneous crabs) in addition to some fish and offal (Tables 29 and 30).

The longspine thornyhead diet was also moderately similar to the diets of Pacific grenadier and giant grenadier (Table 34). In addition to diet overlap based on cephalopods and miscellaneous vertebrates, longspine thornyhead and Pacific grenadier both consumed an array of benthic invertebrates (thalassinid shrimp, polychaete worms, hippolytid shrimp, *Chionoecetes* sp., and miscellaneous crabs) while longspine thornyhead and giant grenadier both consumed bathylagid fish and miscellaneous shrimp.

The very high diet overlap between Dover sole and deepsea sole is based mostly on the broad taxonomic category of polychaete worms in 1991 and 1992 (Tables 29 and 30). Although indices of similarity are higher when prey species are grouped and higher taxa are compared (Pearcy and Hancock 1978), the polychaete prey category is representative of a well-defined ecological group. It is likely that some differences in the diets would be found if families or species of polychaetes were compared.

In general, the species of fish sampled in this study can be grouped into three major categories based on their dietary habits. The pelagic group - Pacific hake, arrowtooth flounder, and juvenile sablefish - ate mostly euphausiids and other euphausiid consumers. The large-mouthed benthic group - adult sablefish, shortspine thornyhead, longspine thornyhead, Pacific grenadier, and giant grenadier - were omnivorous, eating a variety of fishes, crustaceans, and other invertebrates. Most, but not all, of these prey were bottom-dwellers. The small-mouthed flatfish - Dover sole and deepsea sole - consumed mainly polychaetes and brittle stars.

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Table 27.--The percentage weight composition of the stomach contents of groundfish south of Cape Blanco in the summer of 1989. (HAK = Pacific hake, SAB = sablefish, SST = shortspine thornyhead, DOV = Dover sole).

Predator:	HAK	SAB	SST	DOV
Prey groups:				
Cnidaria & Ctenophora				0.01
Polychaeta		0.94	1.20	55.92
Gastropoda	0.00	0.01		0.08
Heteropoda				
Pteropoda				
Bivalvia	0.00			1.27
Cephalopoda	9.14	7.10		1.52
Copepoda	0.00	0.01		
Mysidacea			0.50	
Cumacea	0.00			0.13
Isopoda				
Hyperiid Amphipoda		0.01	0.10	
Other Amphipoda	0.00	0.03	0.03	0.47
Euphausiacea	15.62	18.31	0.14	2.00
Sergestidae	0.88	0.05		
Pasiphaeidae				
Hippolytidae	0.92			
Pandalidae	0.78	0.14		
Crangonidae			2.17	
Thalassinidea				
Misc. shrimp	0.02		1.31	0.05
Galatheidae				
<i>Chionoecetes</i> sp.				
Other majid crabs				
Cancriidae				
Misc. crabs		1.98	0.49	0.00
Misc. crustacea	0.00	0.00	0.00	0.00
Sipuncula & Echiura		0.17		
Asteroidea				
Ophiuroidea		0.00		25.66
Echinoidea	0.00	0.33		0.01
Holothuroidea				0.10
Ascidiacea		0.83		0.12
Thaliacea & Larvacea		0.00		

Table 27.--Continued.

Predator:	HAK	SAB	SST	DOV
Myxinidae				
Chimaeridae				
Clupeidae	6.57	0.62		
Engraulidae	53.06	6.38		
Salmonidae				
Osmeridae	0.20	0.10		
Bathylagidae				
Myctophidae	0.19	0.36		
Other deepsea fishes	0.02			
Gadidae	1.36		84.64	
Zoarcidae				
Macrouridae				
Scomberesocidae				
Gasterosteidae				
Scorpaenidae	5.20	17.50		
Anoplopomatidae				
Agonidae				
Cottidae				
Embiotocidae	1.70			
Stichaeidae				
Centrolophidae	1.41			
Stromateidae		3.16		
Pleuronectiformes	2.34	18.77		
Misc. vertebrata	0.56	4.54	9.41	0.00
Offal		17.87		
Misc. organic material	0.01	0.30		11.47
Misc. prey		0.47		1.17

Table 28.--The percentage weight composition of the stomach contents of groundfish north of Cape Blanco in the summer of 1989. (HAK = Pacific hake, ATF = arrowtooth flounder, SAB = sablefish, SST = shortspine thornyhead, DOV = Dover sole).

Predator:	HAK	ATF	SAB	SST	DOV
Prey groups:					
Cnidaria & Ctenophora		0.01	0.27		
Polychaeta		0.02	0.49	1.33	41.54
Gastropoda		0.01	0.02	0.08	1.37
Heteropoda					
Pteropoda					0.49
Bivalvia	0.00		0.00	0.26	2.77
Cephalopoda	0.34		1.00	0.07	
Copepoda			0.00	0.00	0.00
Mysidacea	0.05	0.00	0.00	0.12	
Cumacea					0.18
Isopoda			0.01	0.58	0.09
Hyperiid Amphipoda	0.00		0.01	0.07	
Other Amphipoda		0.00	0.13	0.28	0.35
Euphausiacea	23.43	3.39	13.42	0.20	0.08
Sergestidae	0.50		0.01		
Pasiphaeidae	0.03	0.10			
Hippolytidae	0.00			4.45	
Pandalidae	3.43	3.31	2.90	39.00	0.82
Crangonidae	0.42	0.11	0.07	5.80	
Thalassinidea				10.63	0.55
Misc. shrimp	0.01	0.03	0.24	1.92	0.23
Galatheididae	0.00	0.01	0.52	10.79	
<i>Chionoecetes</i> sp.					
Other majid crabs				0.43	
Cancridae	0.14		0.01		
Misc. crabs			0.71	0.23	0.02
Misc. crustacea			0.01	0.12	1.64
Sipuncula & Echiura			0.93		5.71
Asteroidea					
Ophiuroidea	0.00		0.22		30.67
Echinoidea	0.06		0.01	0.08	4.11
Holothuroidea			0.01		0.28
Ascidiacea			0.09		0.61
Thaliacea & Larvacea			2.99		

Table 28.--Continued.

Predator:	HAK	ATF	SAB	SST	DOV
Myxinidae			8.04		
Chimaeridae			1.50		
Clupeidae	48.42	19.77	22.39		
Engraulidae	0.76				
Salmonidae			0.96		
Osmeridae	17.76	0.96	0.55		
Bathylagidae					
Myctophidae	0.09	0.29	0.04		
Other deepsea fishes		0.37			
Gadidae	2.10	63.92			
Zoarcidae	0.01		0.74	8.62	
Macrouridae					
Scomberesocidae			1.25		
Gasterosteidae			0.01		
Scorpaenidae	0.00	0.64	0.17	4.80	
Anoplopomatidae			2.63		
Agonidae			0.32	1.28	
Cottidae					
Embiotocidae					
Stichaeidae		0.20	0.12		
Centrolophidae					
Stromateidae					
Pleuronectiformes	1.90	6.35	3.76	2.06	
Misc. vertebrata	0.33	0.46	2.37	0.91	0.60
Offal	0.17		29.81	5.81	
Misc. organic material	0.01	0.02	0.92	0.05	4.21
Misc. prey	0.03	0.02	0.34		3.68

Table 29.--The percentage weight composition of the stomach contents of groundfish in the autumn of 1991. (HAK = Pacific hake, SAB = sablefish, SST = shortspine thornyhead, LST = longspine thornyhead, DOV = Dover sole, DSS = deepsea sole).

Predator:	HAK	SAB	SST	LST	DOV	DSS
Prey groups:						
Cnidaria & Ctenophora					0.39	6.26
Polychaeta			2.20	7.07	84.51	77.67
Gastropoda		0.00	0.83	0.03	0.16	2.93
Heteropoda				0.24		
Pteropoda					0.05	
Bivalvia		0.00	0.00	1.93	2.46	
Cephalopoda	0.94	10.49	1.20	8.08	0.01	
Copepoda	0.00			0.02	0.00	0.00
Mysidacea	0.02	0.00	0.08	0.56	0.01	0.35
Cumacea			0.01	0.10	0.21	
Isopoda			0.09	3.06	0.19	
Hyperiid Amphipoda	0.00	0.08	0.00	0.05	0.12	
Other Amphipoda			0.01	0.37	2.92	0.61
Euphausiacea	2.00	0.00	0.00	0.03		
Sergestidae	5.11	0.10	0.06	0.96	0.34	
Pasiphaeidae	0.35		0.16			
Hippolytidae	0.06		0.97	1.78		
Pandalidae			0.03			
Crangonidae			0.17	0.65		
Thalassinidea			0.60	9.86		1.74
Misc. shrimp	0.01		0.04	1.70	0.20	
Galatheidae				0.03		
<i>Chionoecetes</i> sp.		3.81	60.70	21.18		
Other majid crabs		2.62	1.51	1.59	0.06	
Cancriidae						
Misc. crabs	0.00		0.13	1.32	0.16	0.09
Misc. crustacea	0.00		0.00	0.35		0.00
Sipuncula & Echiura						
Asteroidea				1.65		
Ophiuroidea			0.01	2.82	3.77	4.94
Echinoidea	0.03		0.00	0.24	1.27	
Holothuroidea				2.24		
Ascidacea		3.83		0.04		1.66
Thaliacea & Larvacea						

Table 29.--Continued.

Predator:	HAK	SAB	SST	LST	DOV	DSS
Myxinidae		0.14				
Chimaeridae						
Clupeidae						
Engraulidae						
Salmonidae						
Osmeridae	0.56					
Bathylagidae	4.25	0.26	0.19	2.94		
Myctophidae	3.94	0.42	0.10	10.52	0.22	
Other deepsea fishes		1.26				
Gadidae	77.46	5.89	1.66	0.88		
Zoarcidae			5.24	1.26		
Macrouridae			2.80			
Scomberesocidae						
Gasterosteidae						
Scorpaenidae	0.83	28.85	12.62	4.96		
Anoplopomatidae						
Agonidae						
Cottidae			0.09			
Embiotocidae						
Stichaeidae						
Centrolophidae						
Stromateidae						
Pleuronectiformes	4.25	2.38				
Misc. vertebrata	0.17	0.22	0.28	5.16	0.00	
Offal	0.02	37.22	8.14	5.03		
Misc. organic material	0.01	1.98		1.08	1.89	2.43
Misc. prey		0.42		0.19	1.06	1.31


Table 30.--The percentage weight composition of the stomach contents of groundfish in the autumn of 1992. (HAK = Pacific hake, ATF = arrowtooth flounder, SAB = sablefish, SST = shortspine thomyhead, LST = longspine thornyhead, DOV = Dover sole, DSS = deepsea sole, PGN = Pacific grenadier, GGN = giant grenadier).

Predator:	HAK	ATF	SAB	SST	LST	DOV	DSS	PGN	GGN
Prey groups:									
Cnidaria & Ctenoph.	1.56		0.04			0.98	5.91		
Polychaeta			0.04	0.39	5.21	49.20	51.20	8.18	
Gastropoda			0.04		0.00	0.15			
Heteropoda									
Pteropoda				0.02			1.43		
Bivalvia			0.03	0.00	0.02	0.32	0.05		
Cephalopoda	1.12		1.07	0.71	9.17	0.05		29.17	7.46
Copepoda				0.00	0.02	0.01	0.01	0.42	
Mysidacea	0.06			0.01	0.13	0.01	0.51	0.94	37.02
Cumacea				0.00	0.27	0.46		0.01	
Isopoda				0.08		0.00		0.12	
Hyperiid Amphipoda			0.01	0.01	0.02	0.00		0.52	
Other Amphipoda			0.02	0.06	0.20	2.37	1.28	0.71	
Euphausiacea	7.79		0.24					0.28	
Sergestidae	14.81				0.91	0.95		8.58	
Pasiphaeidae	0.50			0.14	7.15	0.34			15.22
Hippolytidae			0.02	1.43	4.06			5.82	
Pandalidae	23.53	0.07	0.02	0.11					1.98
Crangonidae				0.17			0.03		
Thalassinidea					14.24			5.94	
Misc. shrimp	0.17			0.39	2.08	0.14		0.49	12.98
Galatheidae						5.35	1.01		
<i>Chionoecetes</i> sp.			4.16	17.94	10.78			2.10	
Other majid crabs			0.12	0.58	2.02		0.25		
Canceridae						0.01			
Misc. crabs			0.29	1.20	1.37	0.08		3.35	
Misc. crustacea			0.30	0.01	0.17	1.26		1.57	0.04
Sipuncula & Echiura			0.09	0.02		2.90			
Asteroidea									
Ophiuroidea			0.03	0.04	3.36	34.53	22.99		0.32
Echinoidea	0.00		0.01		0.05	0.26			
Holothuroidea									
Ascidiacea					0.08		1.15		

Table 30.--Continued.


Predator:	HAK	ATF	SAB	SST	LST	DOV	DSS	PGN	GGN
Thaliacea & Larvacea									
Myxinidae									
Chimaeridae									
Clupeidae	7.07	13.94	3.56	1.23					
Engraulidae									
Salmonidae									
Osmeridae			0.28						
Bathylagidae			0.25		18.39			7.55	
Myctophidae	2.66			0.20					
Other deepsea fishes	7.63								
Gadidae		83.57	20.19	16.65					
Zoarcidae			0.16	0.55	2.60				
Macrouridae									
Scomberesocidae	28.77			0.37					
Gasterosteidae									
Scorpaenidae	3.22		52.13	28.81	0.96				
Anoplopomatidae									
Agonidae									
Cottidae									
Embiotocidae									
Stichaeidae									
Centrolophidae									
Stromateidae									
Pleuronectiformes		2.42							
Misc. vertebrata	0.87		4.01	19.38	11.06			19.05	17.44
Offal	0.26		12.92	9.48	5.48				
Misc. organic material				0.00	0.17	0.08	12.60	11.81	
Misc. prey						0.55	1.57	0.94	

Table 3 1.--Percent similarity index of dietary overlap among Pacific hake (HAK), arrowtooth flounder (ATF), sablefish (SAB), shortspine thornyhead (SST), and Dover sole (DOV) caught north of Cape Blanco in the summer of 1989.

Diet overlap: Low Moderate High Very high

 0-24% 25-49% 50-74% 75-100%

	HAK	ATF	SAB	SST	DOV
HAK		32	42	6	1
ATF			31	7	1
SAB				14	4
SST					4
DOV					

Table 32.--Percent similarity index of dietary overlap among Pacific hake (HAK), sablefish (SAB), shortspine thornyhead (SST), and Dover sole (DOV) caught south of Cape Blanco in the summer of 1989.

Diet overlap: Low Moderate High Very high

 0-24% 25-49% 50-74% 75-100%

	HAK	SAB	SST	DOV
HAK		38	2	4
SAB			1-6	5
SST				1
DOV				

Table 35.--Length-ranges of predators and their schooling fish-prey. The predator length-range includes only the predators, sampled during the bottom-trawl surveys in 1989, 1991 and 1992, that consumed these schooling fish-prey. (HAK = pacific hake, SAB = sablefish, SST = shortspine thornyhead, ATF = arrow-tooth flounder).

Predator:	HAK	SAB	SST	ATF
Length-range (cm FL):	29-69	21-62	22-45	18-71
Prey type:	Prey length-range (mm SL):			
<i>Clupea pallasii</i> (Pacific herring)	40-225	56-259	221	55-224
Osmeriidae (Smelts)	37-190	42-160		38-98
<i>Engraulis mordax</i> (northern anchovy)	43-160	80-124		
<i>Merluccius productus</i> (Pacific hake)	106-240	93-398	28-125	400-422
<i>Sebastes</i> spp. (Rockfish)	26-96	122-204	45-96	50

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The juvenile Pacific hake samples were collected by A. Hollowed in 1987 and T. Wilderbuer in 1988. Other stomachs were collected primarily by M. Dom, D. Molenaar, R. Pacunski, and J. Parkhurst in 1989; A. Ward in 1991; and M. Grader and J. McClelland in 1992. We appreciate their efforts and the efforts of other survey participants who assisted in collecting the stomach samples.

Our gratitude also extends to those who assisted in the laboratory analysis of the stomach contents presented in this report. The stomach contents of the 1987 and 1988 juvenile Pacific hake were analyzed by G. Lang and D. Molenaar. The stomach contents of sablefish, arrowtooth flounder, and some shortspine thornyhead from 1992, as well as some Dover sole from 1989 were analyzed by K. Craig.

