

AN ABSTRACT OF THE DISSERTATION OF

Chadwick V. Jay for the degree of Doctor of Philosophy in Fisheries Science presented on April 25, 1996. Title: Spatial and Temporal Characteristics of Bottom-Trawl Fish Assemblages of the Continental Shelf and Upper Slope of the Pacific Coast of the United States, 1977-1992.

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Abstract approved: _____,

David Sampson

Twenty-three bottom-trawl fish assemblages were identified from the relative biomass of 33 dominant species that occurred in the National Marine Fisheries Services' triennial trawl surveys over the continental shelf and upper slope off California, Oregon, and Washington from 1977 to 1992. The assemblages accounted for about 70% of the total variation in species composition among 2,565 hauls. Although the assemblages persisted over the 15-yr study period and occurred within broad geographic boundaries, some had substantially different spatial distributions among surveys. The ability to differentiate assemblages across five environmental variables (latitude, depth, surface and bottom water temperatures, and surficial substrate) was low. The preponderance of hake-dominated assemblages throughout the study area suggests that Pacific hake (*Merluccius productus*) may play a large role in the dynamics of demersal fish communities off the

west coast of the United States. The same data were used to establish general features regarding the abundance and distribution of the 33 dominant fish, and investigate intersurvey regional variation in species composition. Flatfish were generally widespread and at low density within areas of their occurrence. In contrast, rockfish were comparatively less widespread, and were at higher density within areas of their occurrence. Pacific hake, spiny dogfish, and sablefish were both widespread and occurred in high density. The greatest amount of variation in species composition occurred in the shallow shelf region off California, and the shallow and deep regions between Cape Mendocino and Cape Blanco. These regions corresponded to areas with the greatest amount of annual variation in upwelling. Contrary to upwelling, intersurvey variation in surface temperature did not appear to correspond to variation in species composition, but there was an unanticipated negative correlation between variation in bottom temperature and variation in species composition. Species composition was influenced in most regions by Pacific hake, spiny dogfish, and sablefish. A conceptual model was developed to explore the relationship between regional changes in a species' biomass, incidence, and density, and their potential affect on species composition. Empirical examination of the model was difficult. Five of six flatfish species (Pacific sanddab, rex sole, Pacific halibut, Dover sole, and English sole) exhibited a significant positive linear relationship between incidence and log-transformed biomass which is consistent with density-dependent habitat selection. There was evidence (albeit weak) from patterns in the occupancy of substrate types by these flatfish, that marginal habitats are associated with areas of mud for Pacific sanddab and areas of sand for rex sole, Pacific halibut, and Dover sole.

Spatial and Temporal Characteristics of Bottom-Trawl Fish Assemblages
of the Continental Shelf and Upper Slope of the Pacific Coast
of the United States, 1977-1992

by

Chadwick V. Jay

A DISSERTATION

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Doctor of Philosophy dissertation of Chadwick V. Jay presented on April 25, 1996

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Spatial and Temporal Characteristics of Bottom-Trawl Fish Assemblages of the
Continental Shelf and Upper Slope of the Pacific Coast of the United States, 1977-1992

Chapter 1

INTRODUCTION

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Fisheries science was established at the turn of the century from efforts to understand the variability and predict the future abundance of fish stocks. Those efforts have resulted in the proliferation of single-species management practices (Smith 1988). However, single-species practices are inadequate, particularly for mixed-species fisheries such as a trawl fishery (Mercer 1982, Pikitch 1988). They are particularly hampered by their incorporation of simple abstractions from a complex system of interacting species undergoing changes in spatial distributions within a dynamic and often unpredictable environment. Studies on the spatial dynamics of co-occurring species may lead to insights on the significance of physical and biological processes in structuring fish communities and aid in discussions on alternative management approaches.

Since 1977, the National Marine Fisheries Service (NMFS) has conducted triennial standardized bottom-trawl surveys over the continental shelf and upper slope off California, Oregon, and Washington to assess the abundance of bottom fish. Data from these surveys have provided researchers the opportunity to quantify the co-occurrence of species over large geographic regions. Gabriel (1982) identified fish assemblages from the NMFS 1977 survey data, and Gabriel and Tyler (1980) suggested that the assemblages off Oregon in 1977 had some similarity with assemblages that were identified from an unrelated trawl survey in 1973. Since the onset of the present study, Weinberg (1994) used the 1977-92 survey data to examine the persistence of rockfish assemblages within the northern region of the survey area.

Now that a significant amount of time series data has been collected from the surveys, it is possible to study changes in the spatial distribution of fish assemblages. Such studies have been conducted on the Atlantic Coast of North America using trawl survey data and have led to a greater understanding of the relative impact of fishing and environmental variability on the structure of fish communities (Colvocoresses and Musick 1984, Overholtz and Tyler 1985, Murawski and Finn 1988, Gomes et al. 1995).

The purpose of this dissertation is to gain understanding of the organization and spatial variability of the summertime bottom-trawl fish assemblages off the U.S. West Coast using the NMFS 1977-92 survey data. The approach taken in this dissertation is inherently descriptive; thus, assigning causal mechanisms to observed patterns is speculative. However, given the spatial scale of large marine ecosystems, and assuming that any given state of the system is contingent upon its previous state, such an inductive approach may be the only method of uncovering the larger patterns and processes involved in structuring fish communities in these large systems (e.g. Francis and Hare 1994).

It should be kept in mind that the triennial surveys were standardized for comparability. Commercial landing data were not used because of the biases associated with unknown fish discards, non-standardized effort, and non-random “sampling” of the study area. Many of the generalizations that are made herein may be unjustified if large biases occurred between surveys, such as those that may result from differences in vessel specifications, weather, or modifications to survey design (Byrne et al. 1981).

In Chapter 2, I identify fish assemblages based on the relative abundance of dominant species, then assess the variability in their spatial distributions. In addition, I examine the segregation of assemblages across five environmental variables. In Chapter 3, I address a few of a multitude of potential factors associated with the occurrence and distribution of fish assemblages by looking at relationships between the incidence and abundance of dominant species.