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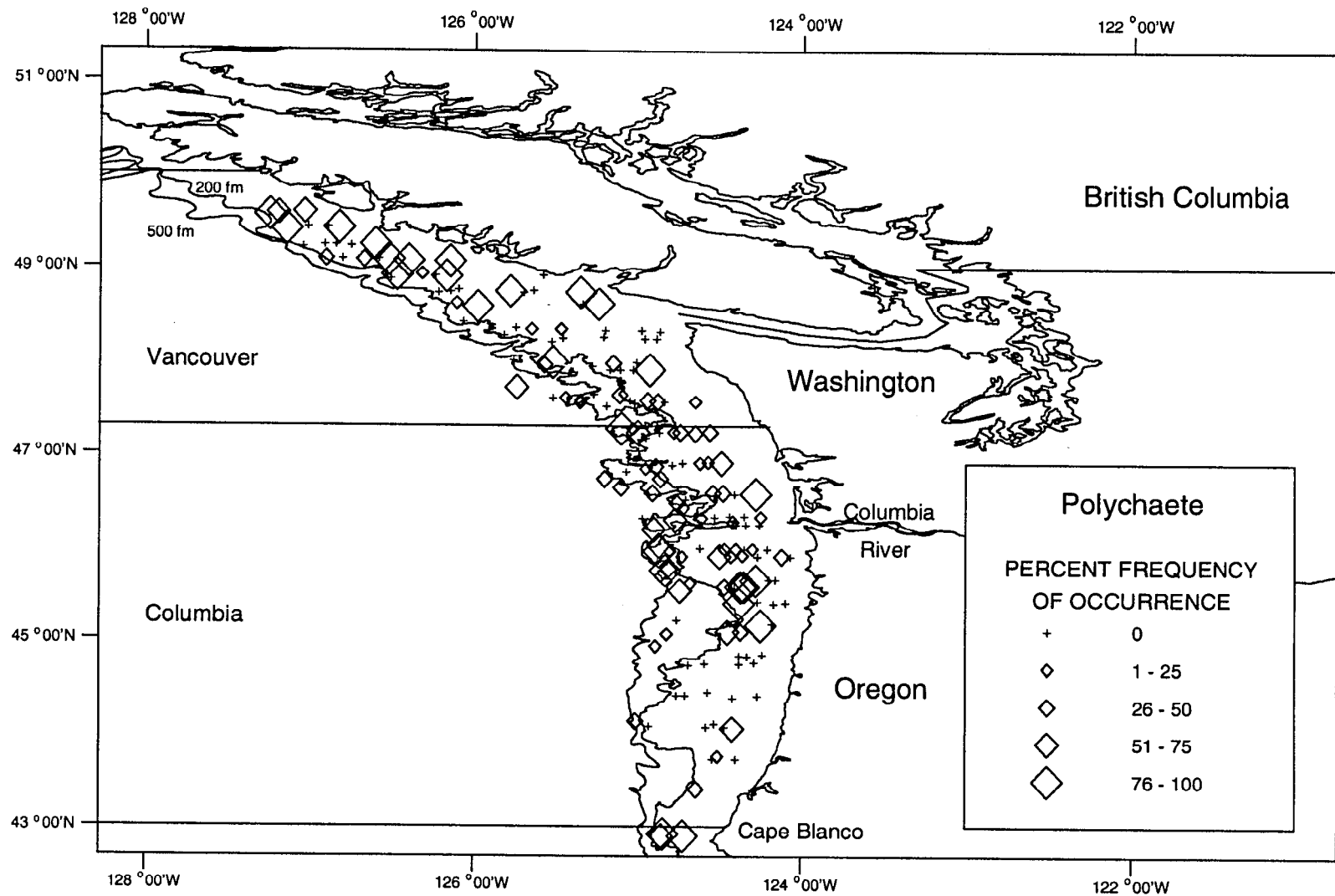
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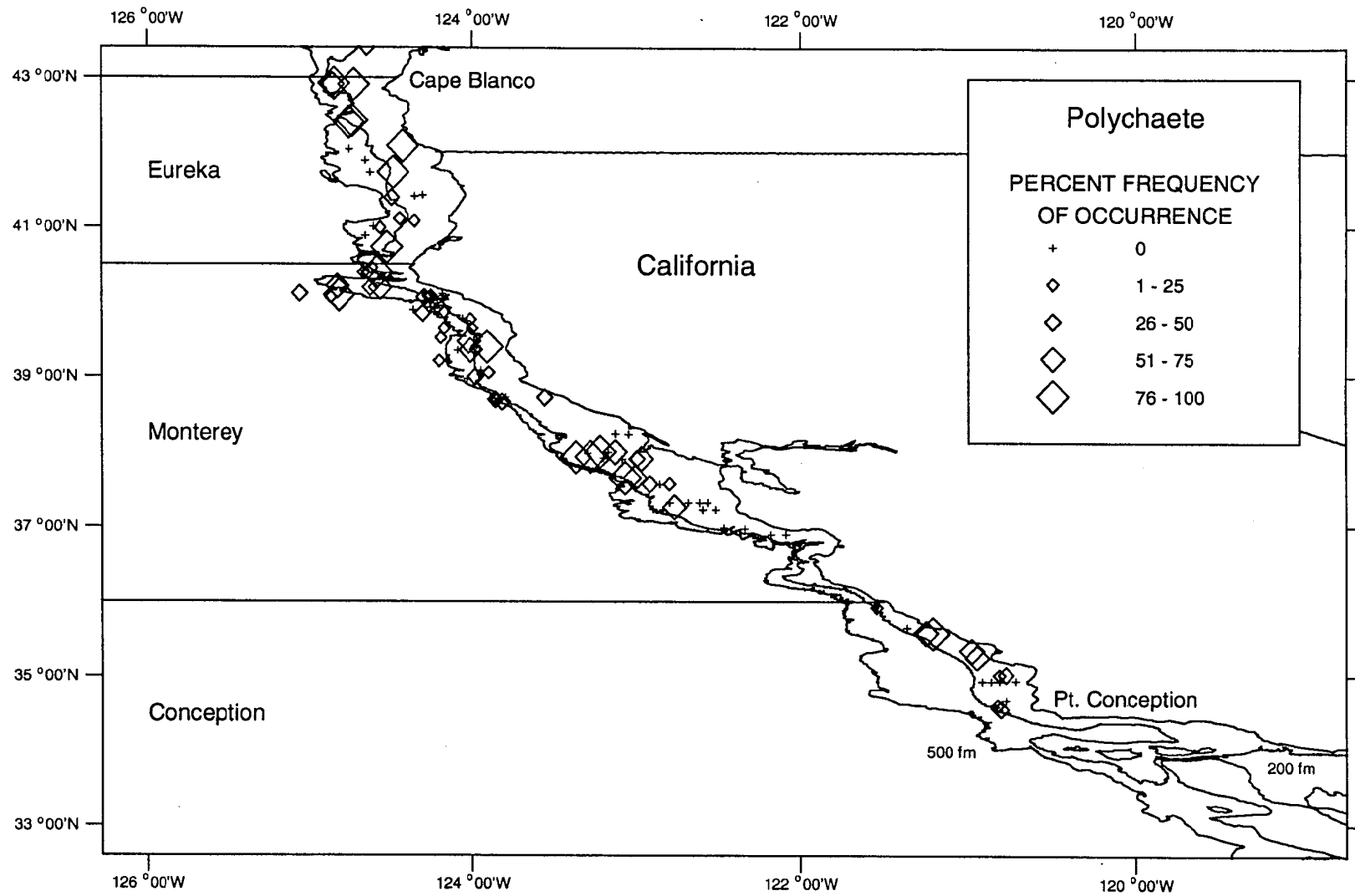
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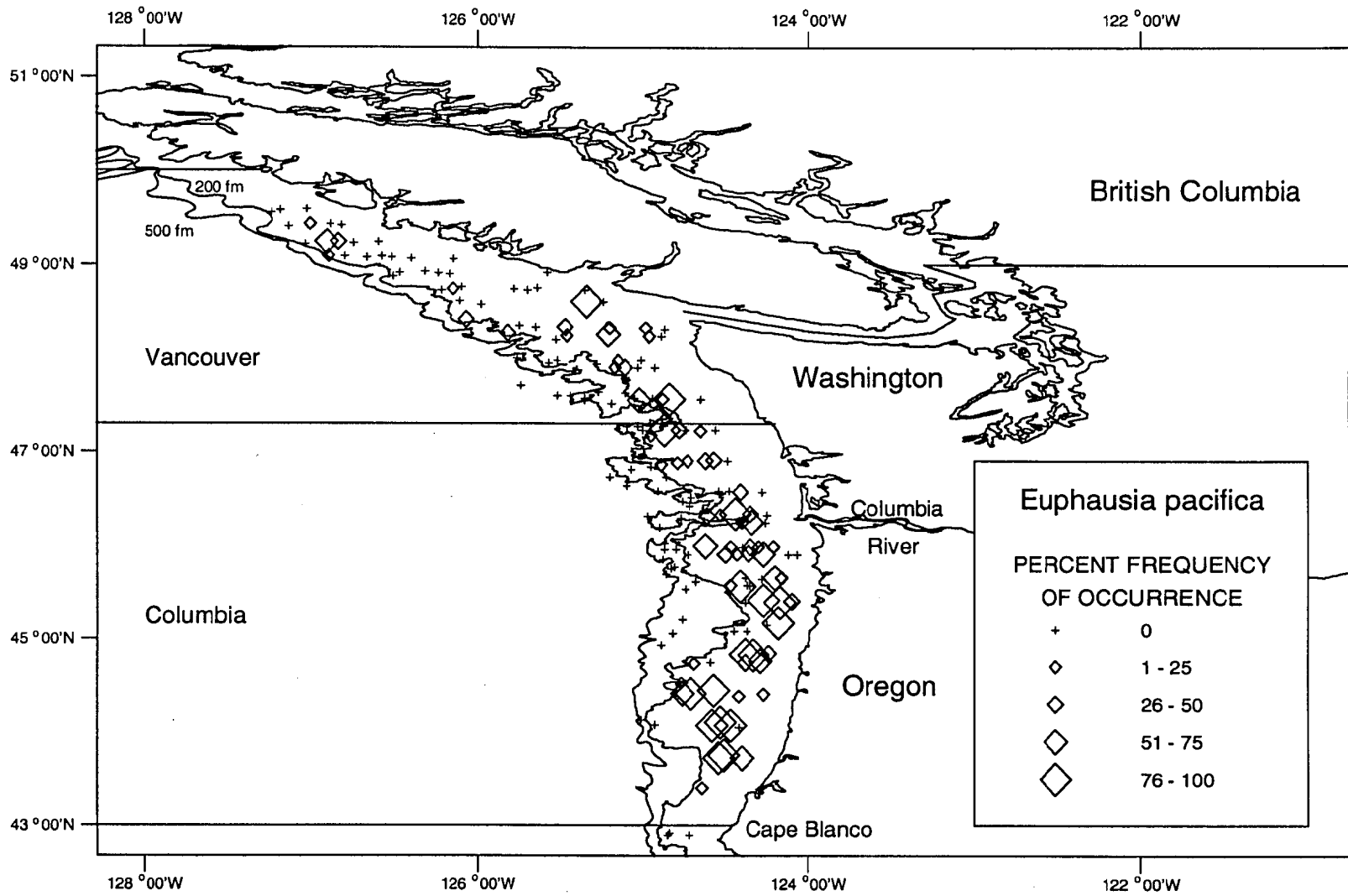
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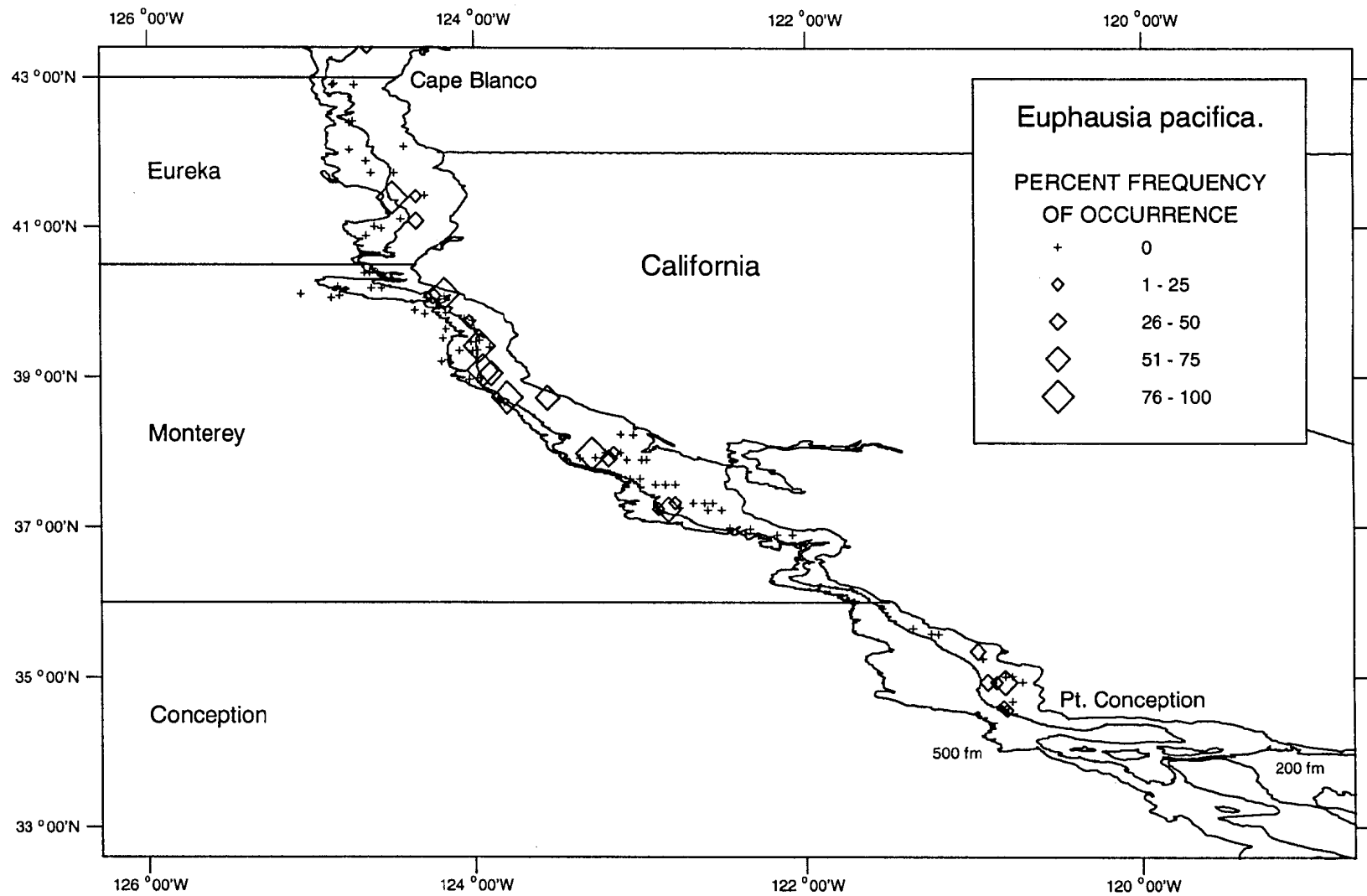
APPENDIX

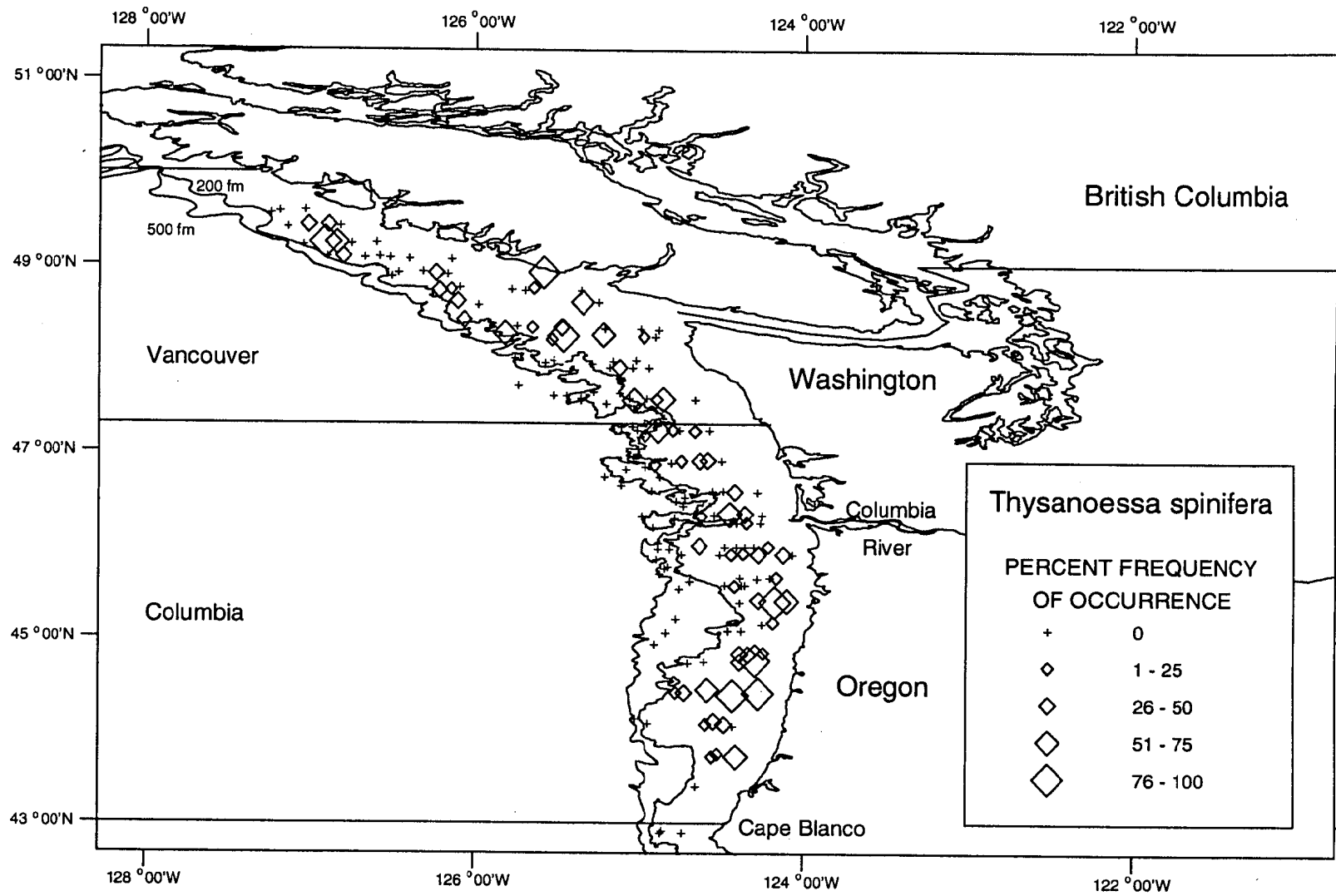
The geographical distributions of important prey groups are illustrated by plotting their percent frequency of occurrence in all predators sampled at each haul location. The charts on facing pages show the geographical distribution of a prey group north of Cape Blanco and south of Cape Blanco. The 200-fm and 500-fm isobaths are shown.

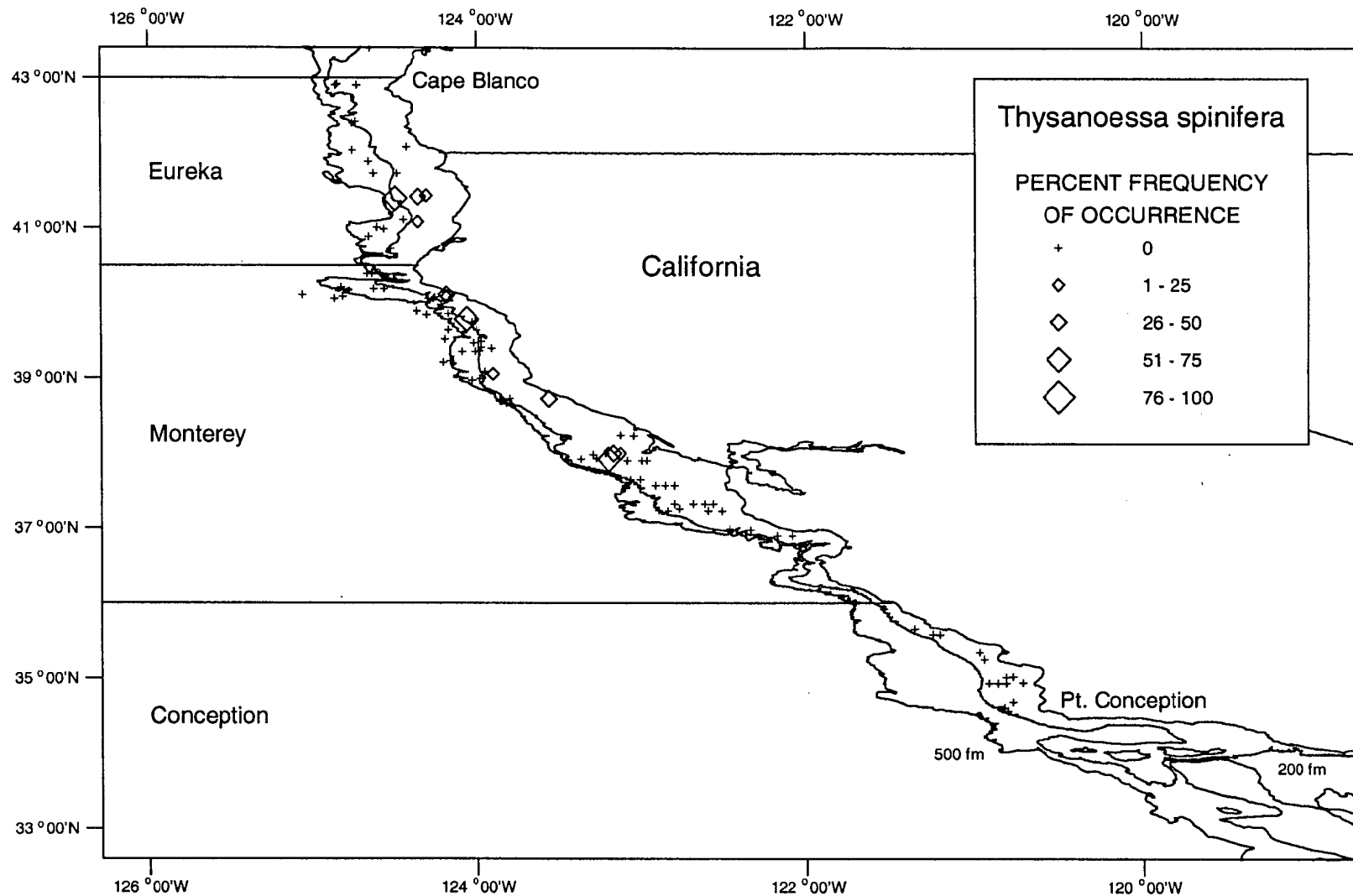


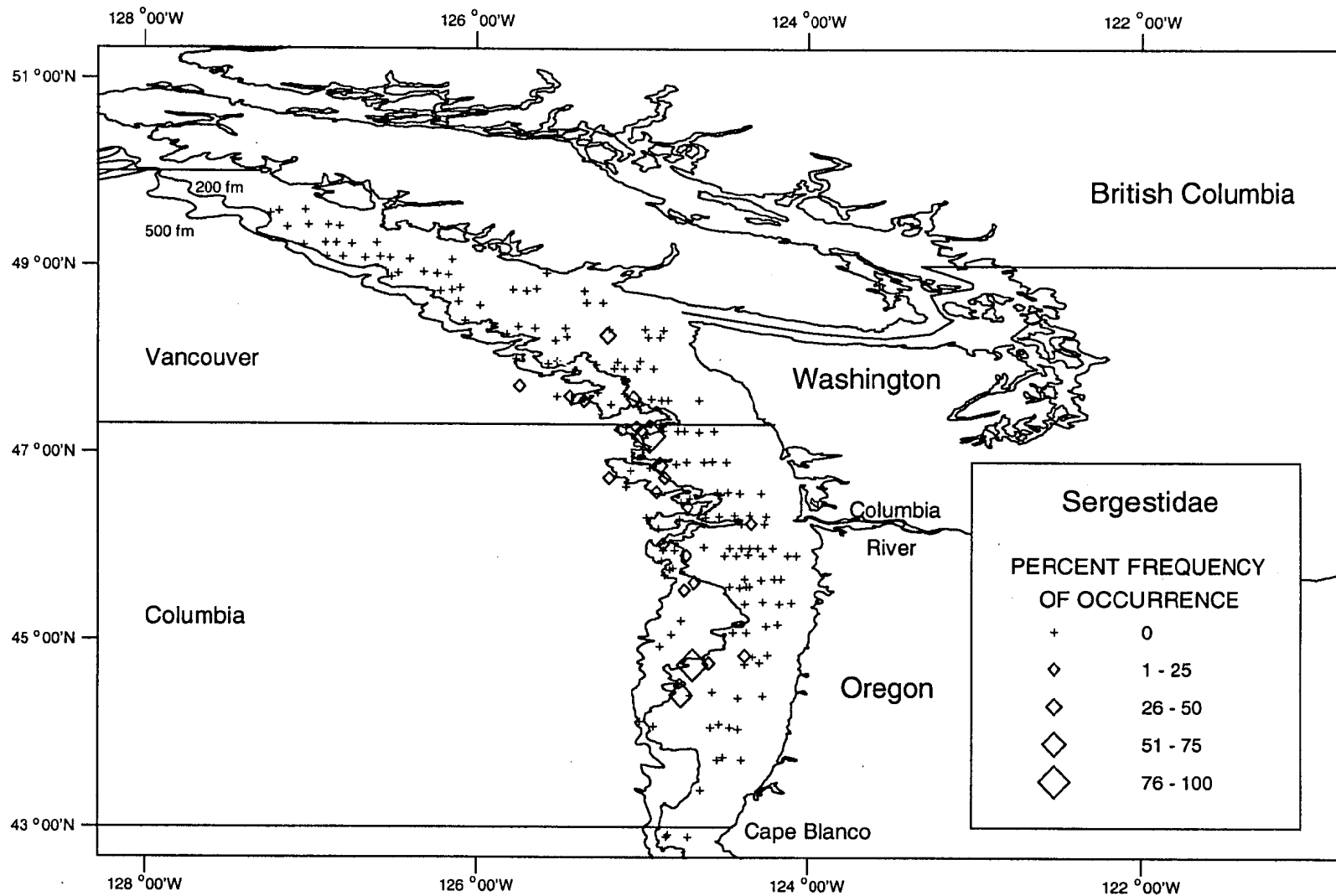


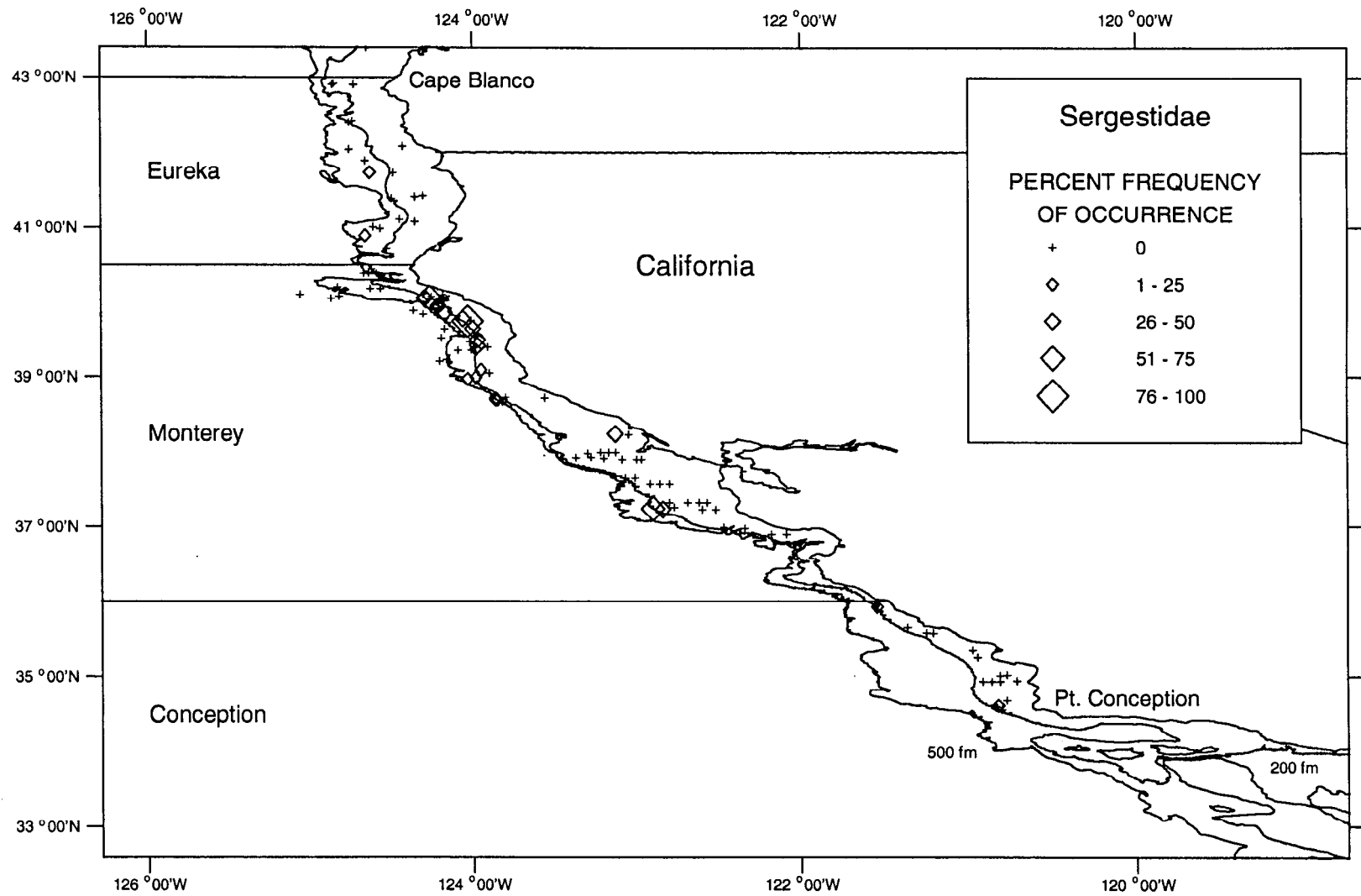


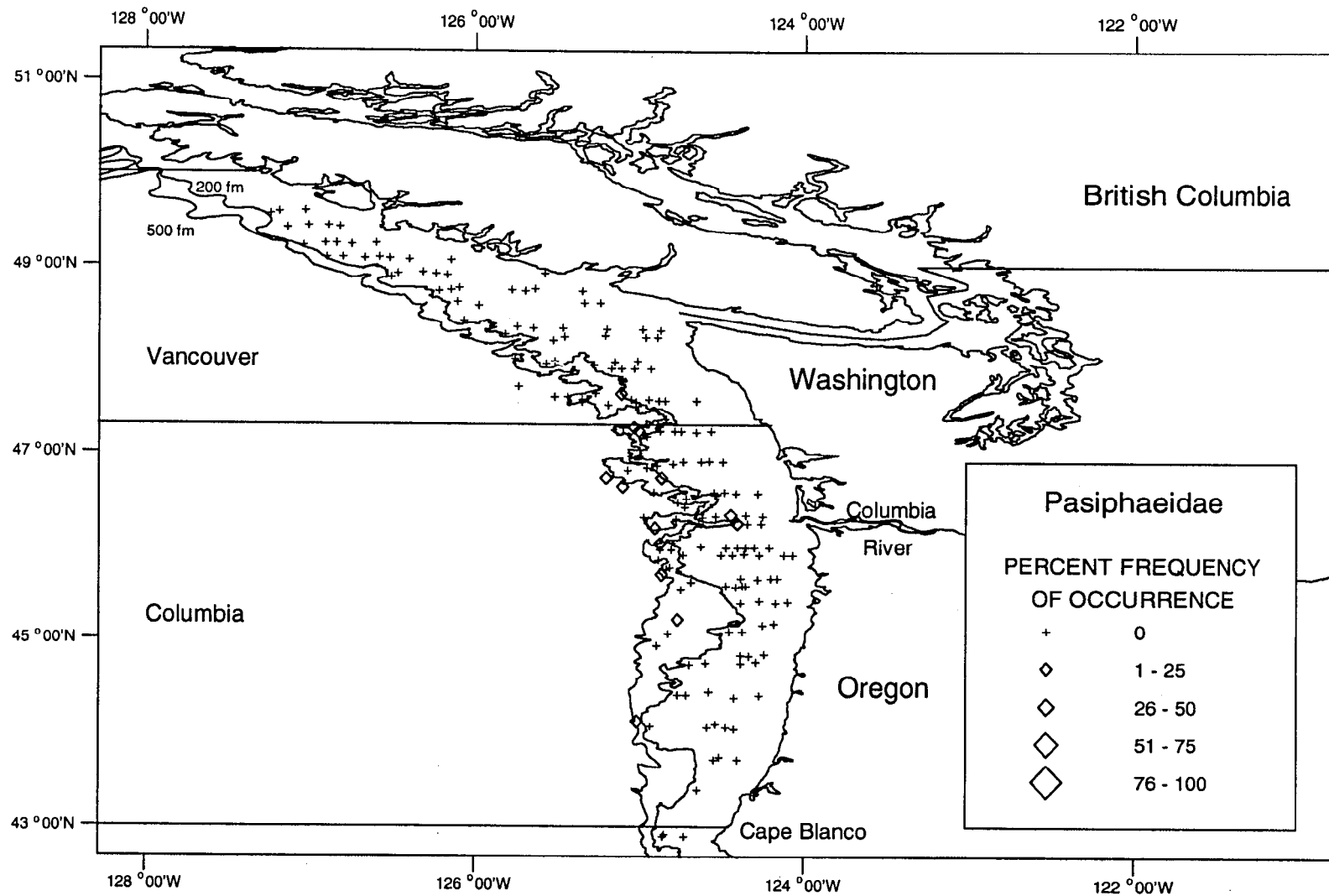


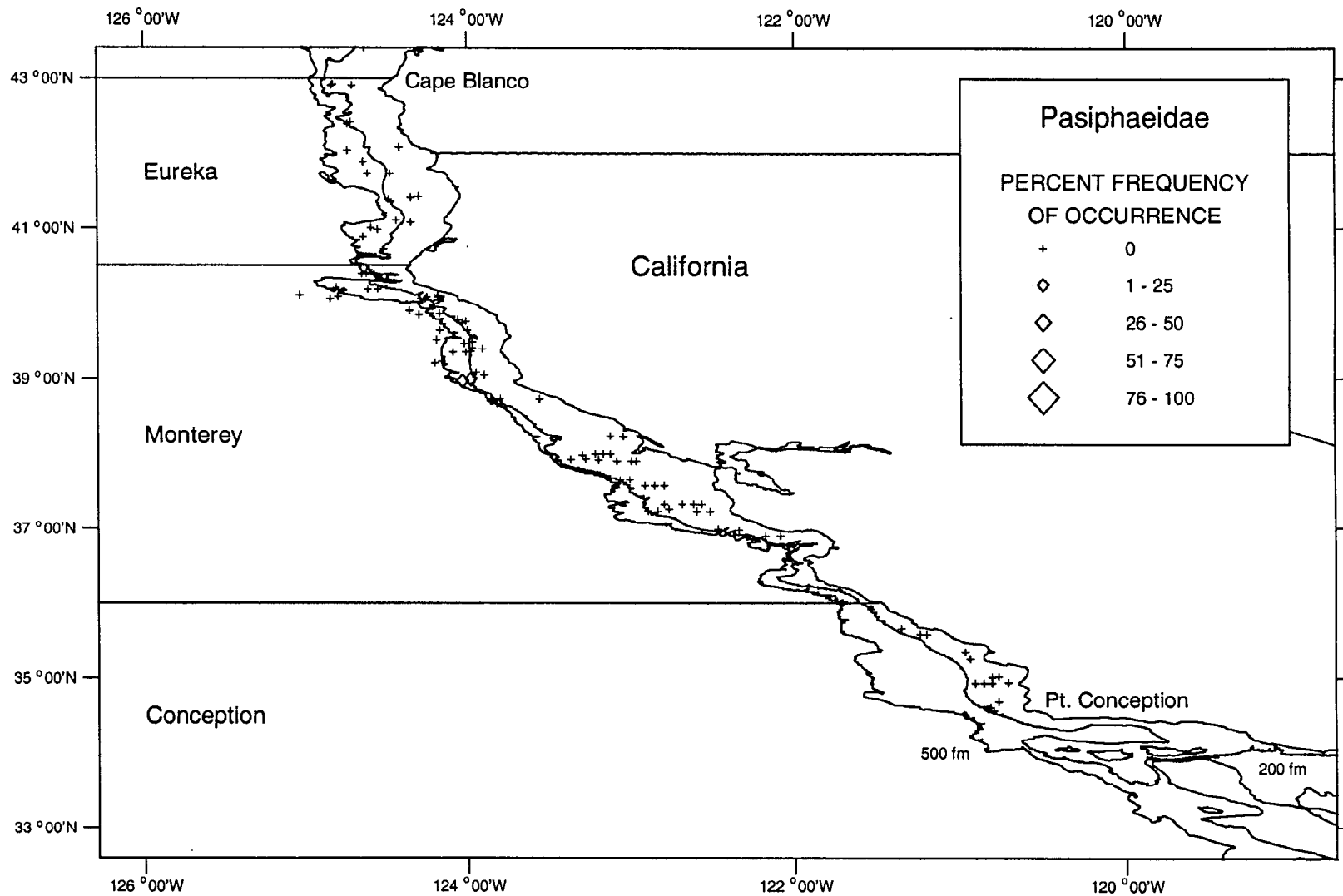


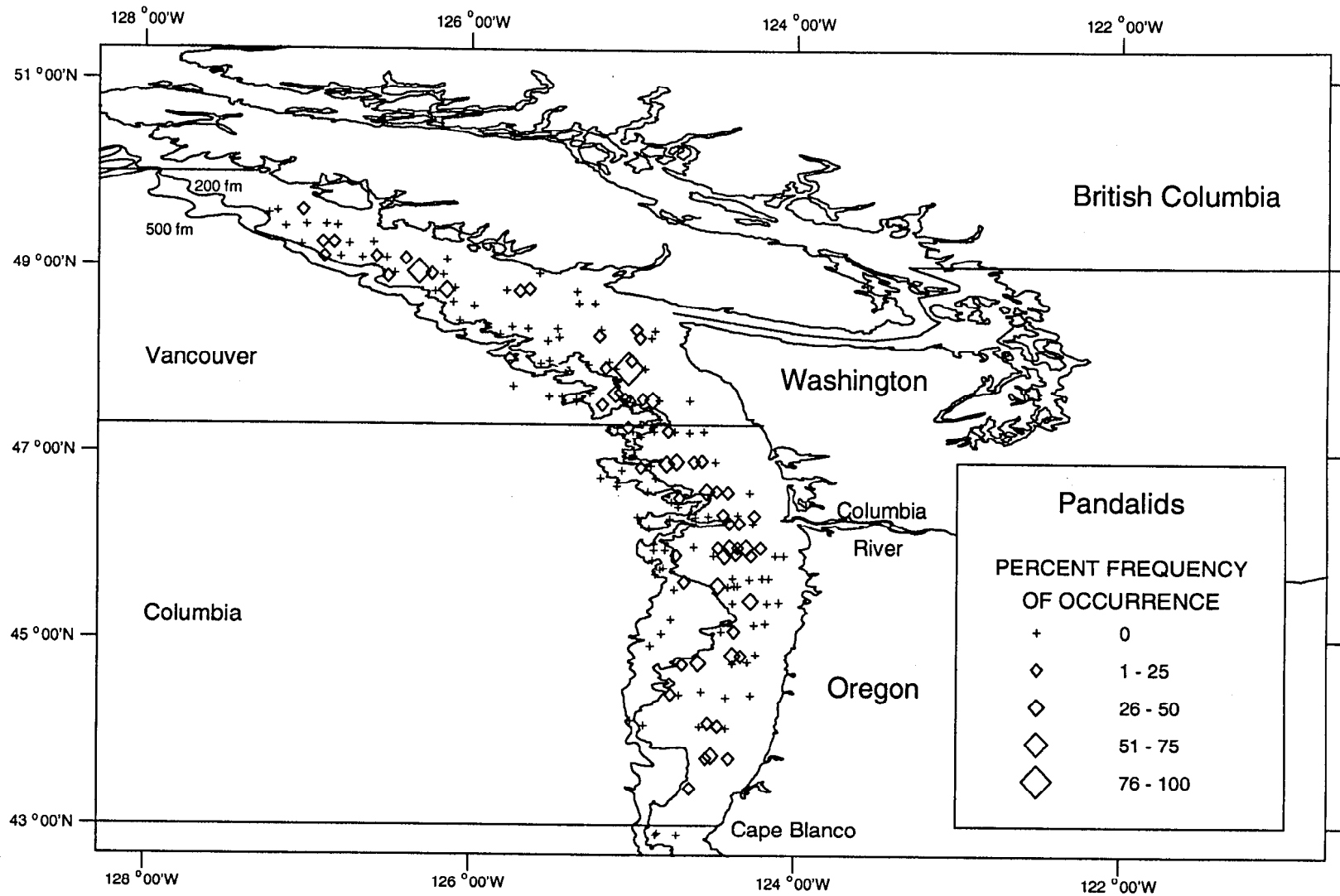