Chapter 2

DISTRIBUTION OF BOTTOM-TRAWL FISH ASSEMBLAGES OVER THE CONTINENTAL SHELF AND UPPER SLOPE OF THE U.S. WEST COAST, 1977-1992

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Introduction

Fish associations can be affected directly or indirectly from fishing. Trawl gear is relatively nonselective, such that any organism that is not able to move out of its path, or pass through its mesh will be captured. Because of differential productivity among species, less productive species may be overfished while fishers strive for the “optimal” catch level of a more productive species. Two general approaches have been suggested to alleviate overfishing in a trawl fishery: (1) to identify areas, times, or gear types that will achieve a catch of a more desirable mix of species (e.g. Leaman and Nagtegaal 1987, Murawski and Finn 1988); and (2) to identify assemblages of species that can be managed adaptively as similar units of production (Tyler et al. 1982). To identify strategies that may optimize the catch of a given mix of species, knowledge of the spatial and temporal co-occurrence of species is required. Similarly, assemblage management would require that one knows what assemblages exist, their location, and to what extent their spatial distribution may change. Furthermore, studying relationships between assemblages and their environment may provide insight into the relative importance of environmental characteristics to the distribution of assemblages.

The National Marine Fisheries Service (NMFS) has conducted standardized bottom-trawl surveys triennially since 1977 over the continental shelf and upper slope off California, Oregon, and Washington to assess the abundance of bottom fish. These data have provided researchers the opportunity to quantify the co-occurrence of species over large geographic regions. Gabriel (1982) identified fish assemblages from the NMFS

1977 survey data, and Gabriel and Tyler (1980) suggested that the assemblages off Oregon in 1977 had some similarity with assemblages that were identified from an unrelated trawl survey in 1973. Since the onset of the present study, Weinberg (1994) used the 1977-92 survey data to identify rockfish assemblages within the northern region of the survey area and identified the persistence of three assemblages.

The purpose of the present study is to use the NMFS 1977-92 triennial survey data to assess the variability in the spatial distribution of summertime bottom-trawl fish assemblages off the west coast of the United States. In addition, I examine the segregation of assemblages across five environmental variables.

The term “distribution” has several meanings in the ecological literature (Pielou 1977, Wright 1991). To avoid confusion here, I define “geographic range” as an assemblage’s extent of occupation over a single dimension (e.g. across latitude or depth), and “incidence” as the estimated proportion of sampling units that are occupied by an assemblage. Because, in the present study, the sampling unit was a unit of area, incidence can be interpreted as the estimated proportion of the study area that was occupied by an assemblage. According to the definitions I have adopted, an assemblage can increase its incidence without necessarily increasing its geographic range. Furthermore, I use the term “species composition” when referring to a group of species and their relative abundance. I define an “assemblage” as the composition of species from hauls that have been grouped together such as from cluster analysis.

Methods

Description of Trawl Surveys

The general objective of the NMFS surveys was to determine the distribution, abundance, and biological characteristics of demersal fish off California, Oregon, and Washington (see Gunderson and Sample 1980, Weinberg et al. 1984, Coleman 1986, 1988, and Weinberg et al. 1994 for details of the 1977, 1980, 1983, 1986, and 1989 surveys). The surveys were conducted from the first or second week in June to late September or early October, over the continental shelf and upper slope of the Pacific coast of primarily the United States. The 1977 survey began at 34°00' N, the 1980, 1983, and 1986 surveys began at 36°48' N, and the 1989 and 1992 surveys began at 34°30' N. The 1977 and 1986 surveys concluded at the Washington/Canada border, and the 1980, 1983, 1989, and 1992 surveys concluded near Vancouver, Canada. Sampling extended from 55 m to 366 m deep, except for the 1977 survey, which extended from 91 m to 457 m deep. For comparison purposes, only data collected from 36°48' N to the Washington/Canada border were used in the present study (Fig. 2.1).

In each survey, sampling was conducted during daylight from at least two fishing vessels. All vessels deployed a Nor'Eastern otter trawl with rollers and a cod-end liner with 3.2-cm mesh. Only data from hauls with satisfactory or better fishing performance were used in the present study, resulting in the exclusion of not more than 6% of the hauls from each survey. A haul with only satisfactory fishing performance is one where

Fig. 2.1. Sampling locations with satisfactory or better fishing performance within the present study area in each of the NMFS triennial surveys from 1977 to 1992 (50- and 250-m isobaths are shown).

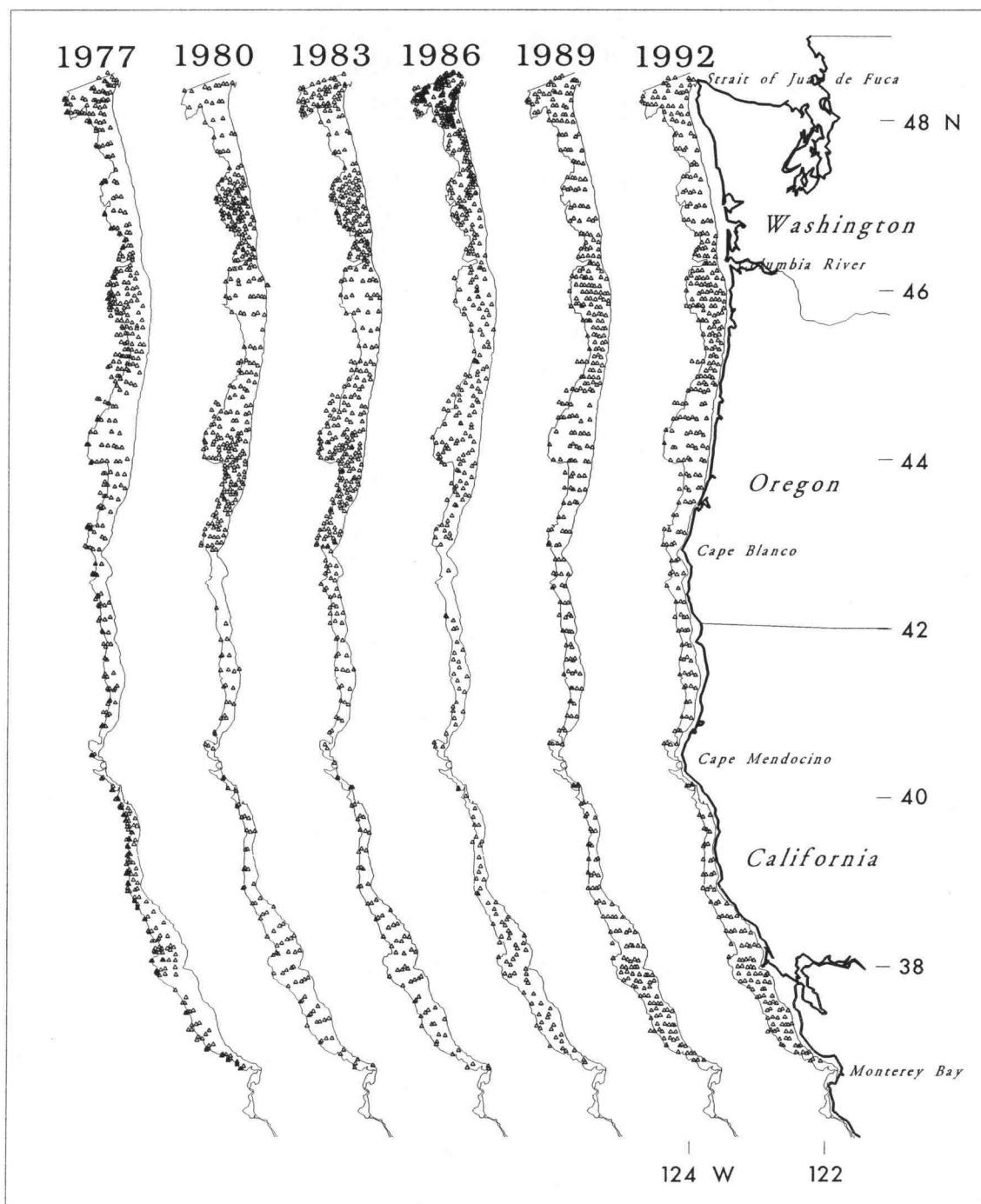


FIGURE 2.1

“the chief scientist and head fisherman agree that despite a trawl hang-up, fish loss due to net damage or slowed retrieval was minimal, and the tow should still be used in data analysis” (NMFS 1991, page 9).

Conceptually, the sampling unit is a constant volume of water that would be sampled by the bottom trawl over a distance of 2.8 km ($5.6 \text{ km/h tow rate} \times .5 \text{ h tow duration}$). Thus, the conceptual sampling unit is the volume of water corresponding to the product of the vertical opening of the mouth of the trawl (headline height), the horizontal opening of the trawl (wing-tip width), and the distance that the trawl is towed. However, in practice, although headline height was held sufficiently constant among hauls, the trawl’s wing-tip width sometimes varied among fishing vessels. Furthermore, even though tow duration was held constant for all hauls, the distance that the trawl was towed varied among hauls, because of variable fishing conditions and differing vessel specifications. Hence, the sampling unit was variable.

For statistical analyses, I treated the sampling unit as a two-dimensional unit of a constant area of seafloor by adjusting species catch weights (measured to the nearest kg) from each tow to a “standardized” sampling unit of 1-km^2 of seafloor. The adjustment was achieved by dividing the actual catch weight of each species by the actual area trawled, resulting in the catch equivalent of one standard unit of effort (CPUE). Such adjustments for the analysis of survey catch data are common. The actual area trawled was derived by multiplying the distance towed, which was recorded for each haul, by the trawl’s wing-tip width for a given vessel (Table 2.1). A sample observation is herein

Table 2.1. Trawl wing-tip width used to adjust catch weights from each survey vessel to a standardized sampling unit of 1-km².

Survey year	Vessel	Trawl width (m)
1977	Commando	13.40
	David Starr Jordan	13.40
	Pacific Raider	13.40
	Tordenskjold	13.40
1980	Mary Lou	13.40
	Pat San Marie	13.40
1983	Nordfjord	13.40
	Warrior II	13.40
1986	Alaska	13.30*
	Pat San Marie	12.69
1989	Golden Fleece	12.40**
	Pat San Marie	13.40**
1992	Alaska	12.76**
	Green Hope	12.55**

*average from polyethylene net of 13.82 m and nylon net of 12.78 m.

**trawl width was measured for many individual hauls in the 1989 and 1992 surveys; however, for simplification, overall mean width was used.

Source: Gunderson and Sample 1980, Weinberg et al. 1984, Coleman 1986, 1988, Weinberg et al. 1994, 1992 survey: M. Wilkins, NMFS, Seattle, personal communication.

referred to as a “haul” and consists of a set of species catch weights that have been adjusted to a “standardized” sampling unit of 1-km² of seafloor.

A stratified random sampling design was employed in each survey, with strata defined by latitudinal and depth boundaries (Table 2.2, also see Fig. 2.1).

Table 2.2. Surface area (km² = number of sampling units) and boundaries of sampling strata ("border" indicates Washington/Canada border). The number of hauls in each stratum is indicated in parentheses.