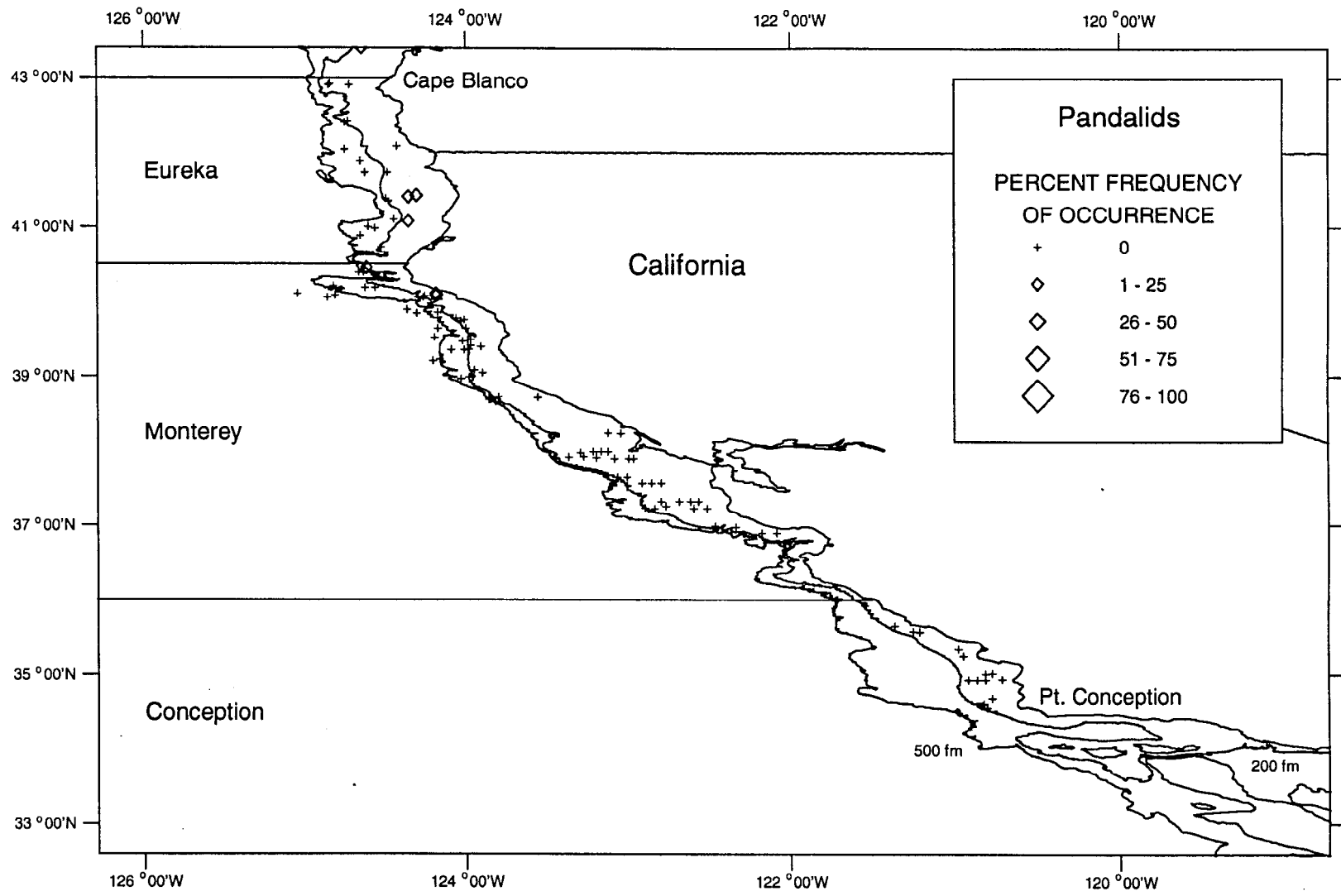


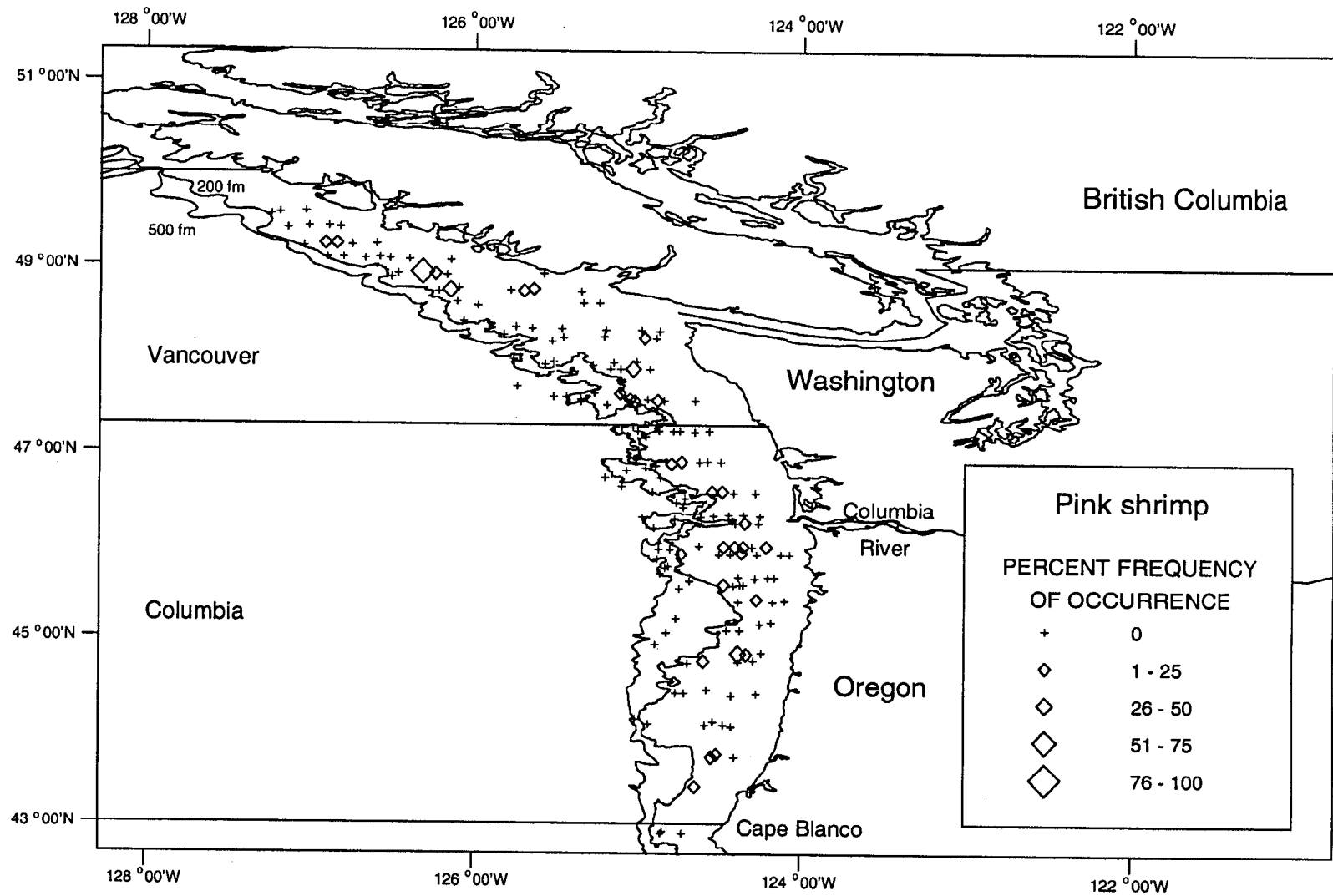


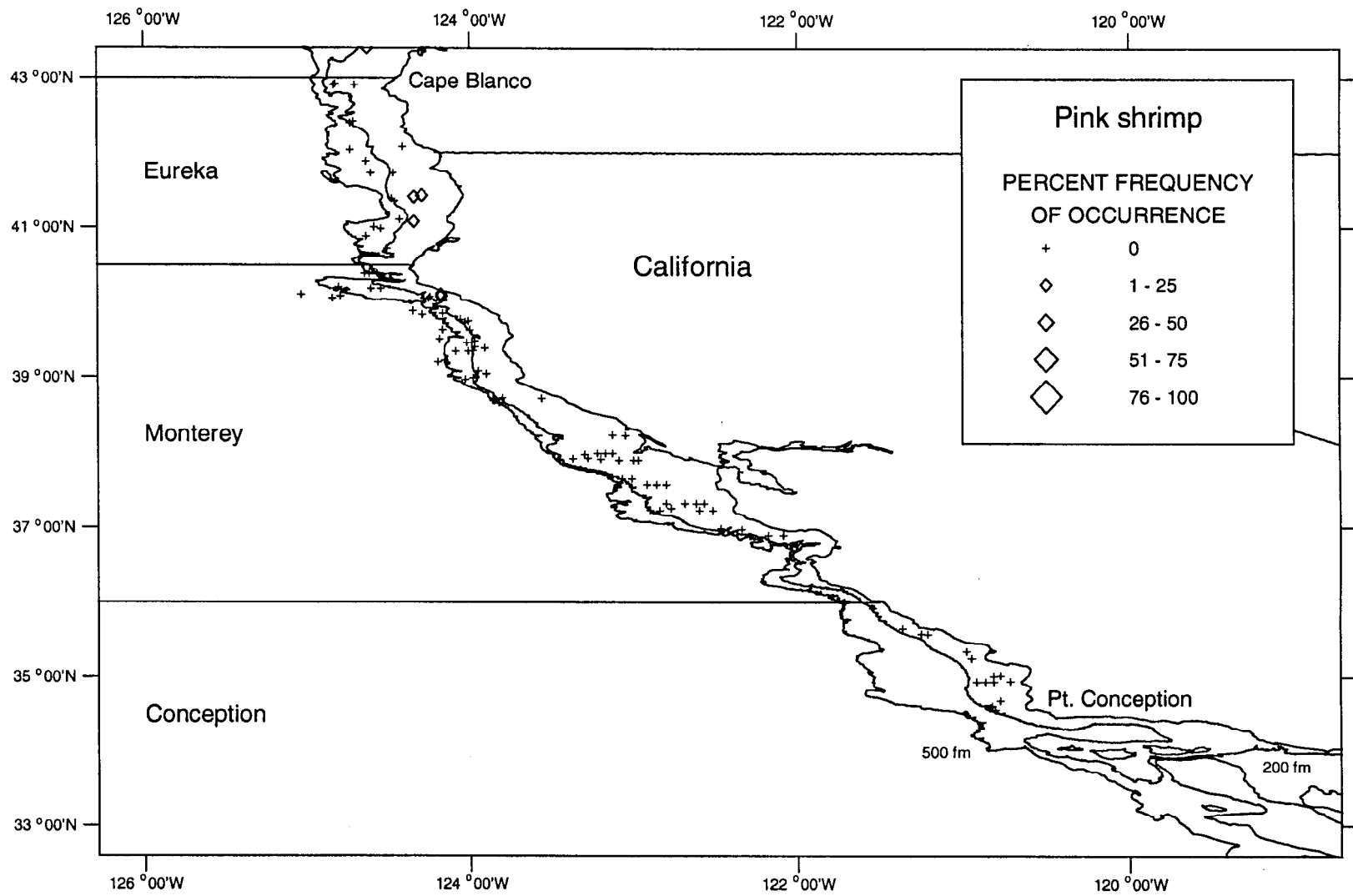


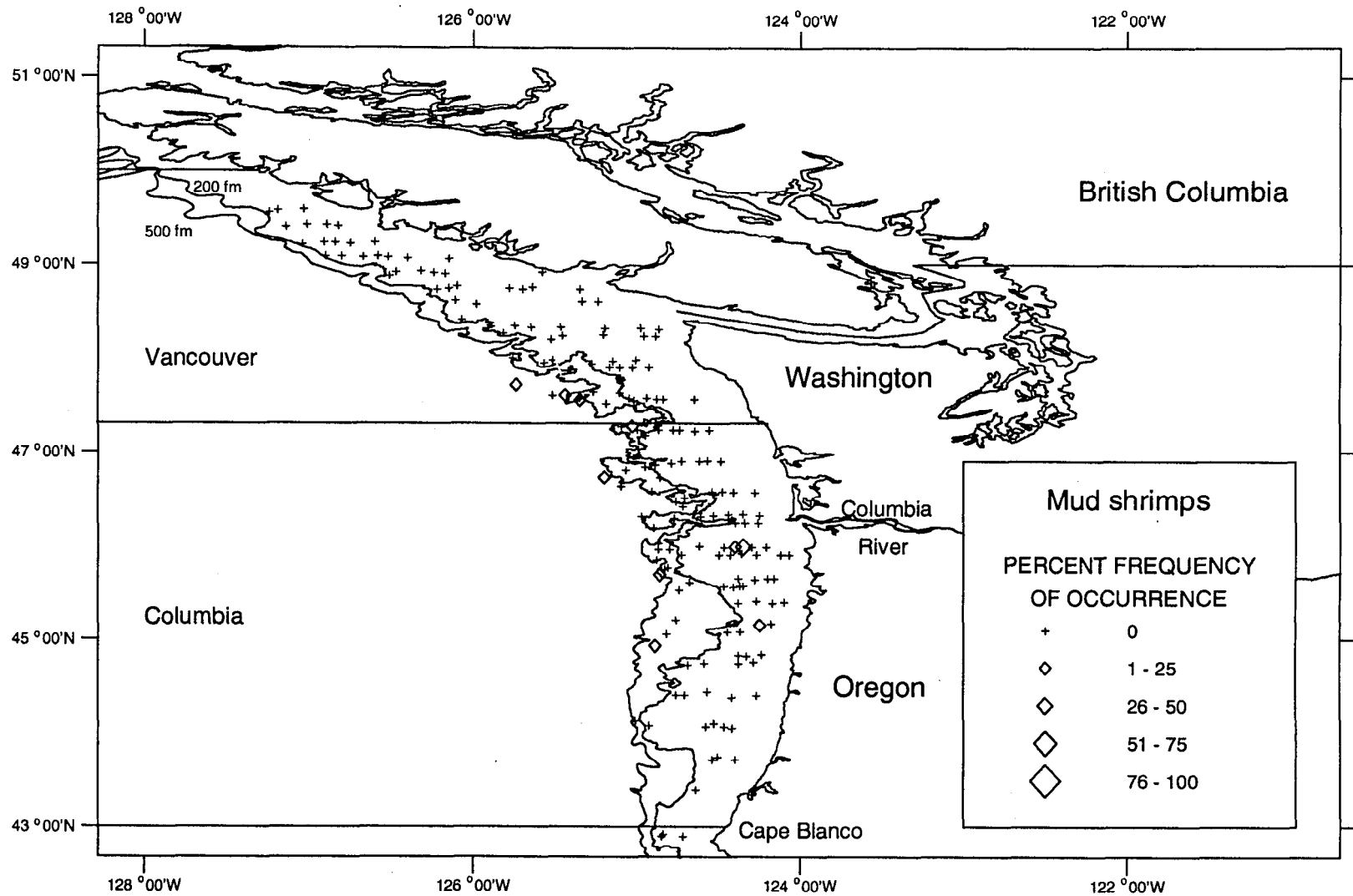


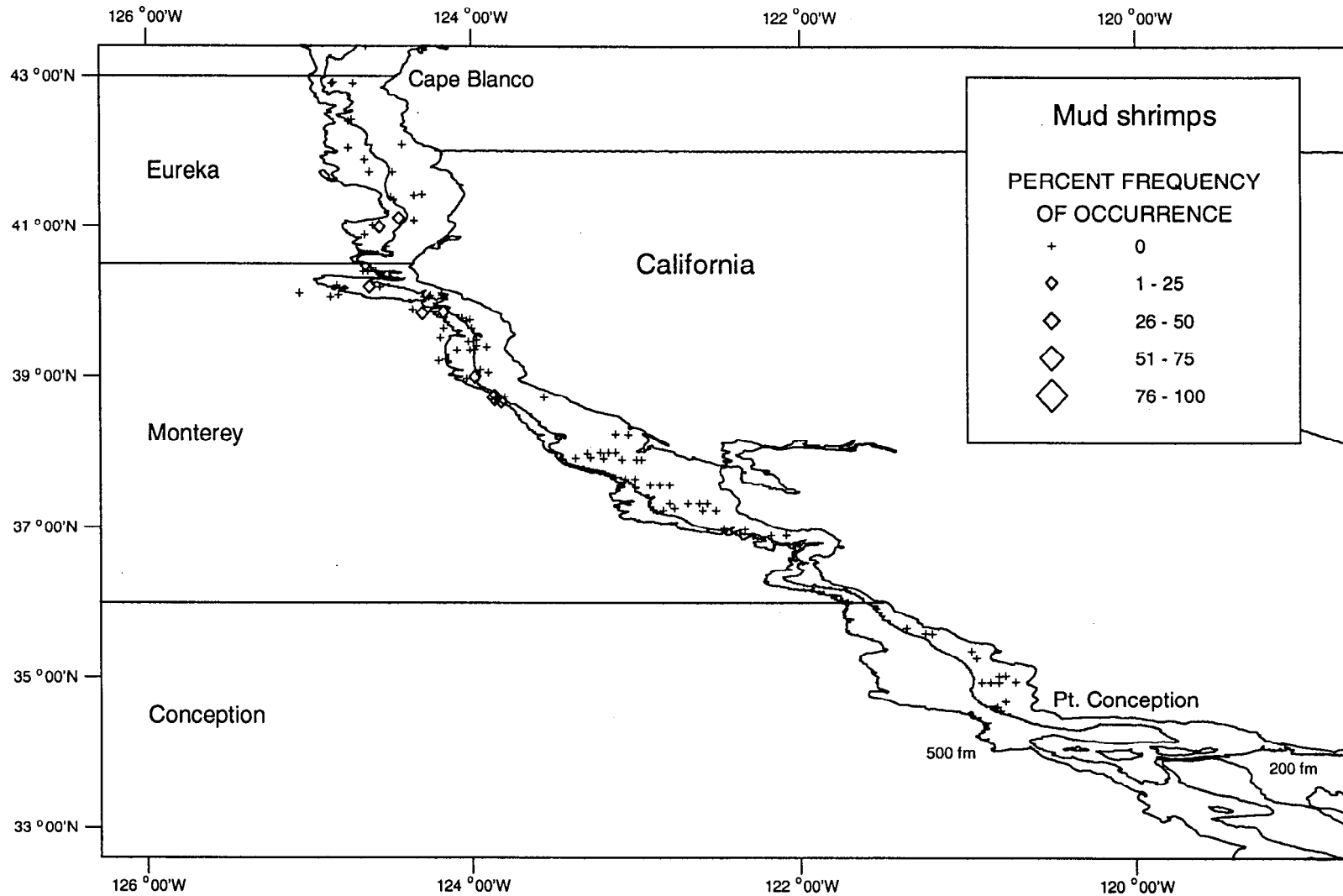


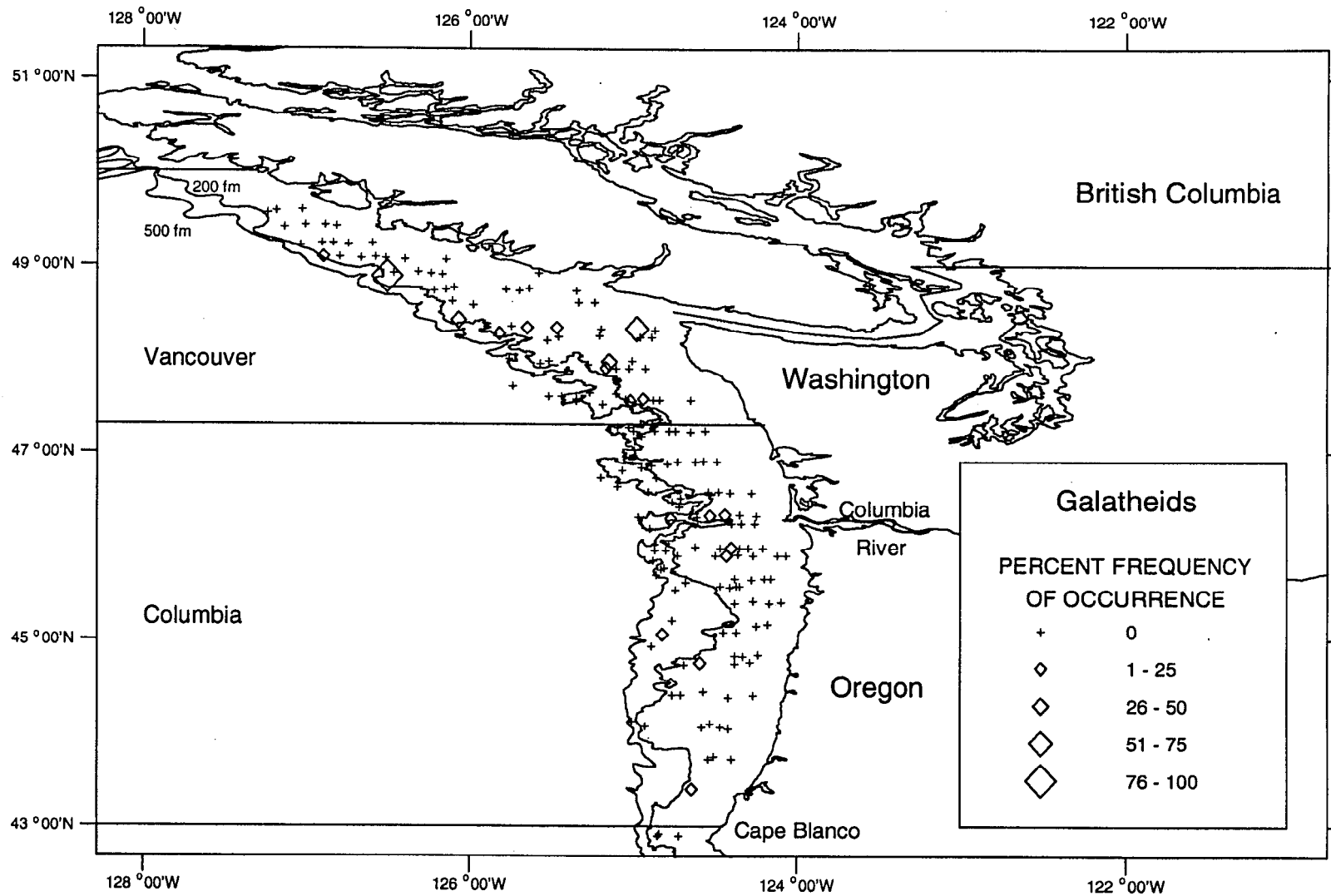


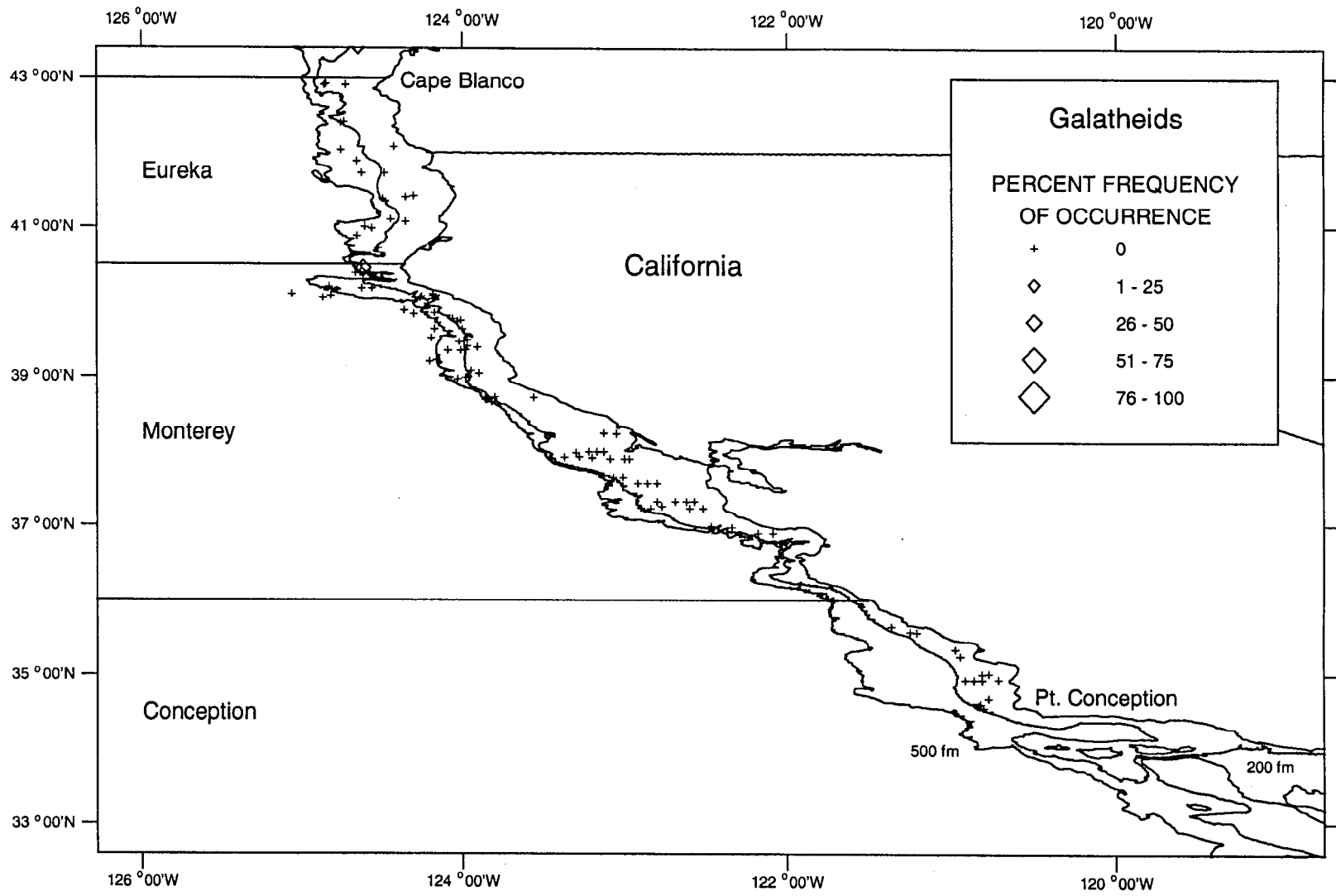