1977	Depth boundaries (m)			
	91 - 181	182 - 272	273 - 364	365 - 457
Latitudinal boundaries (°N)				
36°48' - 37°07'	467 (7)	87 (5)	88 (5)	100 (2)
37°07' - 37°56'	1,157 (13)	183 (3)	160 (5)	185 (5)
37°56' - 38°19'	936 (11)	138 (6)	106 (5)	64 (6)
38°19' - 38°49'	1,042 (10)	221 (4)	95 (4)	50 (3)
38°49' - 40°02'	1,332 (24)	171 (15)	172 (14)	190 (13)
40°02' - 45°00'	7,547 (55)	1,815 (35)	1,506 (28)	1,513 (26)
45°00' - 46°44'	4,028 (60)	1,023 (30)	641 (17)	1,136 (25)
46°44' - 47°51'	2,304 (17)	245 (4)	172 (5)	178 (5)
47°51' - border	2,150 (26)	727 (15)	319 (12)	124 (5)
<hr/>				
1980	Depth boundaries (m)			
	55 - 183	184 - 220	221 - 366	184 - 366
Latitudinal boundaries (°N)				
36°48' - 42°00'	10,896 (71)	---	---	2,190 (27)
42°00' - 42°50'	1,375 (0)*	---	---	382 (1)*
42°50' - 44°18'	5,012 (101)	357 (16)	895 (8)	---
44°18' - 45°00'	2,647 (26)	---	---	973 (8)
45°00' - 46°10'	4,092 (34)	---	---	1,432 (9)
46°10' - 47°20'	3,915 (128)	219 (9)	272 (7)	---
47°20' - border	3,871 (20)	---	---	1,232 (9)

(Table 2.2 — continued)

1983	Depth boundaries (m)			
Latitudinal boundaries (°N)	55 - 183	184 - 220	221 - 366	184 - 366
36°48' - 42°00'	10,896 (87)	---	---	2,190 (35)
42°00' - 42°50'	1,375 (0)*	---	---	382 (0)*
42°50' - 44°18'	5,012 (98)	357 (18)	895 (15)	---
44°18' - 45°00'	2,647 (31)	---	---	973 (12)
45°00' - 46°10'	4,092 (24)	---	---	1,432 (12)
46°10' - 47°20'	3,915 (89)	219 (12)	272 (7)	---
47°20' - 47°55'	1,642 (9)	---	---	225 (4)
47°55' - border**	2,230 (39)	377 (11)	631 (10)	---

**I did not recognize the strata within the 47°55' - border latitudinal boundary as distinct strata at the time of analysis, data were analyzed for strata north of 47°20' as indicated in the 1980 survey.

1986	Depth boundaries (m)			
Latitudinal boundaries (°N)	55 - 91	92 - 183	184 - 219	220 - 366
36°48' - 42°50'	4,965 (30)	7,200 (53)	718 (5)	1,843 (11)
42°50' - 45°00'	2,512 (17)	5,173 (56)	501 (4)	1,595 (11)
45°00' - 46°10'	1,057 (7)	3,035 (24)	503 (4)	839 (6)
46°10' - 47°00'	1,033 (9)	1,673 (36)	171 (2)	223 (0)*
47°00' - 47°50'	1,019 (53)	1,556 (17)	112 (2)	139 (0)*
47°50' - border	349 (11)	2,164 (150)	390 (11)	686 (14)

(Table 2.2 — continued)

1989	Depth boundaries (m)	
	55 - 183	184 - 366
Latitudinal boundaries (°N)		
36°48' - 38°00'	3,818 (61)	513 (5)
38°00' - 40°30'	4,724 (40)	1,112 (13)
40°30' - 43°00'	4,090 (39)	1,076 (16)
43°00' - 44°40'	6,250 (40)	1,508 (14)
44°40' - 46°30'	6,014 (97)	2,118 (19)
46°30' - border	6,896 (71)	1,593 (16)

1992	Depth boundaries (m)	
	55 - 183	184 - 366
Latitudinal boundaries (°N)		
36°48' - 38°00'	3,818 (60)	513 (4)
38°00' - 40°30'	4,724 (39)	1,112 (12)
40°30' - 43°00'	4,090 (37)	1,076 (16)
43°00' - 44°40'	6,250 (41)	1,508 (16)
44°40' - 46°30'	6,014 (97)	2,118 (18)
46°30' - border	6,896 (66)	1,593 (14)

*stratum contained one or no hauls, so for estimations, it was combined with its adjacent southern stratum. Source: Gunderson and Sample 1980, Weinberg et al. 1984, Coleman 1986, 1988, Weinberg et al. 1994, 1992 survey: M. Wilkins, NMFS, Seattle, personal communication.

However, apparently for logistical reasons (see Lenarz and Adams 1980), tracklines were incorporated into the sampling design. Sampling locations were allocated randomly along tracklines which extended across depth, but trackline starting points were allocated systematically. Nevertheless, I assumed random sampling for all estimations. All sampling locations were chosen prior to the commencement of each survey.

In the 1977, 1980, and 1983 surveys, trackline starting points were separated at regular distances within each stratum, with distances prescribed by latitudinal boundaries. Starting points were allocated along the 91-m isobath in the 1977 survey, and along the 55-m isobath in the 1980 and 1983 surveys. Tracklines extended seaward and perpendicular to the isobath from which they started. In the 1986 survey, tracklines extended seaward and parallel to the seabed slope from starting points separated by two minutes of latitude along the 55-m isobath. In the 1989 and 1992 surveys, tracklines extended seaward and parallel to latitude and were separated at regular distances within each stratum, with distances prescribed by latitudinal boundaries.

Sampling locations were allocated randomly along each stratum's trackline segment. The number of sampling locations allocated along a given segment was prescribed by segment length. Hence, the sampling fraction within strata was controlled by the distance between trackline starting points and the number of sampling locations allocated to each trackline segment. During sampling, if a designated sampling location was untrawlable, a radius of one nautical mile around the original location was searched for an alternative sampling location. If a suitable location was not found within a reasonable period (about .5 h), the sampling location was abandoned.