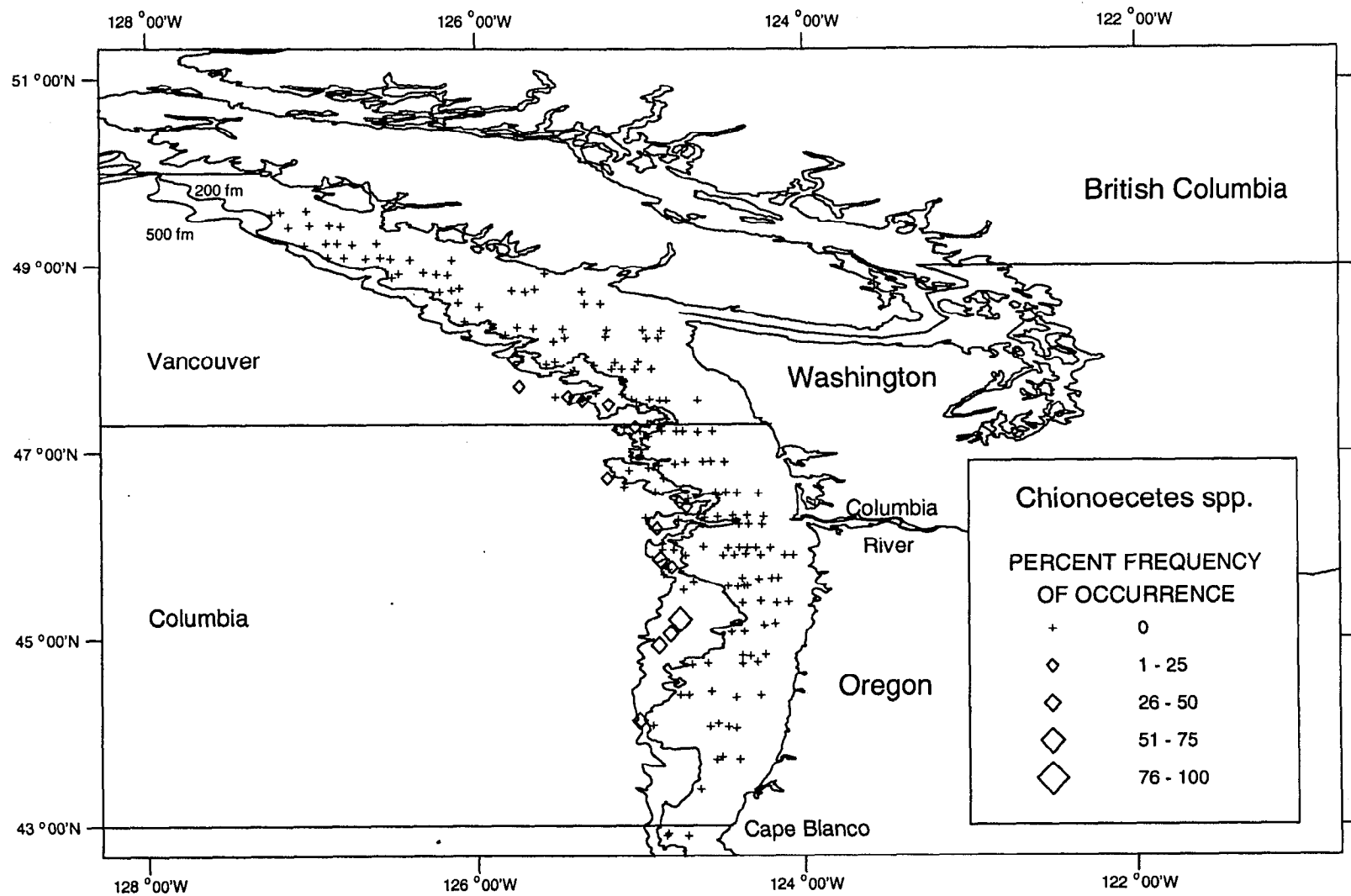


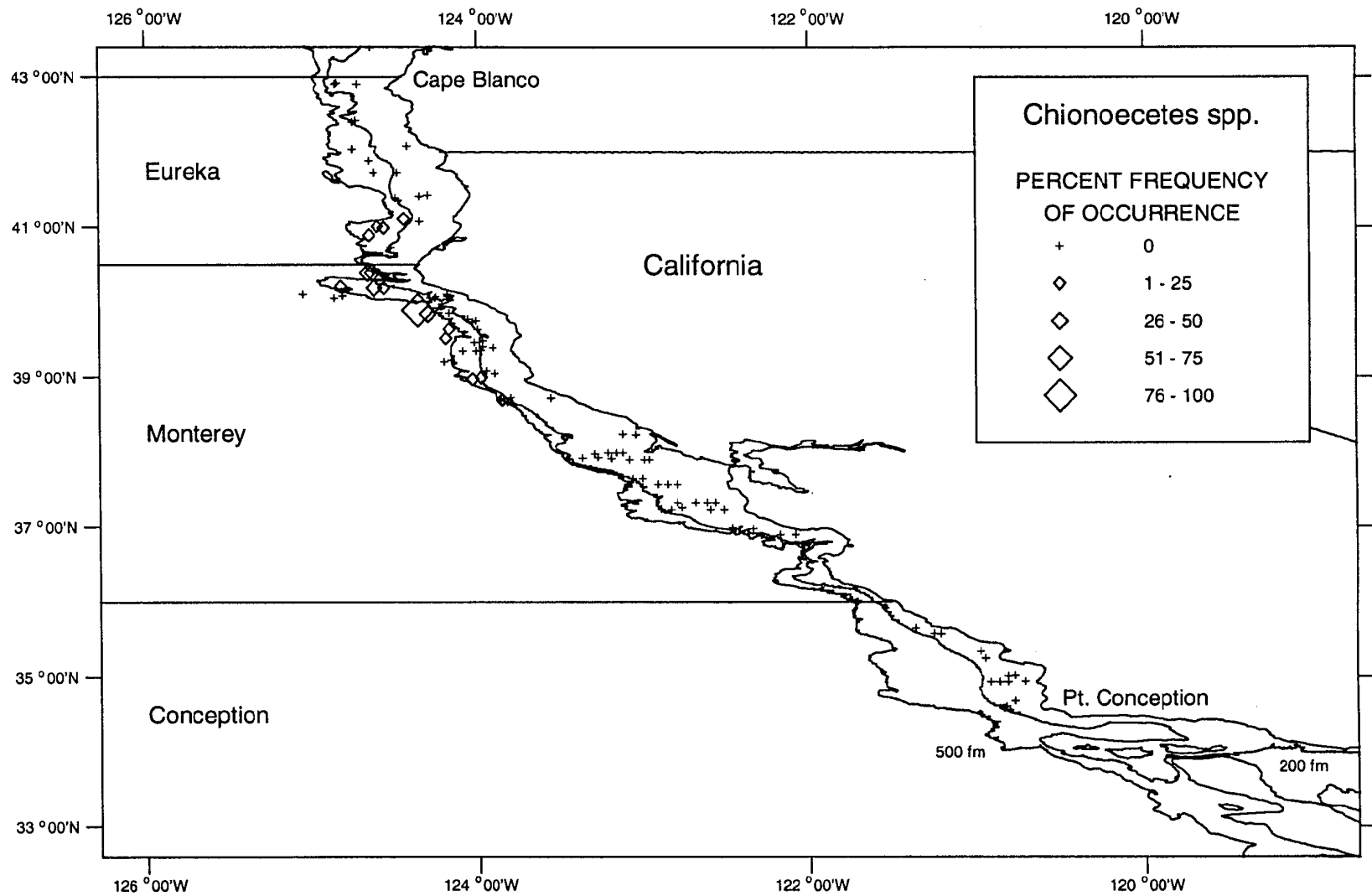


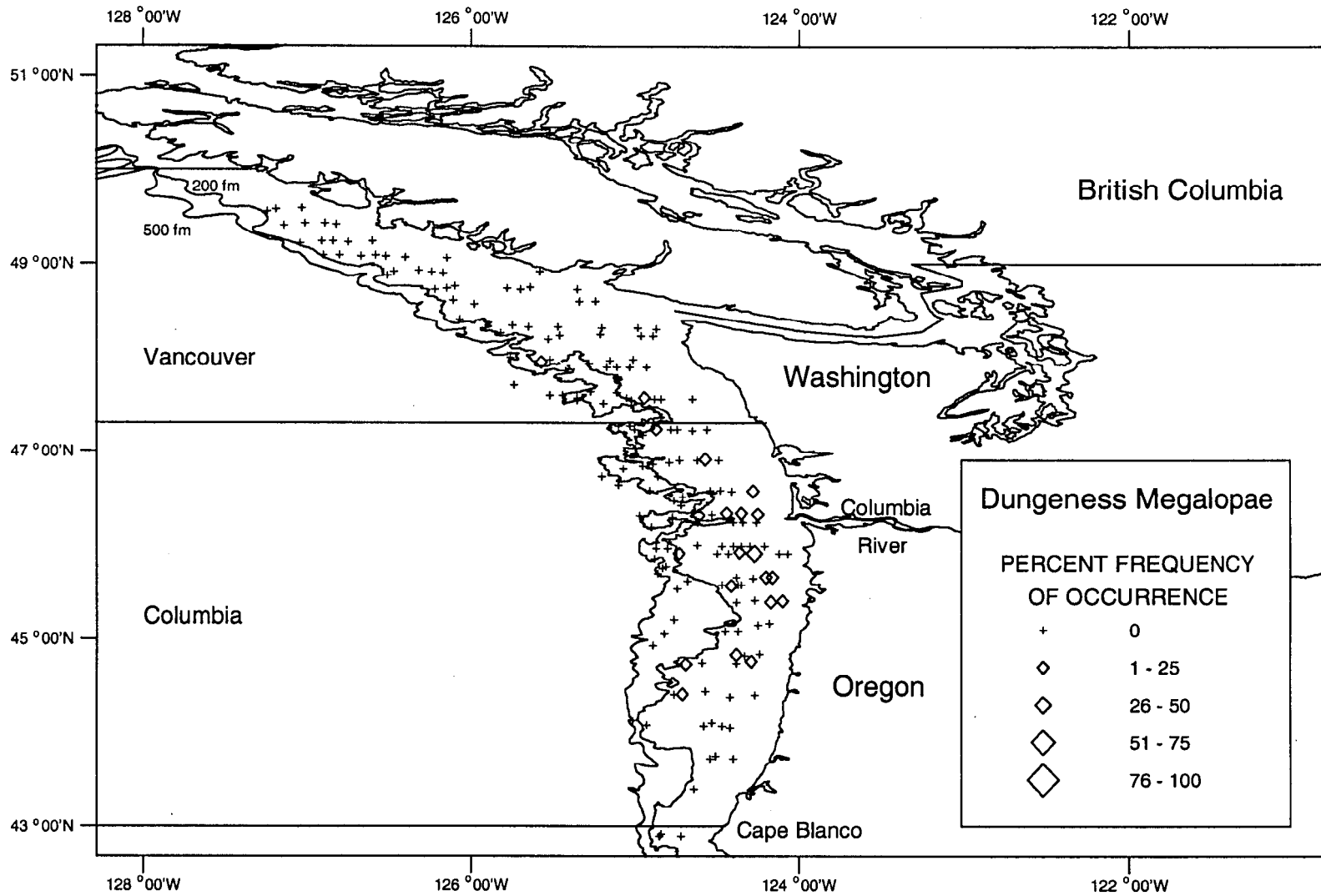


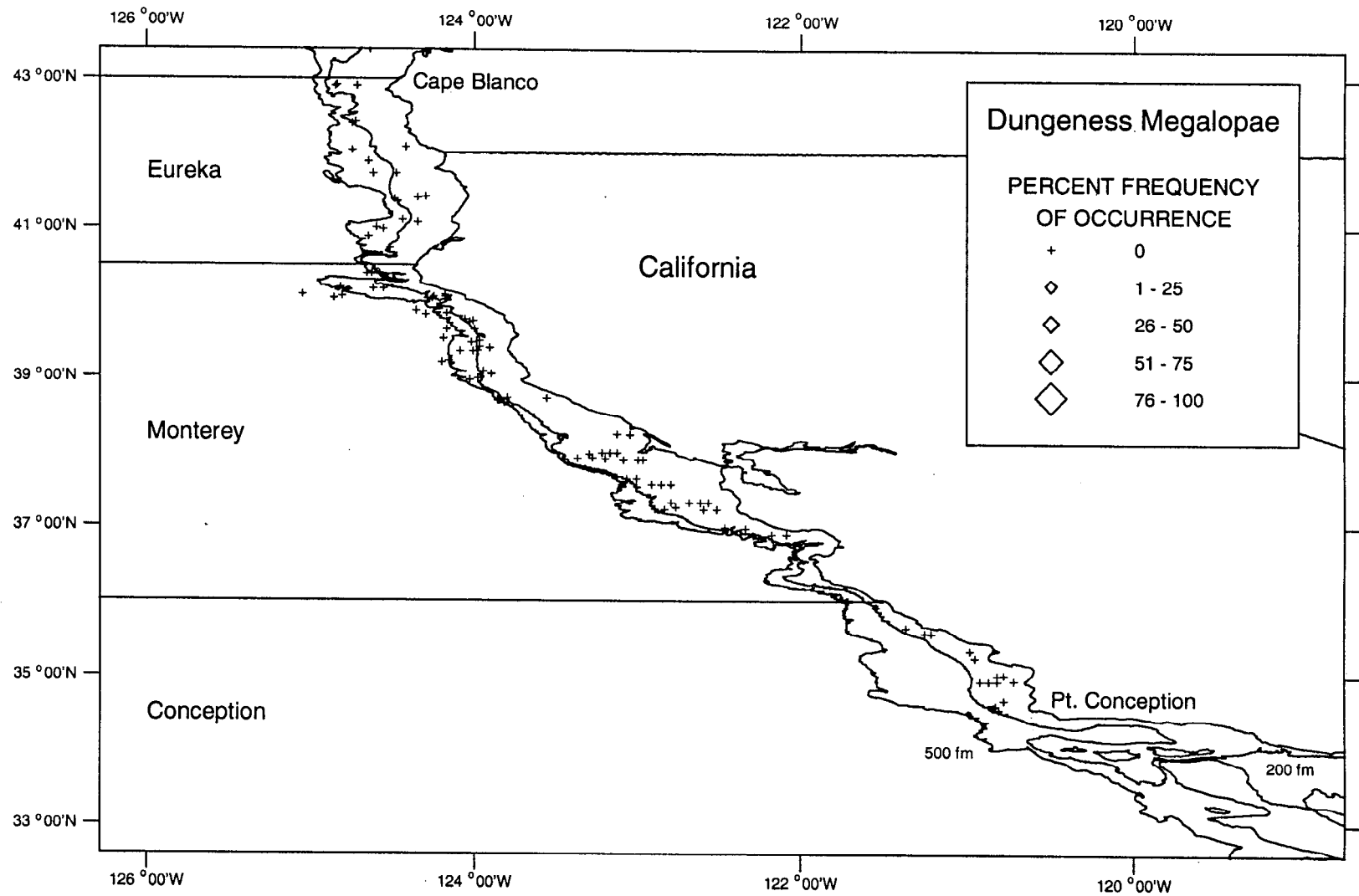


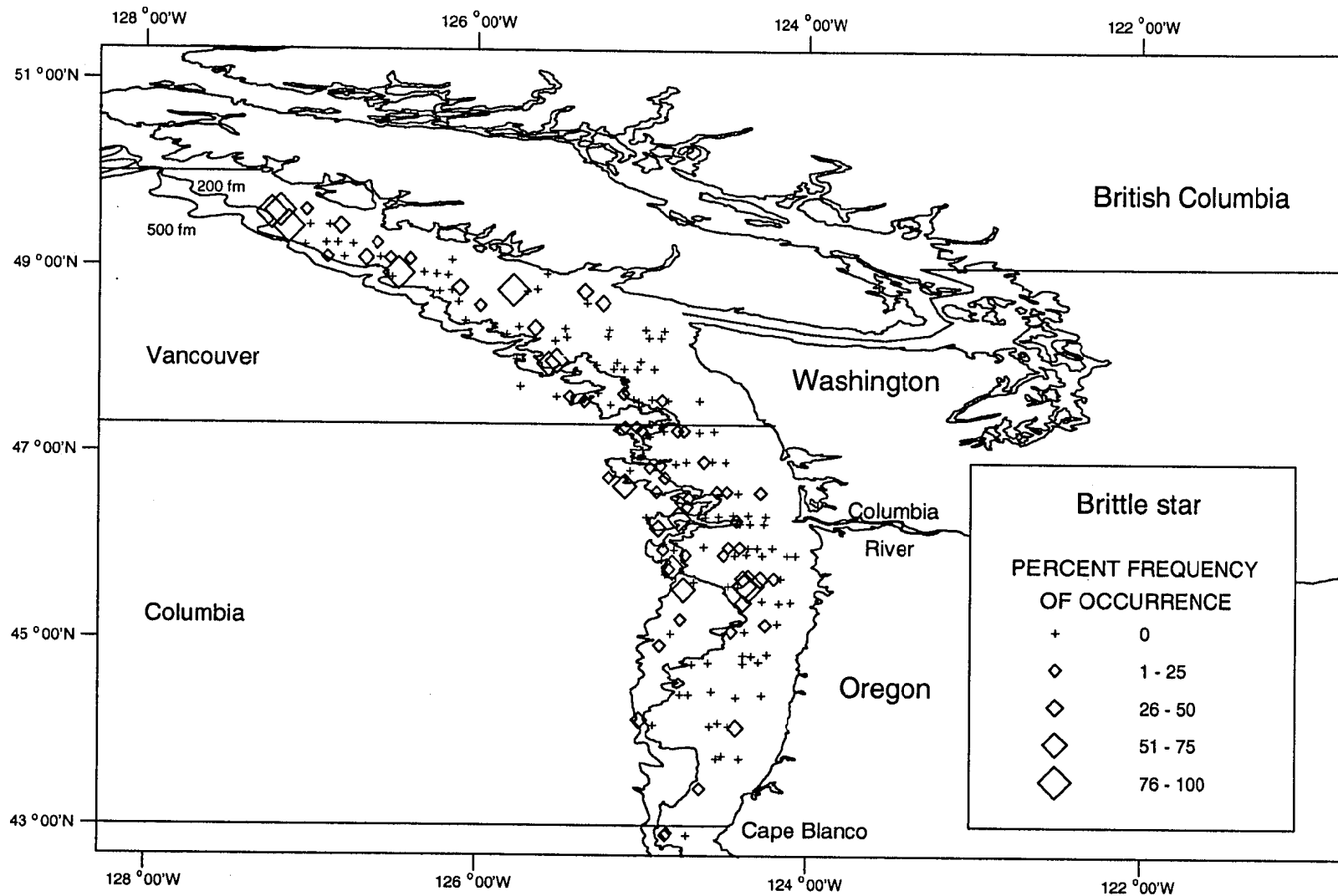


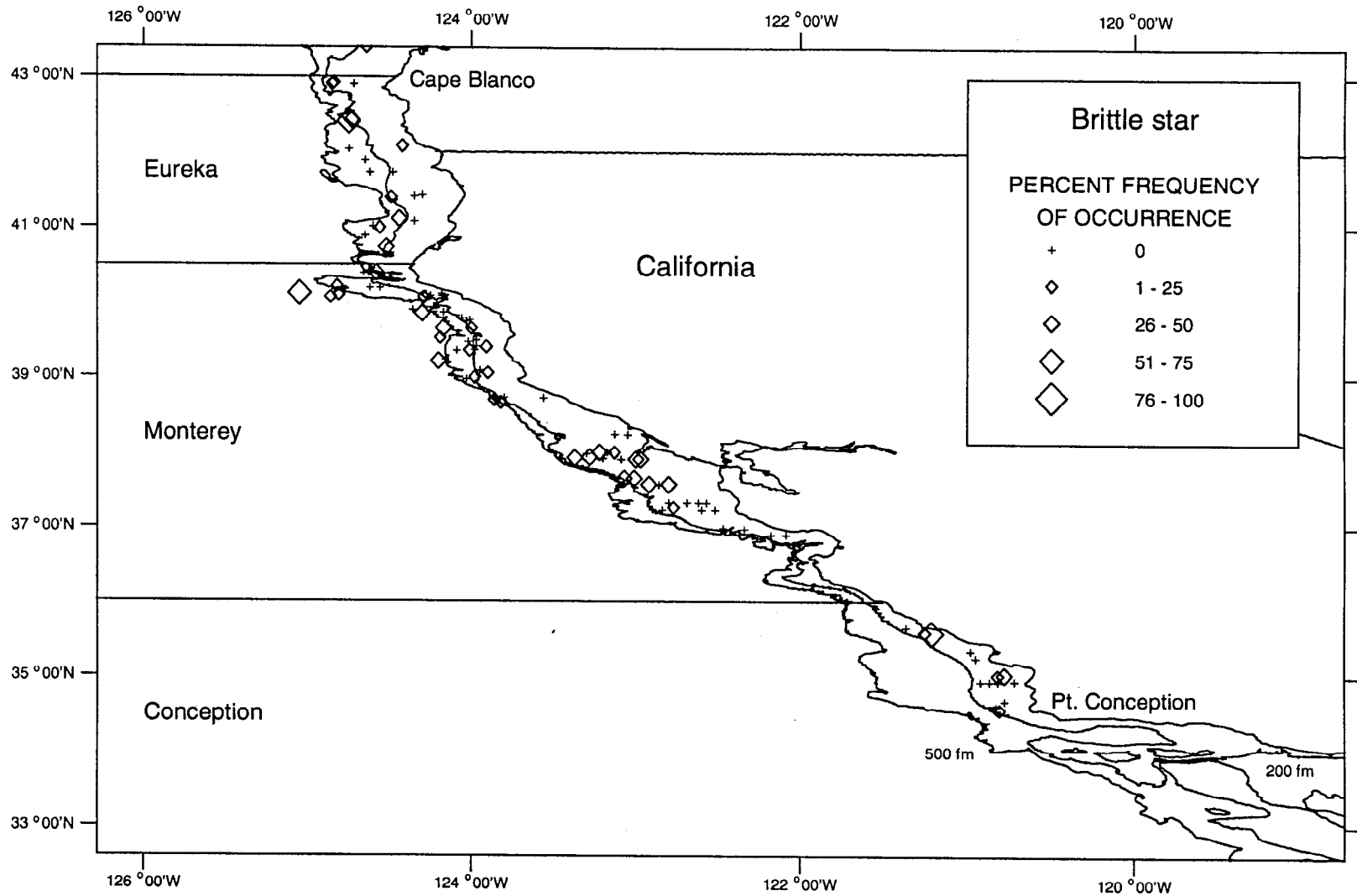