Identification of Dominant Species

In the six surveys combined, 180 fish species representing 53 families were caught within the study area (Appendix 1). To identify fish assemblages, I wanted to

focus on species that composed most of the fish biomass, many of which are exploited commercially; and secondarily, to select a manageable number of species to study. Some species are spatially clumped and therefore may be abundant in small areas, but have a low level of abundance within the overall study area. To ensure that such species were adequately represented in the selection process, the following procedure was used to obtain a list of dominant species, which were subsequently used to identify fish assemblages: The study area was divided into eight regions using four latitudinal ($36^{\circ}48'-39^{\circ}30' \text{ N}$, $39^{\circ}30'-42^{\circ}30' \text{ N}$, $42^{\circ}30'-45^{\circ}30' \text{ N}$, and $45^{\circ}30'$ -Washington/Canada border) and two depth intervals ($<200 \text{ m}$ and $>200 \text{ m}$). The number of species that reached or exceeded given levels of mean abundance (CPUE) within any region in any year was determined. The relationship between number of species and abundance was negatively curvilinear (Fig. 2.2), and leveled off at about 26 species at a CPUE of 600 kg/km^2 . This indicated the minimal set of species to study. To include a few commercially valuable species that were not members of these 26 species (e.g. Pacific cod, Pacific halibut, and English sole), I selected those species that had a mean abundance of at least 400 kg/km^2 within any region in any year, resulting in a list of 33 species (Table 2.3). Subsequent estimates of fish biomass indicated that the 33 species composed over 95% of the total bottom-trawl fish biomass in the study area in each survey. The relative abundance of the 33 species in each haul was used to classify hauls into groups with similar species compositions, each group constituting an assemblage.

Fig. 2.2. Number of species that reached or exceeded given levels of mean abundance (CPUE) within any of eight regions in any survey year (curve was derived by fitting a simple linear regression of number of species on $\log_{10}(\text{mean CPUE})$; $r^2 = .76$).

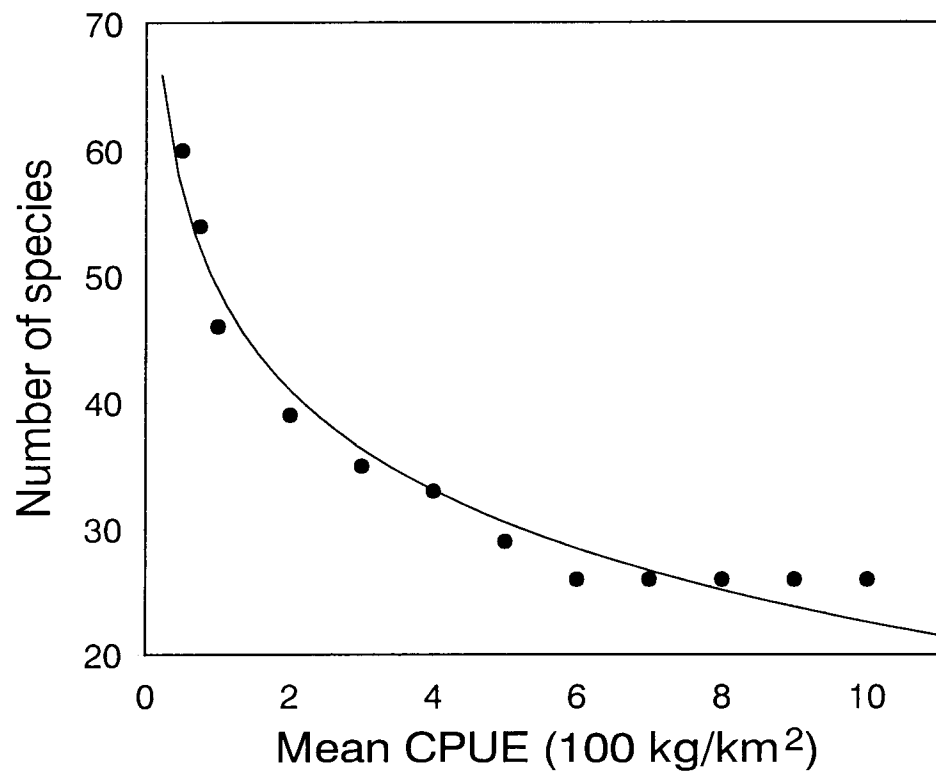


FIGURE 2.2

Table 2.3. Dominant species which were used to identify bottom-trawl fish assemblages from the NMFS 1977-1992 triennial surveys (scientific and common names follow Robins et al. 1980).

Common name	Scientific name
spiny dogfish	<i>Squalus acanthias</i>
American shad	<i>Alosa sapidissima</i>
Pacific herring	<i>Clupea harengus pallasii</i>
Pacific cod	<i>Gadus macrocephalus</i>
Pacific hake	<i>Merluccius productus</i>
walleye pollock	<i>Theragra chalcogramma</i>
jack mackerel	<i>Trachurus symmetricus</i>
white croaker	<i>Genyonemas lineatus</i>
chub mackerel	<i>Scomber japonicus</i>
Pacific ocean perch	<i>Sebastes alutus</i>
silvergray rockfish	<i>Sebastes brevispinis</i>
darkblotched rockfish	<i>Sebastes crameri</i>
splitnose rockfish	<i>Sebastes diploproa</i>
widow rockfish	<i>Sebastes entomelas</i>
yellowtail rockfish	<i>Sebastes flavidus</i>
chilipepper	<i>Sebastes goodei</i>
shortbelly rockfish	<i>Sebastes jordani</i>
bocaccio	<i>Sebastes paucispinis</i>
canary rockfish	<i>Sebastes pinniger</i>
redstripe rockfish	<i>Sebastes proriger</i>
yellowmouth rockfish	<i>Sebastes reedi</i>
bank rockfish	<i>Sebastes rufus</i>
stripetail rockfish	<i>Sebastes saxicola</i>
sharpchin rockfish	<i>Sebastes zacentrus</i>
shortspine thornyhead	<i>Sebastolobus alascanus</i>
sablefish	<i>Anoplopoma fimbria</i>
lingcod	<i>Ophiodon elongatus</i>
Pacific sanddab	<i>Citharichthys sordidus</i>
arrowtooth flounder	<i>Atheresthes stomias</i>
rex sole	<i>Glyptocephalus zachirus</i>
Pacific halibut	<i>Hippoglossus stenolepis</i>
Dover sole	<i>Microstomus pacificus</i>
English sole	<i>Parophrys vetulus</i>

Identification of Fish Assemblages

Hauls from all six surveys combined were classified into groups with similar species compositions primarily by using hierarchical agglomerative cluster analysis with Ward's minimum variance fusion strategy (SAS Institute Inc. 1988). In striving for adequate representation of species composition at a given sampling location, only those hauls that contained at least 50 specimens of the dominant species combined were used. The 33 classifying variables for each haul were the weight of each of the 33 species relative to the weight of the 33 species combined. Each variable was transformed by $\ln(1 + x)$ to improve distance measures, because species-catch-weights were often non-normally distributed among hauls; they were often highly right skewed and contained a moderate number of zero values, which is typical of many fisheries survey data (Pennington 1983, Smith 1988, 1990). Variables were standardized to a mean of zero and a standard deviation of one to de-emphasize a few of the highly abundant species.