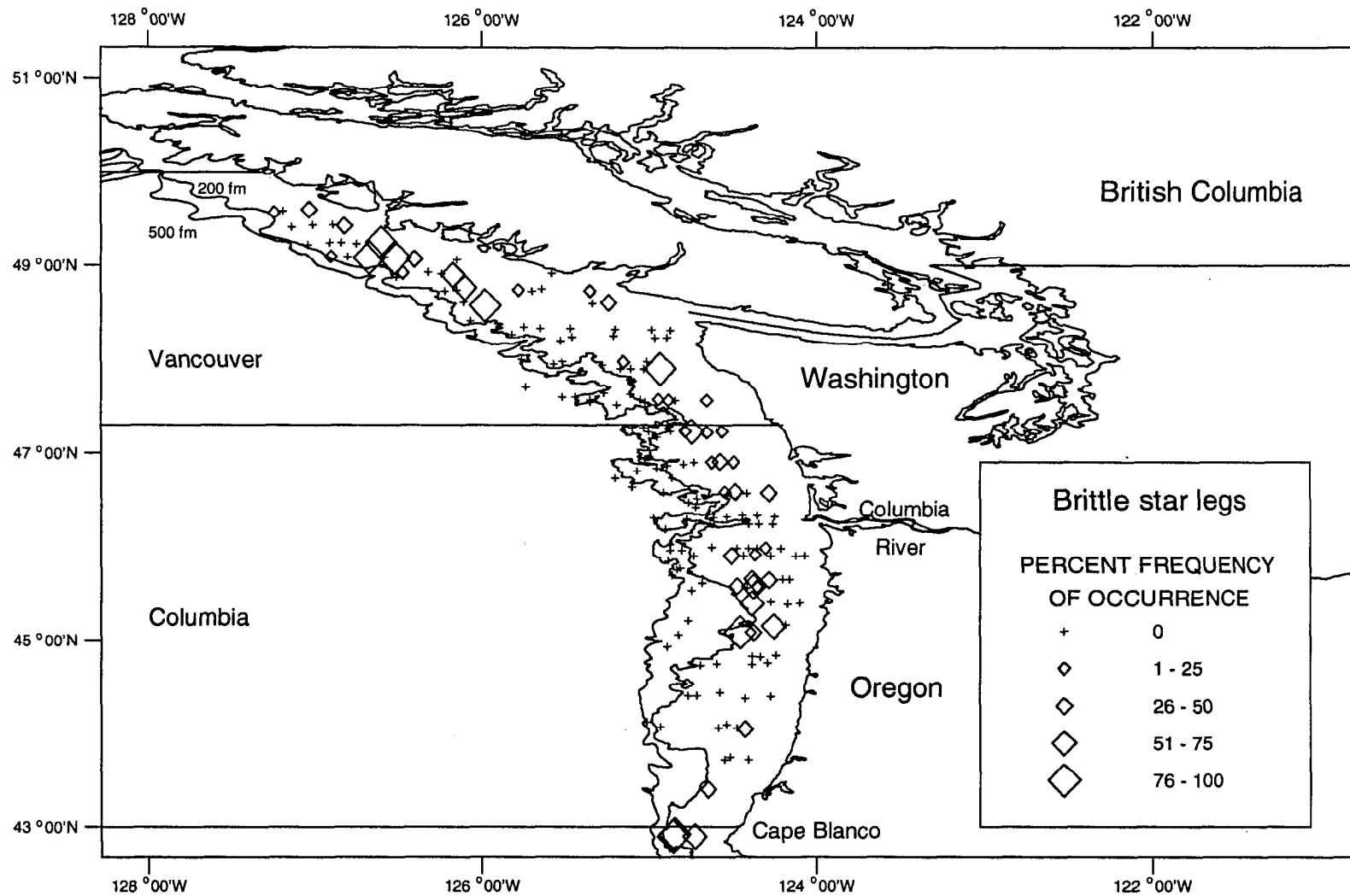


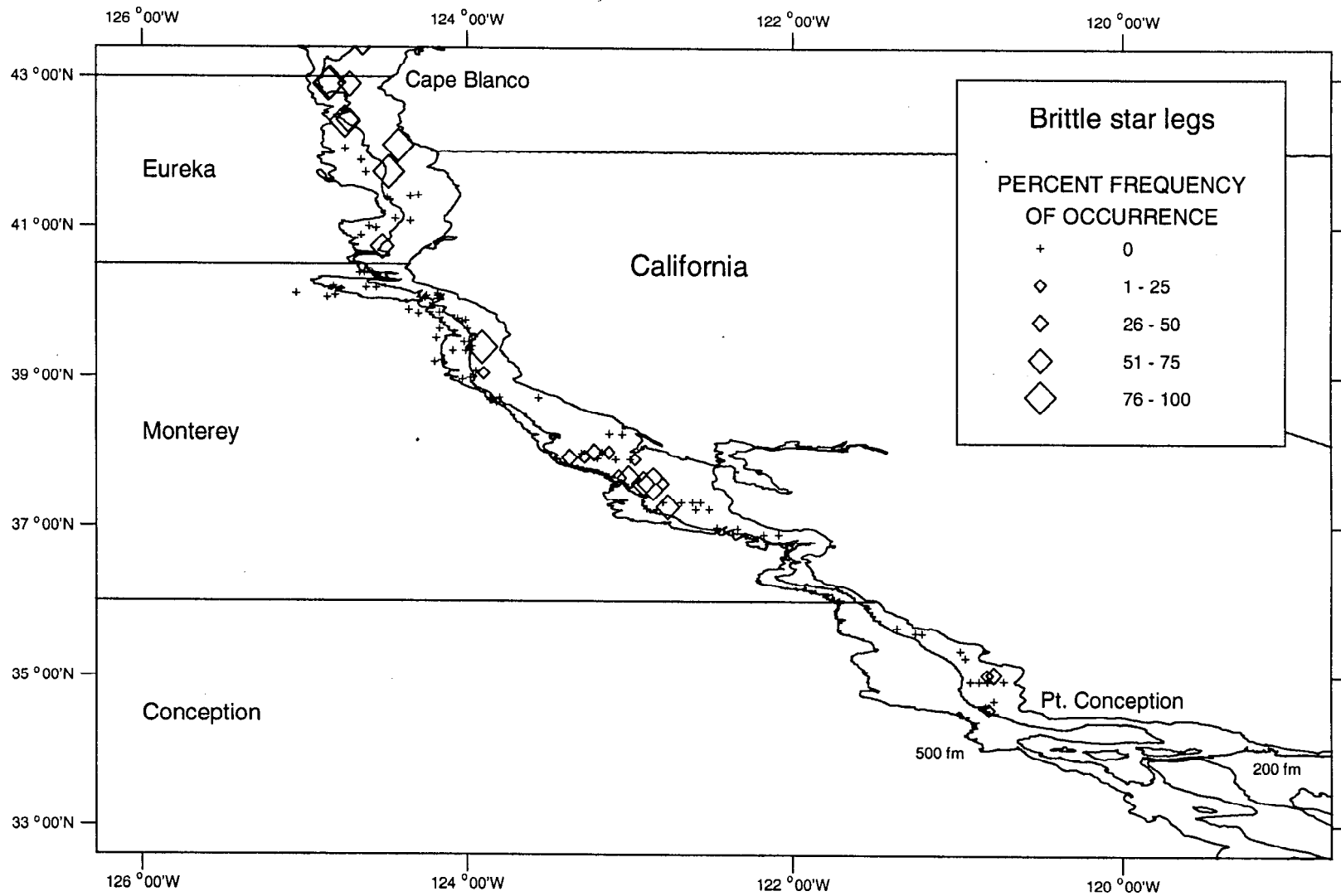


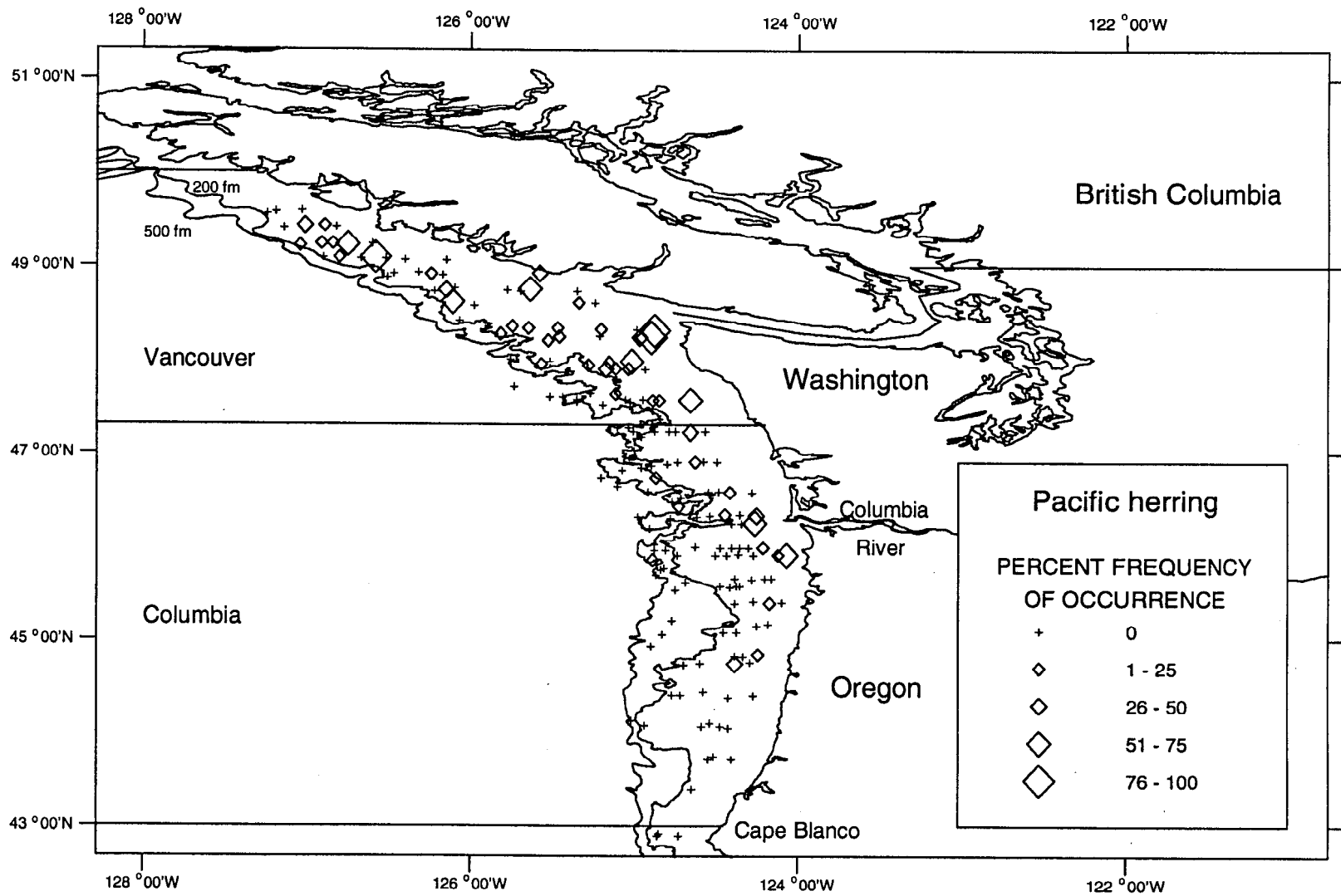


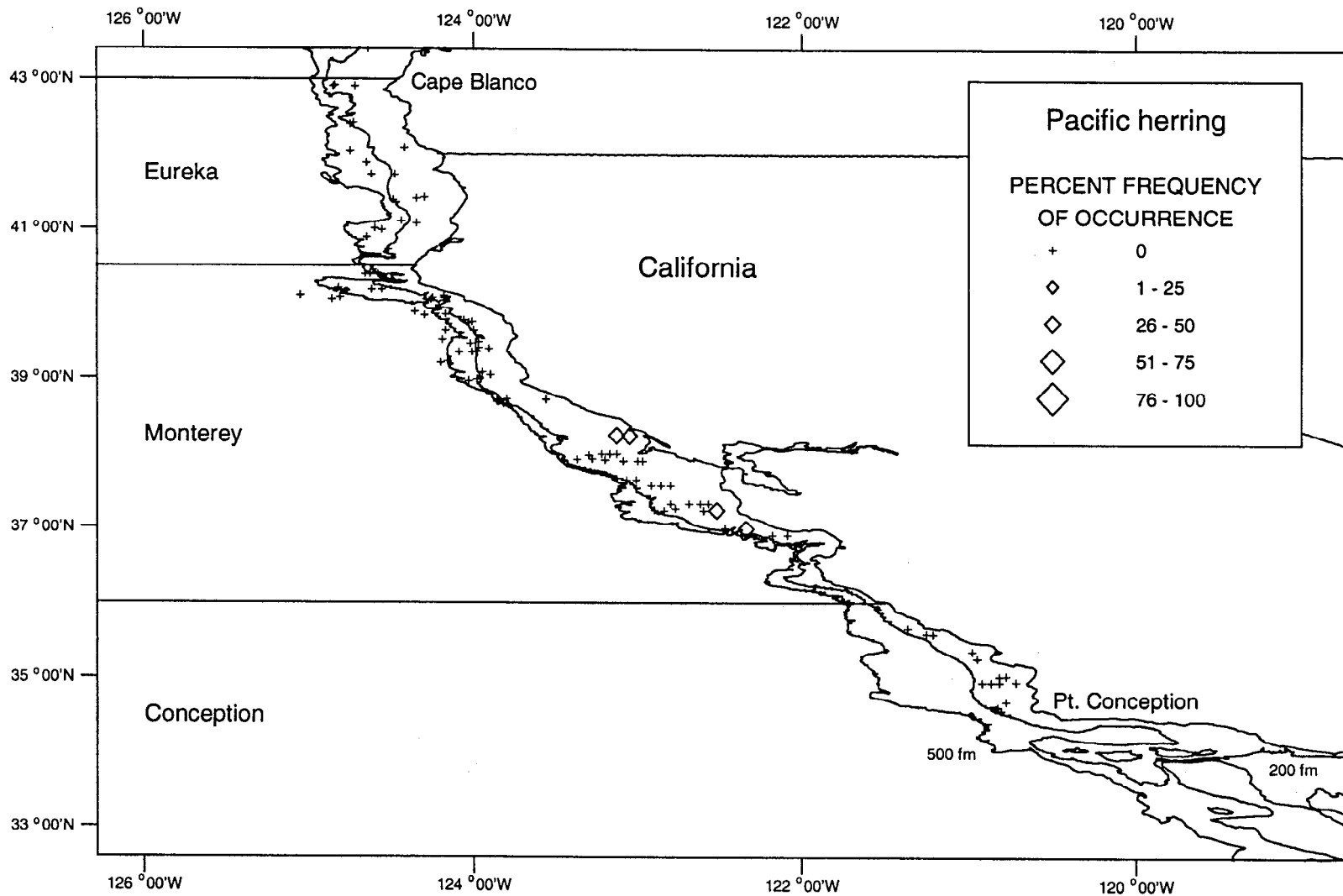


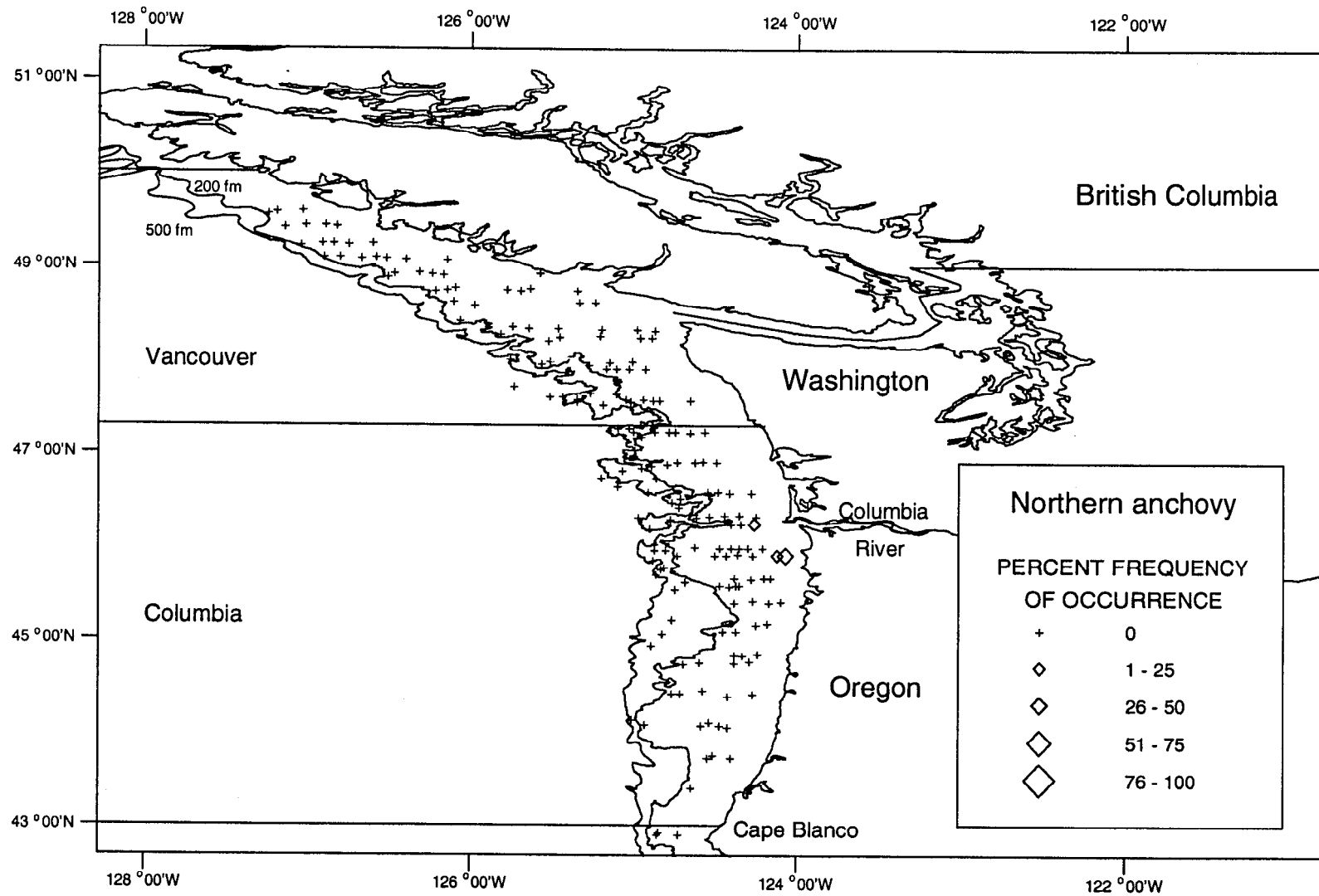


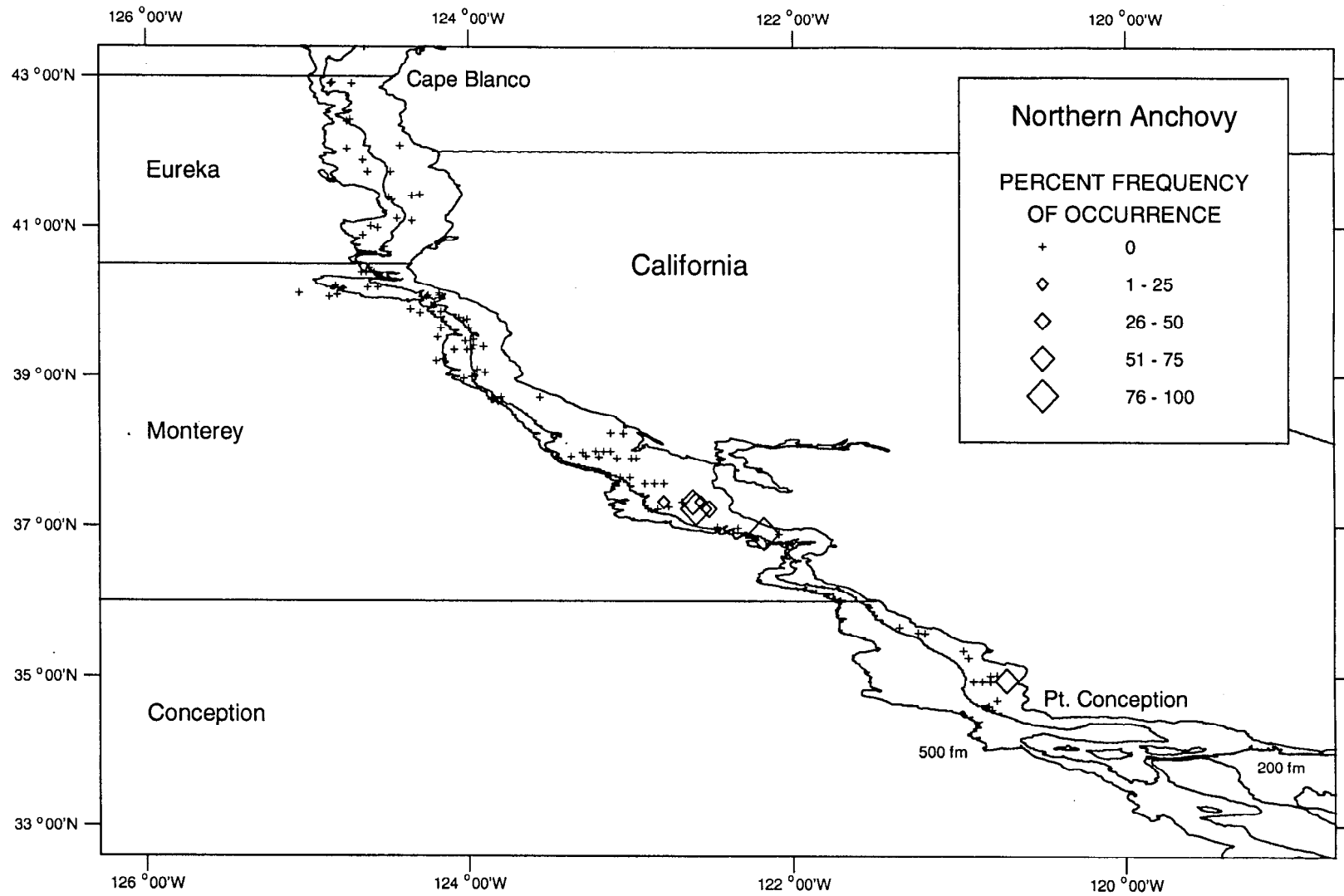


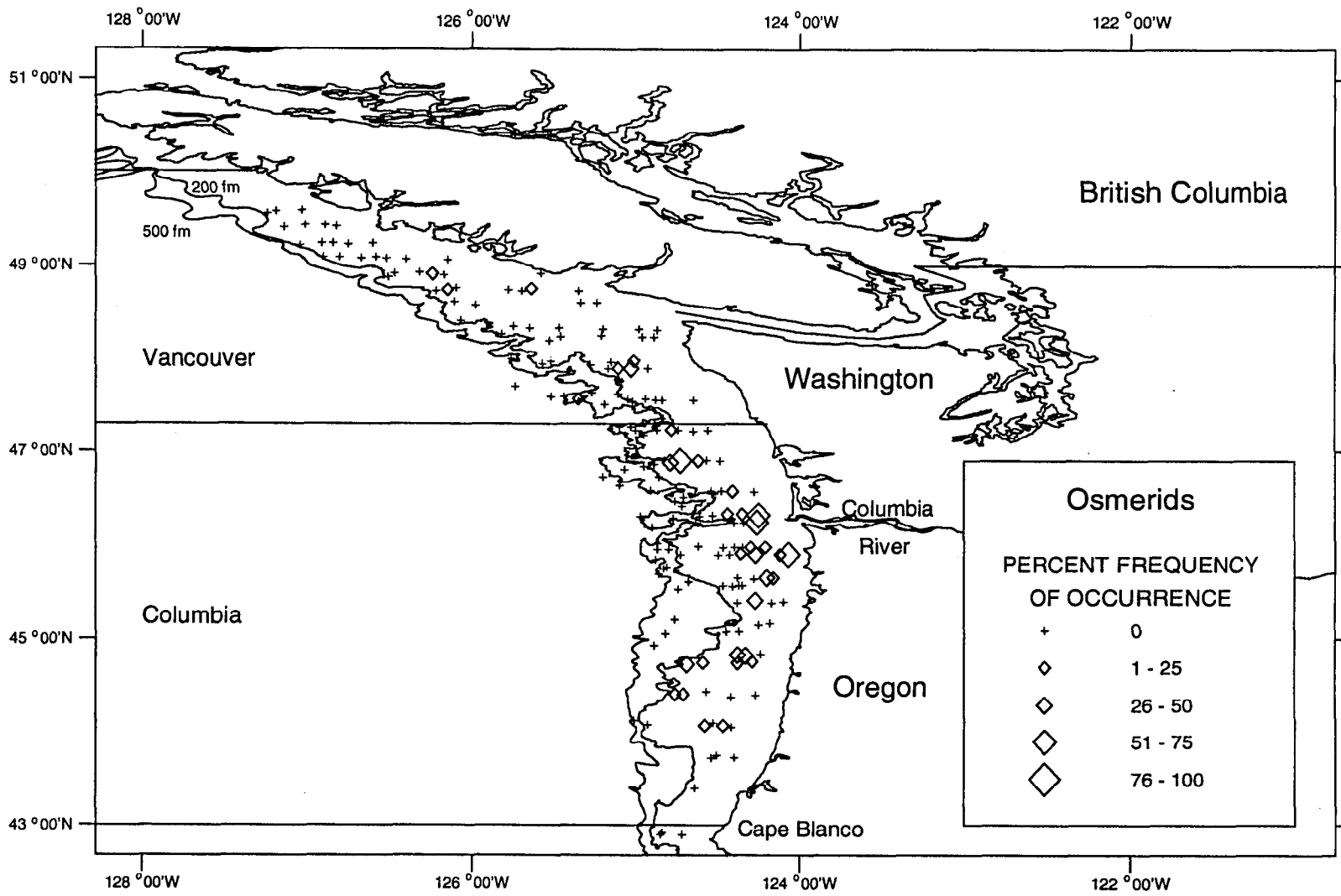


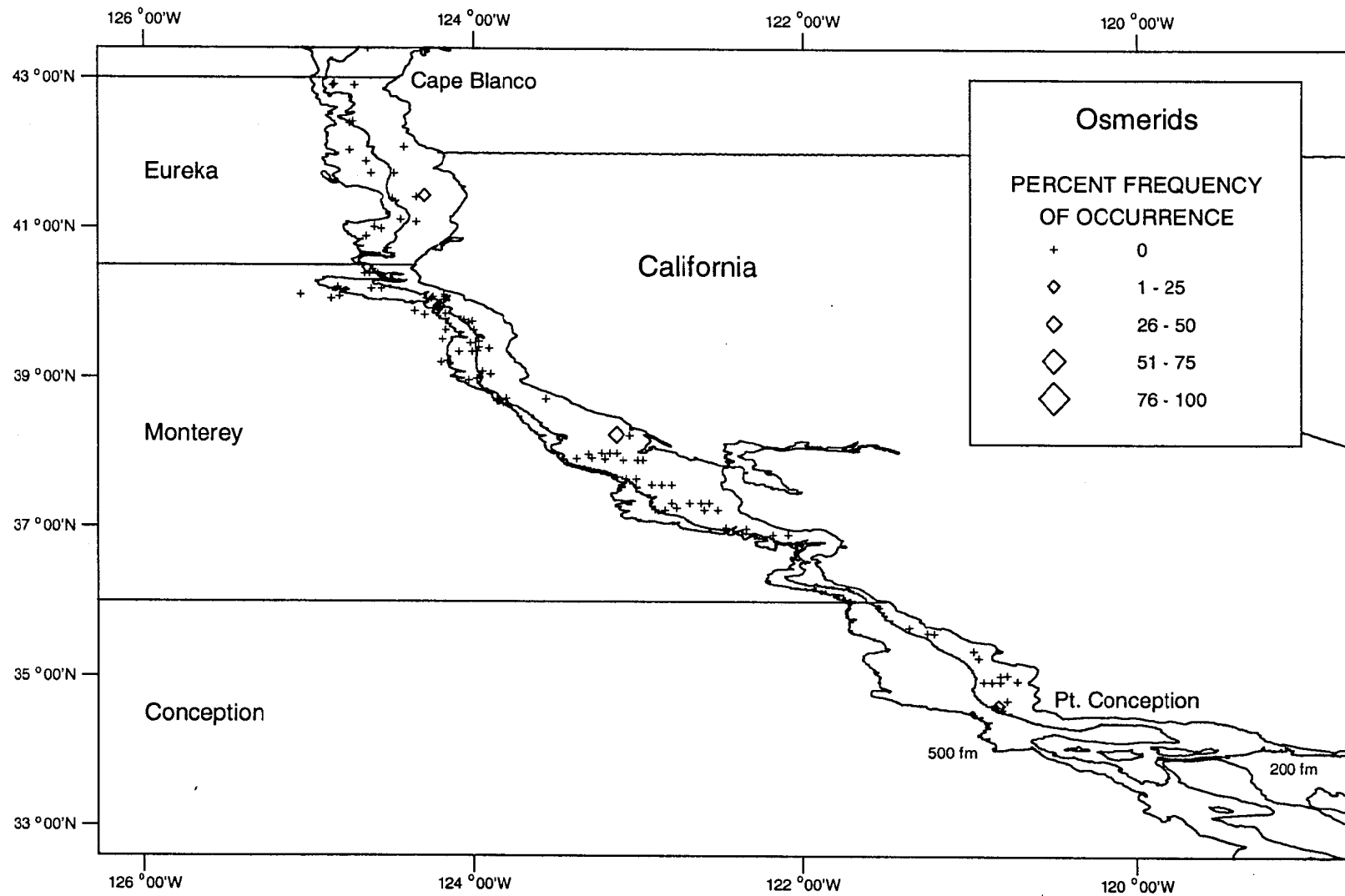


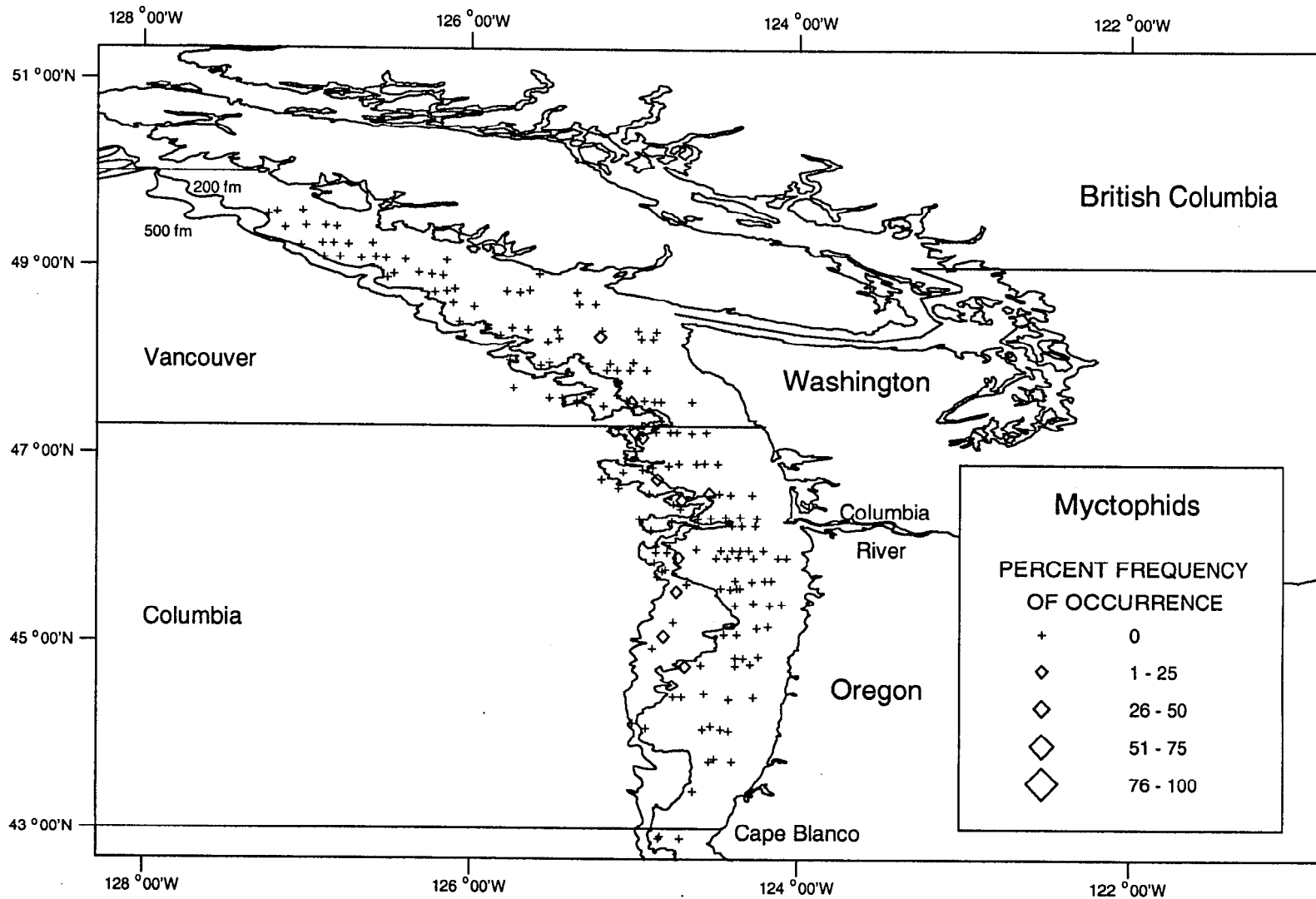


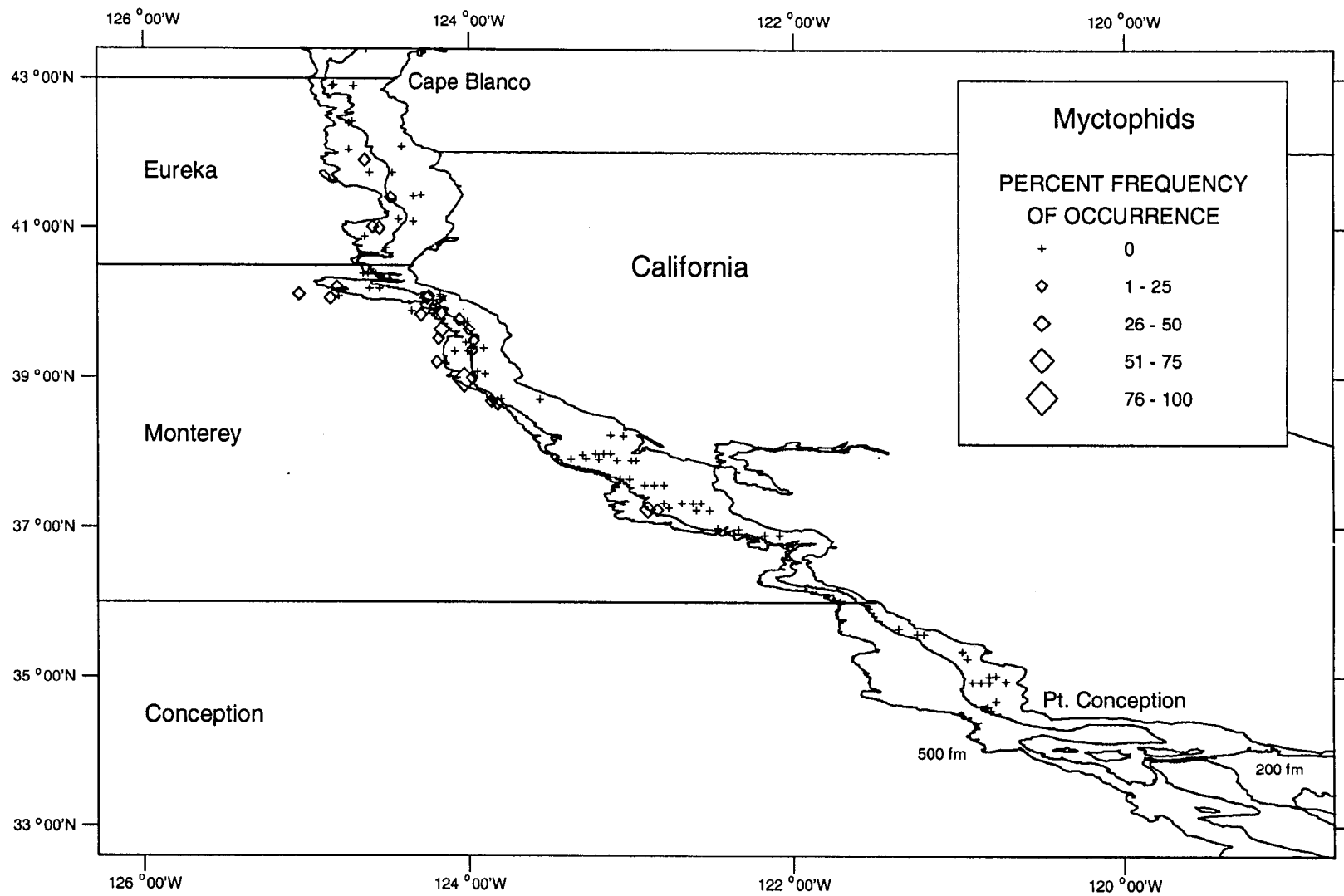


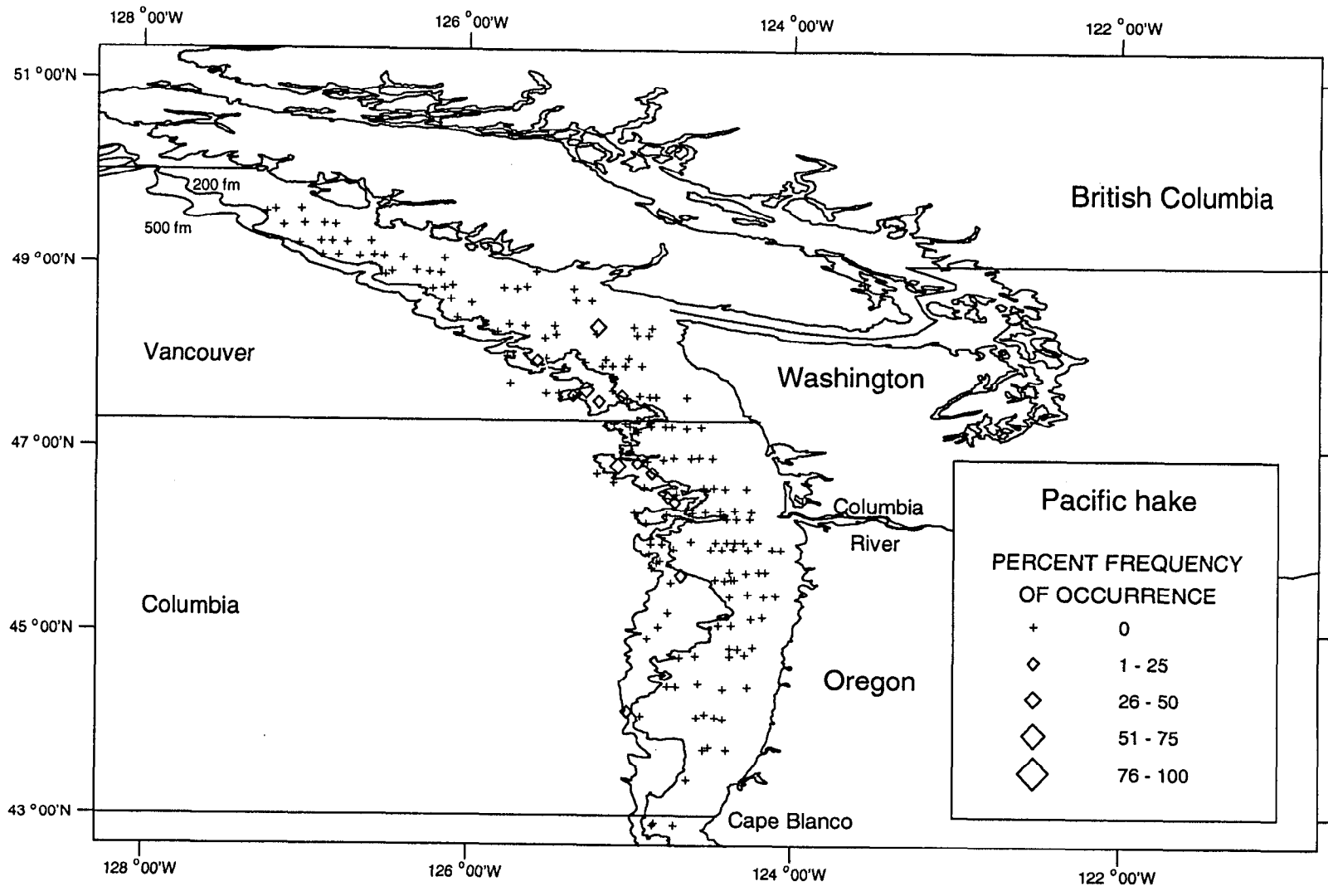


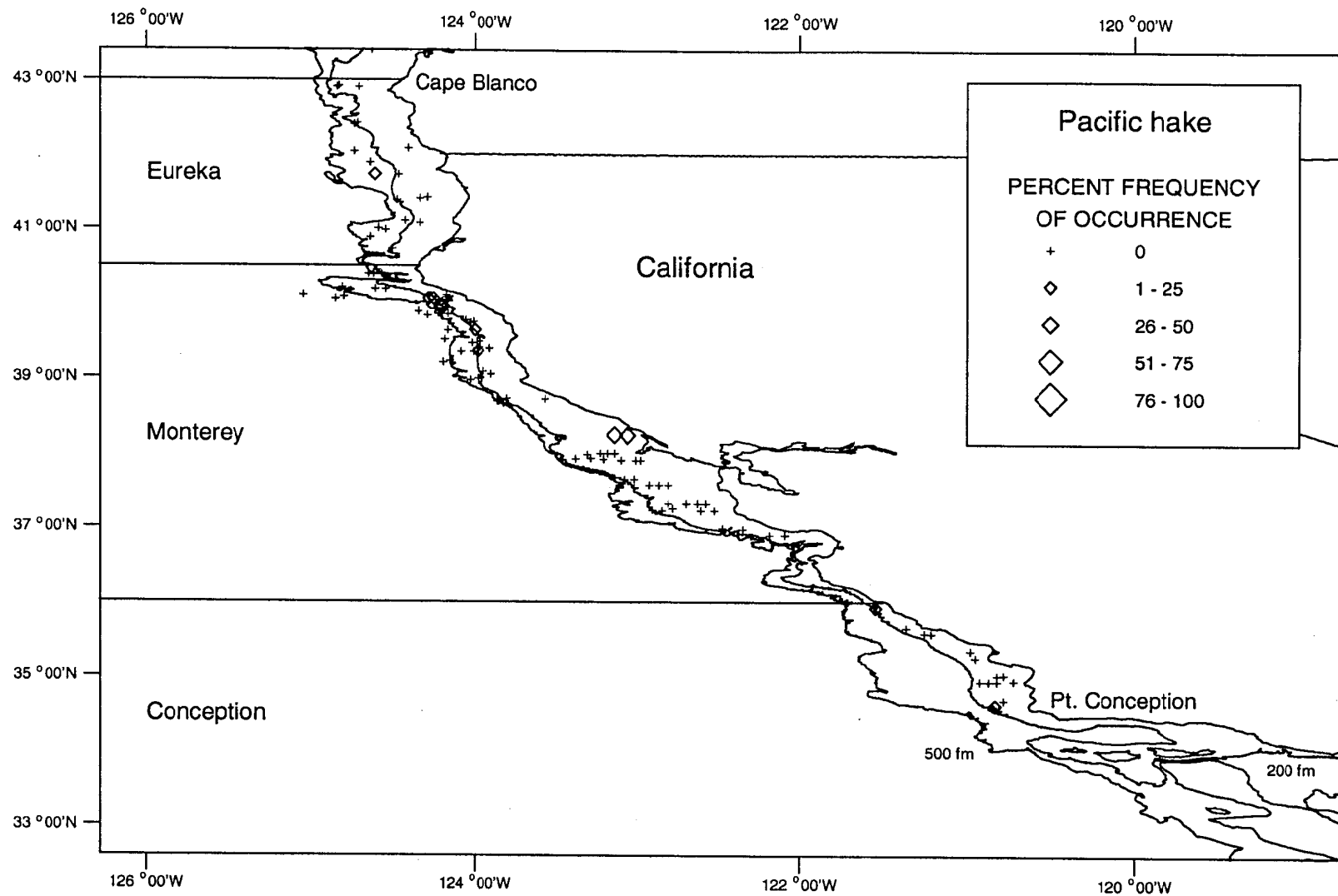


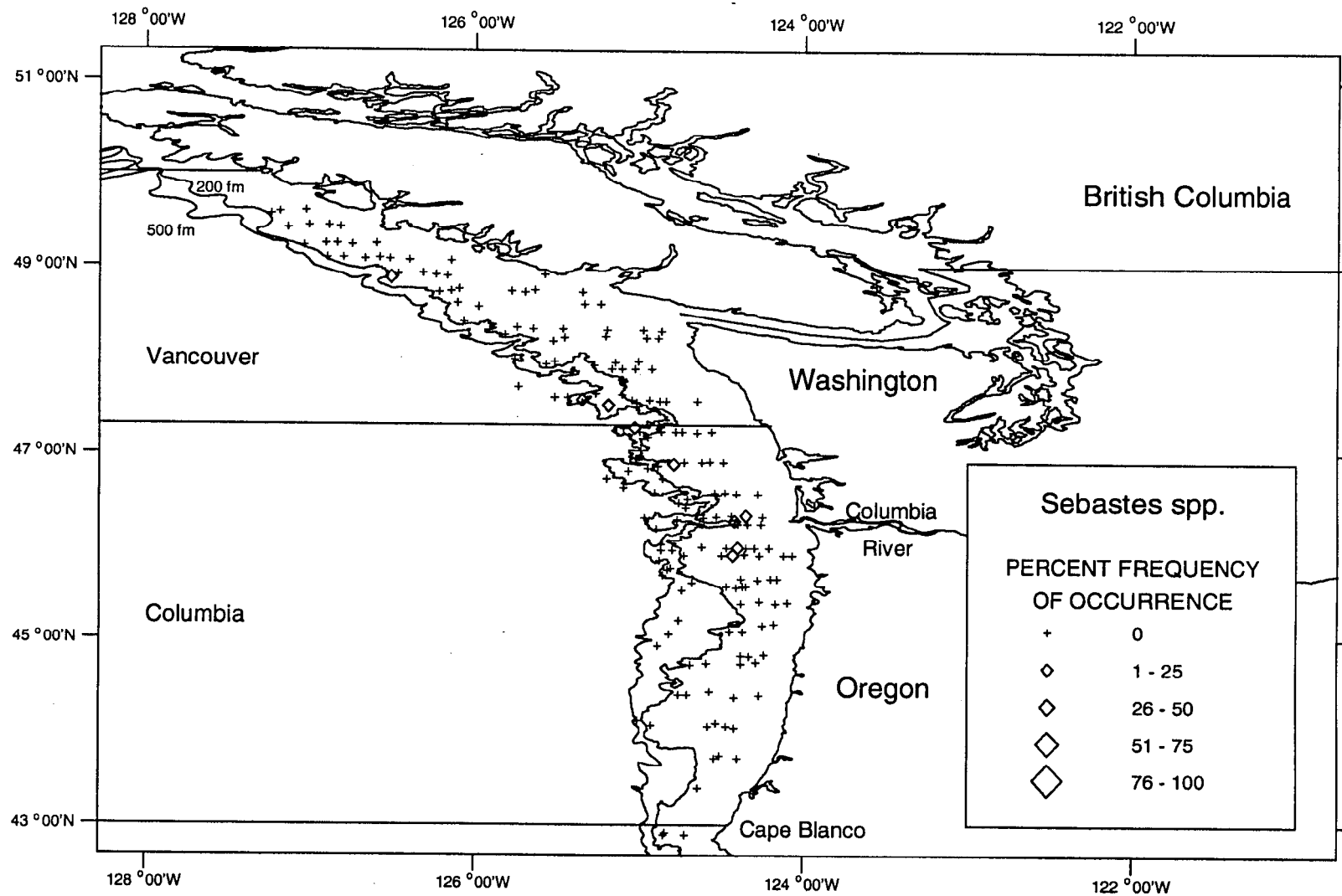