Agglomerative clustering begins with each haul in its own cluster and fuses two clusters at a time until all observations compose a single cluster. Ward's minimum variance fusion strategy combines clusters that minimize within-cluster-sum-of-squares at each step of the clustering process. Because minimum variance clustering weights within-cluster-sum-of-squares by cluster size, as a cluster grows larger during the clustering process, its dissimilarity with other clusters increases, thereby reducing the often undesirable effect of chaining (Orlóci 1978). Chaining is the sequential fusion of single entities with a pre-existing larger cluster.

A difficulty with cluster analysis is deciding on the number of clusters present in the data (Everitt 1980). At each step of the minimum variance clustering, an estimate of the proportion of the total variance that is explained by any specific number of clusters (R^2) can be calculated. In the present study, R^2 can be interpreted as an estimate of the proportion of the total variation in species composition among hauls that is explained by a particular number of clusters. Subsequent to the clustering process, a plot of R^2 on number-of-clusters in each step of the process (Fig. 2.3) was used as an aid indetermining a starting point for identifying the number of clusters that may be present in the data. The R^2 values leveled off at about .80, and the 52 clusters associated with this value were selected for further scrutiny.

For practical interpretations, an assemblage was defined as a distinct composition of species that occurred over a sufficiently large area in any given year. In keeping with this definition, some of the 52 clusters that were identified from the cluster analysis were fused with their adjacent cluster in the cluster dendrogram (Fig. 2.4) if the cluster: (1) did not appear to be distinct in species composition (a qualitative interpretation); or (2) did not contain at least 15 hauls from any given survey. The second criterion was used to ensure that the hauls of an identified cluster occurred over a “sufficiently large area”.

As a minor refinement to the haul assignments, discriminant analysis was used to reclassify potentially outlying hauls stemming from the irreversibility of assignments at successive steps in the clustering process (see Sneath and Sokal 1973, Orlóci 1978). In the reclassification procedure, the clusters were the “known” groups and the relative

Fig. 2.3. Amount of total variation in species composition explained (R^2) by successive agglomeration of clusters during the clustering process that was used to identify bottom-trawl assemblages.

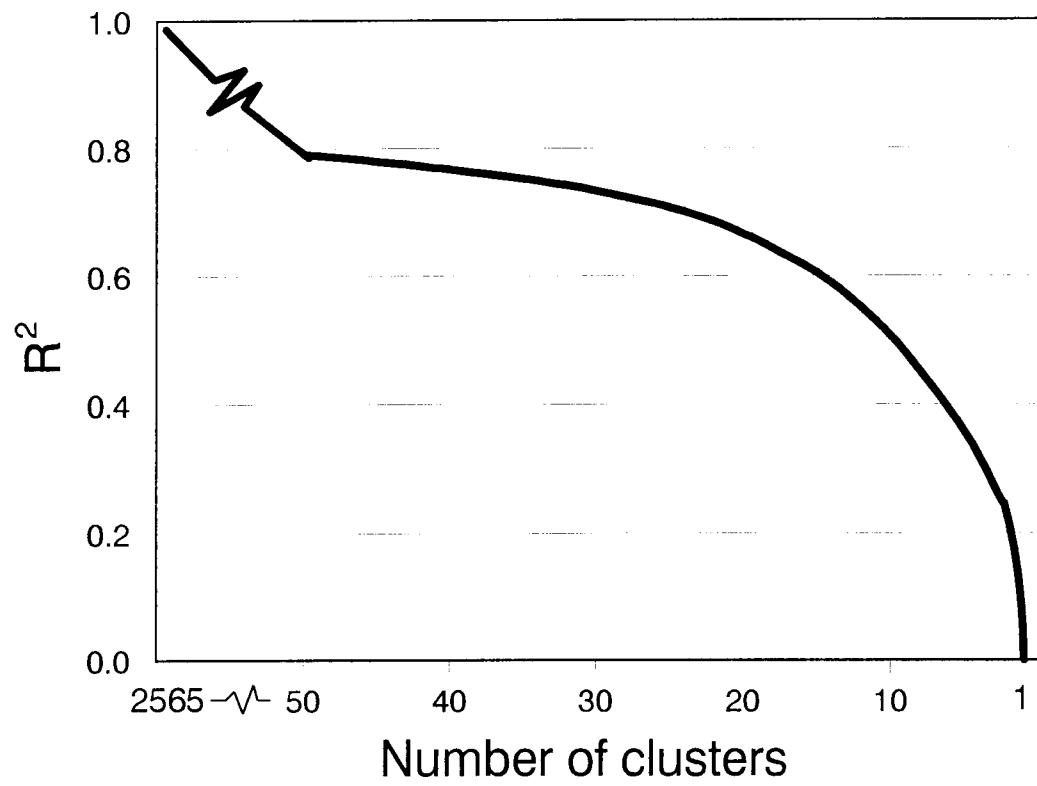


FIGURE 2.3

Fig. 2.4. Partial dendrogram resulting from clustering hauls based on the relative abundance of 33 dominant species in the NMFS triennial surveys from 1977 to 1992. Groups of hauls with similar species compositions constitute an assemblage.