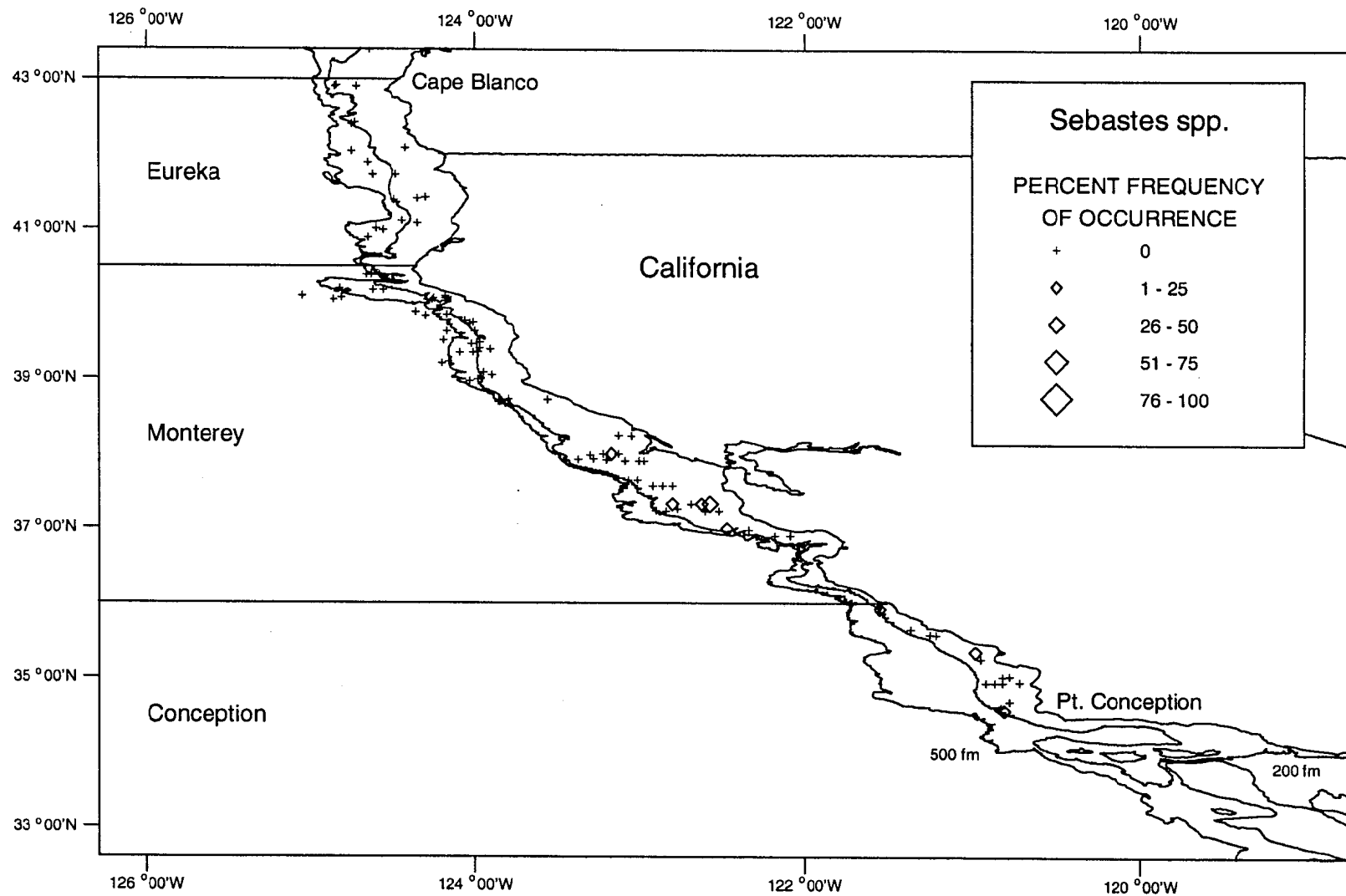


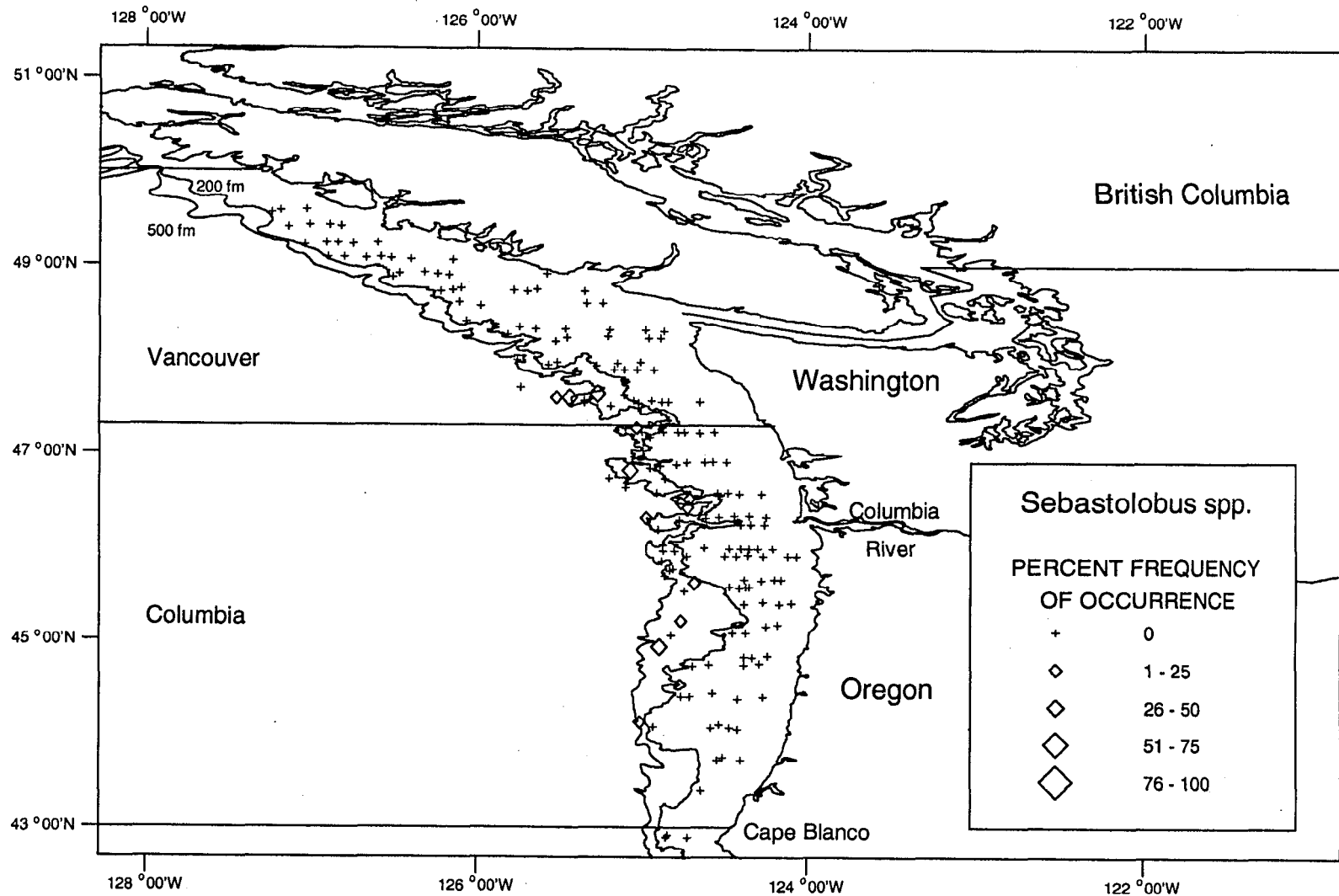


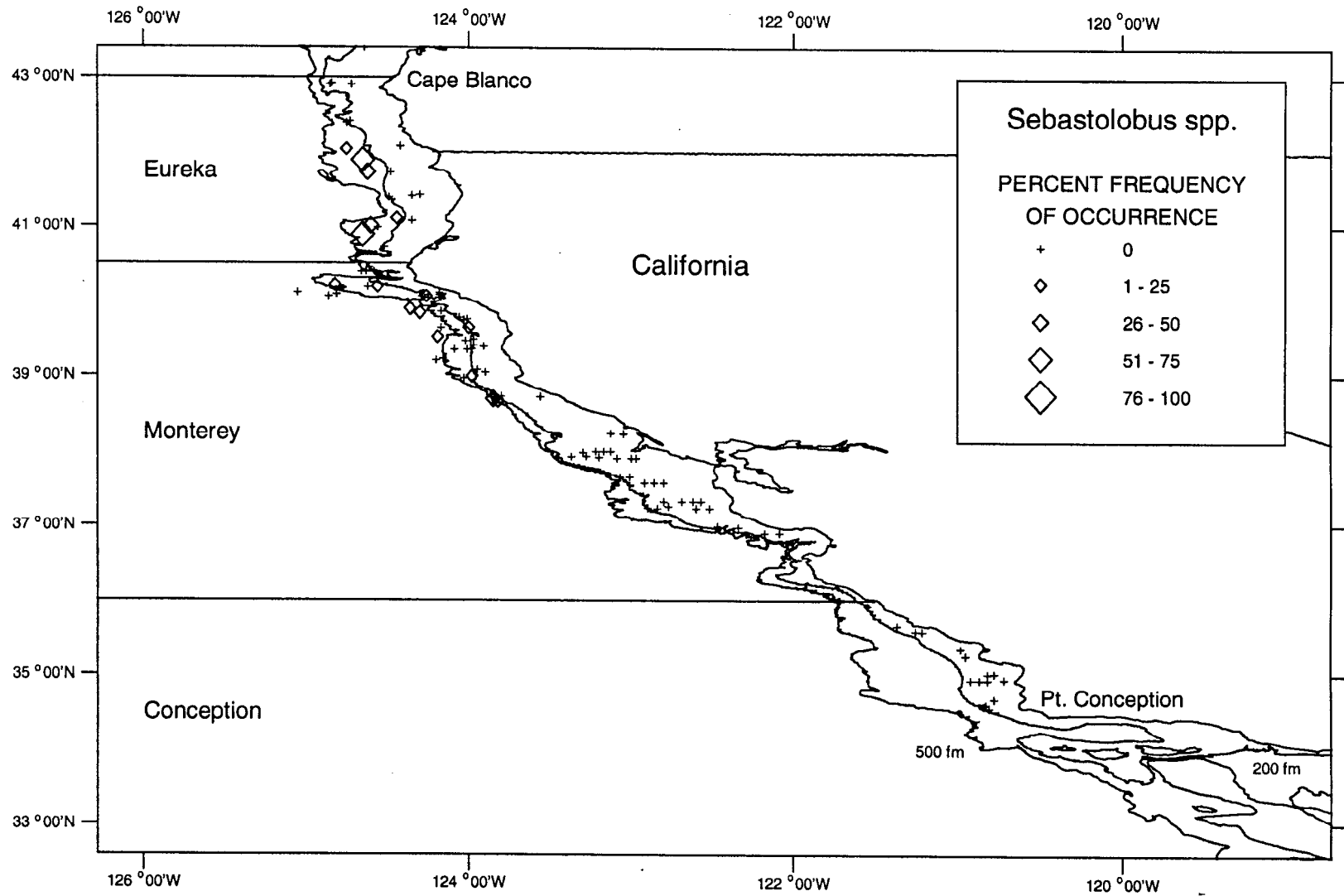


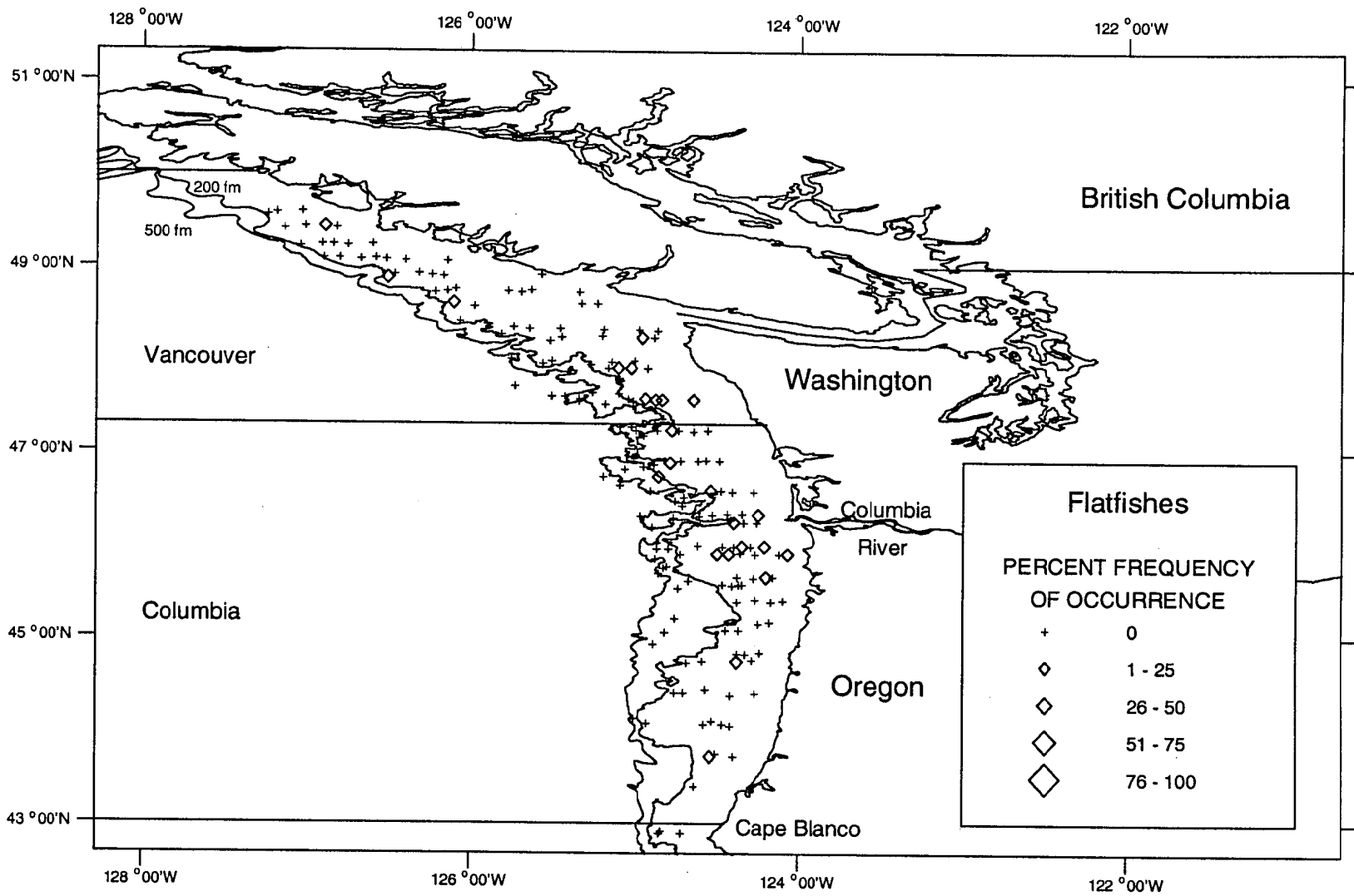


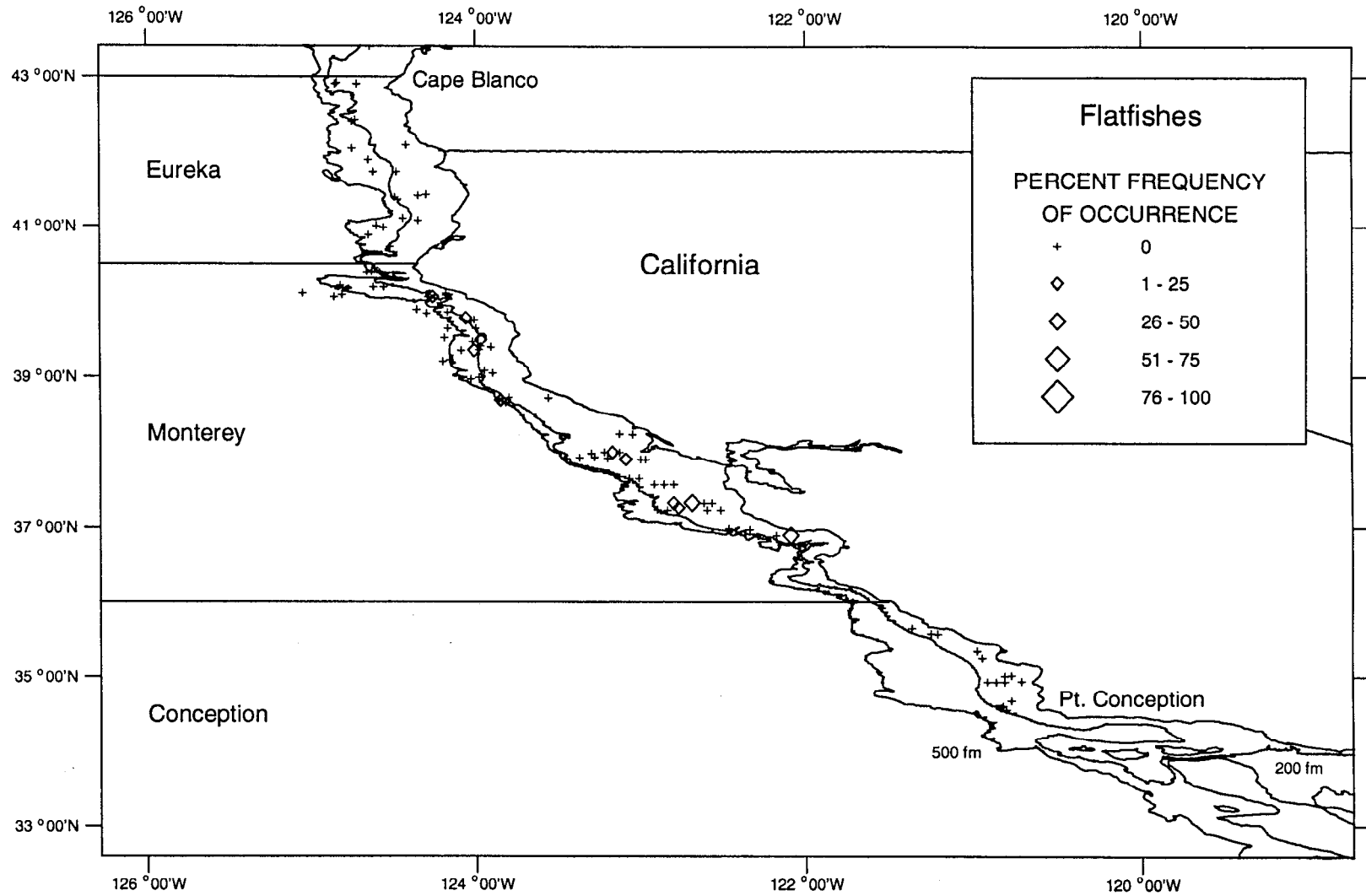












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