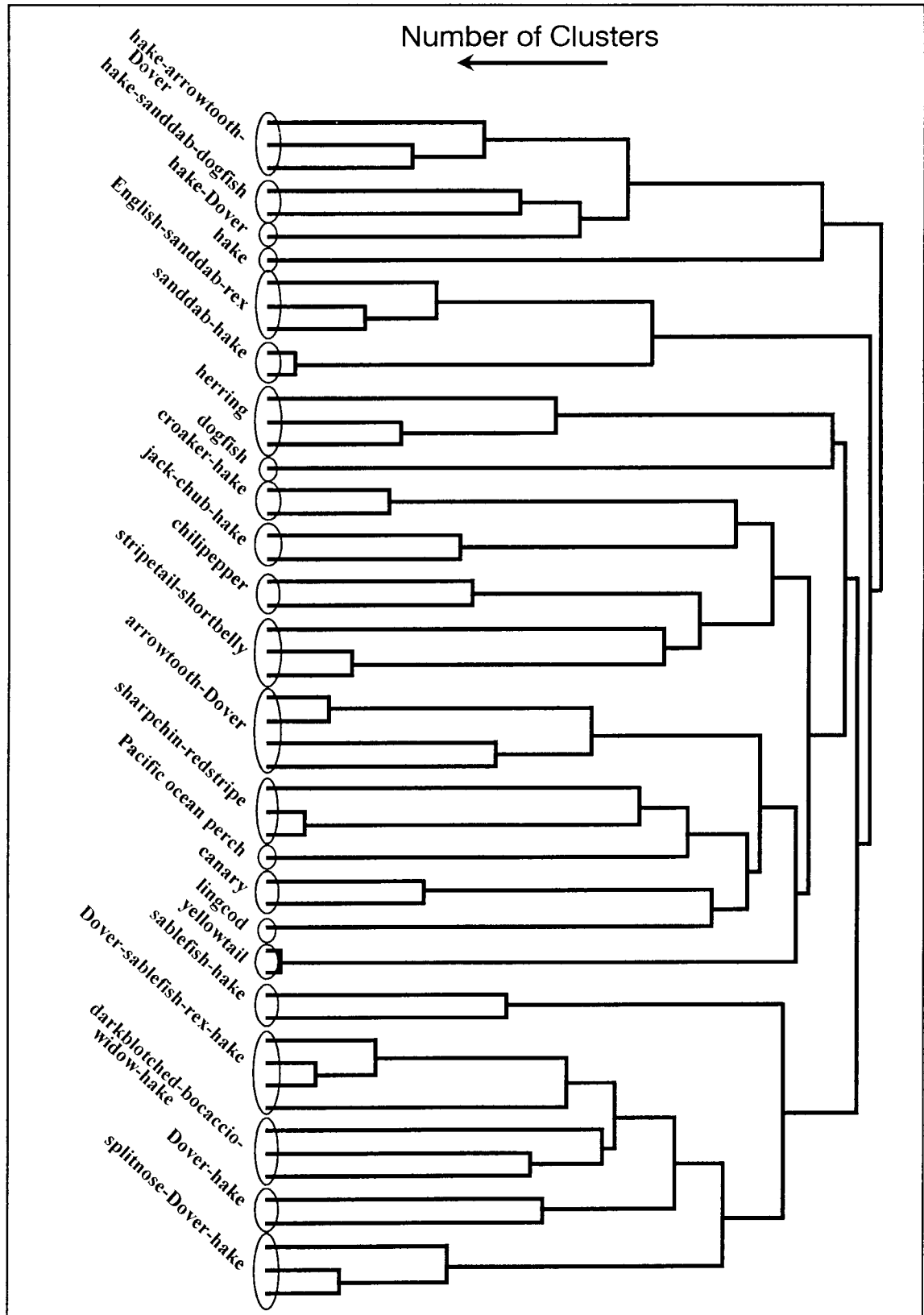


FIGURE 2.4

abundance of the 33 dominant species were the discriminating variables. Generalized distance functions, with prior probabilities of the group memberships set equal, were used for the reclassification. Assumptions for discriminant analysis were assessed using univariate descriptors of canonical scores from the first canonical function, and indicated that although the data set was probably not multivariate normal, the assumption of multivariate normality was not severely violated, and thus the reclassification procedure was considered productive. The classification function derived from the first run of the analysis was used to reclassify hauls, and a second analysis on the reclassified data was performed to obtain an apparent error rate of classification to approximate the performance of the classification functions. The reclassification procedure resulted in reclassifying approximately 10% of the hauls, with a final apparent error rate of classification of 5%.

The composition of species reflected from the hauls within the final clusters constituted the assemblages. The multivariate standard deviation of observations-within-cluster was calculated to obtain a measure of the relative variation in species composition among hauls within each assemblage (“root-mean-square standard deviation”, FASTCLUS, SAS Institute Inc. 1988; subsequently referred herein as the multivariate within-assemblage standard deviation). The univariate sample mean, coefficient of variation, and interquartile range of the relative abundance of each species among hauls within each assemblage were used to describe how assemblages differed and provide a measure of how “tightly” hauls were grouped on a species-by-species basis. An R^2 value (squared multiple correlation) was calculated to assess the amount of total variation in

species composition among hauls that was accounted for by the assemblages (Ward's minimum variance clustering algorithm with input values from FASTCLUS, SAS Institute Inc. 1988).

Geographic Range and Incidence of Assemblages

The geographic range of each assemblage for the 1980 to 1992 surveys combined was ascertained by plotting the 5th, 25th, 50th, 75th, and 95th percentiles of the estimated incidence of each assemblage across latitude and depth. The 1977 survey was not included, because it covered a slightly deeper area than subsequent surveys. To account for unequal sampling densities among strata, each observation was assigned a frequency equal to the inverse of its stratum's sampling fraction.

An assemblage's persistence is indicated by its continued occurrence over survey years. However, a more informative indicator of persistence is a measure of the assemblage's spatial extent, or incidence, over time. Therefore, I estimated the total incidence of each assemblage in each survey, and I made intersurvey statistical comparisons of incidence between smaller regions — contrasting the regions north and south of 42° N, and the regions of the continental shelf (approximated by areas <200 m deep) and upper slope (>200 m). Within-stratum comparisons across surveys were not possible, because the geographic boundaries of sampling strata differed across most surveys. Incidence was estimated using the estimator of the population proportion for stratified random sampling (Scheaffer et al. 1990). In addition to comparing regional

incidence, I mapped the assemblages in each survey year and visually compared their locations. Assemblage boundaries were drawn around single haul positions, or around groups of two or more adjacent positions belonging to the same assemblage.

Differentiating Assemblages Across Environmental Variables

Discriminant analysis was used to examine the level of assemblage segregation across five environmental variables: latitude, depth, surface and bottom water temperatures, and surficial substrate. Because bottom temperature during the 1977 survey was measured unsatisfactorily (Dark and Wilkins 1994), and substrate data were obtained for the area north of 42° N only, the analysis was restricted to data from the northern region of the 1980-1992 surveys.

Latitude and depth were recorded for every haul. Surface temperature was measured by bucket thermometer at 66% of the haul locations in 1980 and at more than 95% of the haul locations in the remaining four surveys. Bottom temperature was measured with either an expendable bathythermograph, a recording device attached to the headrope, a CTD, or a combination of these methods. Bottom temperature was measured less consistently than surface temperature; at only 9% of the haul locations in 1983, but 89% of the haul locations in 1992. Surficial substrate at each haul location was categorized into “mud”, “sand”, “shell and gravel”, or “rock” using a digitized map of the distribution of offshore deposits on the continental shelf and upper slope off Oregon and

Washington (Moore and Luken 1979). Substrate categories were treated as a gradient of substrate coarseness and coded 1, 2, 3, and 4 for analysis purposes.

Although discriminant analysis requires only that there are at least two observations per group and that the total number of observations is at least two more than the number of discriminating variables, enough observations per group are needed to ensure that means and dispersions within each group are estimated with sufficient precision. Within-group sample sizes of approximately three times the number of discriminating variables are suggested (Williams and Titus 1988), which in the present study, requires 15 observations per group. Two groups, the striptail-shortbelly and splitnose-Dover-hake assemblages, contained fewer than 15 observations in the northern region ($>42^{\circ}$ N). Rather than reducing the number of variables in the analysis to meet the minimum within-group sample size requirement, these assemblages were excluded from the analysis. Furthermore, the croaker-hake and chilipepper assemblages did not occur in the northern region, so they were not included in the analysis. The omission of these assemblages, together with the constraint of using only those observations that contained measurements for all five environmental variables resulted in an analysis of nineteen assemblages comprising 1,525 hauls from the northern region of the 1980-1992 surveys.

Discriminant analysis assumes that groups have equal dispersions and that the data structure is multivariate normal. These assumptions were assessed using univariate descriptors of each discriminating variable and within-group canonical scores derived from each canonical function. Tests for homogeneity of variance are sensitive to

normality and within-assemblage residuals of the environmental variables indicated that the data structure was probably not multivariate normal. Although latitude and surface temperature residuals were approximately normally distributed, residuals for depth were heavy tailed; and residuals for bottom temperature and substrate were skewed, particularly for substrate. A large amount of skewness in substrate residuals was due to an imbalance in the number of observations within each substrate (estimates of the proportional abundance of each substrate in the northern region, calculated in the manner that assemblage incidence estimates were calculated, are: mud = 39%, sand = 48%, shell-gravel = 6%, and rock = 8%). A log-transform of the substrate variable made very little difference in the results of the analysis, so the untransformed substrate variable was used. Plots of canonical scores within each group for each of the first three canonical functions indicated that the assumption of multivariate normality was not as severely violated as univariate diagnostics indicated. In summary, assumptions for discriminant analysis were not met entirely, so the analysis was regarded as suboptimal, but useful for exploratory purposes. Canonical functions were derived to describe the discriminating power of the five environmental variables, and generalized distance functions were used for classification with group memberships assigned equal prior probabilities.

Results

Variation in Species Composition Between and Within Assemblages

Twenty-three assemblages were identified (Fig. 2.4, Table 2.4), and named by those species with a mean within-assemblage relative biomass of at least 10%. The assemblages accounted for about 70% of the total variation in species composition among hauls from all surveys combined. Four of the 23 assemblages were dominated by Pacific hake (Table 2.4). Of the remaining 19 assemblages, eight were dominated by rockfish species and five by flatfish species.

The relative amount of variation in species composition among hauls within assemblages is indicated by the multivariate within-assemblage standard deviation (SD_m , Table 2.4), which is analogous to the sample standard deviation in a univariate situation. The hake assemblage had far less variation in species composition among hauls ($SD_m = .016$) than the other assemblages, which have standard deviations ranging from .032 for the hake-Dover assemblage to .066 for the darkblotched-bocaccio-widow-hake assemblage. The sharpchin-redstripe and stripetail-shortbelly assemblages each were derived from fusing two clusters that were distinct qualitatively (criterion 1 was met in Methods Section above; see Fig. 2.4), but did not occur over a sufficiently large area (criterion 2 was not met), and therefore, they have relatively high standard deviations (.062 and .061).

Table 2.4. Bottom-trawl fish assemblages identified from the NMFS 1977 to 1992 triennial surveys. Species with a mean relative biomass (\bar{x}) of at least 5% among hauls within a given assemblage are listed. SD_m = multivariate within-assemblage standard deviation; n = number of hauls classified into a given assemblage; CV_{SD} = univariate within-assemblage standard deviation / mean relative biomass; IQR = interquartile range of relative biomass.

Assemblage	SD_m	Species	n	\bar{x}	CV_{SD}	IQR
hake	.016	Pacific hake	409	.87	.10	.80 - .95
hake-Dover	.032	Pacific hake	227	.55	.20	.47 - .64
		Dover sole		.10	.77	.04 - .15
		sablefish		.06	1.12	.01 - .09
		rex sole		.05	1.07	.01 - .06
hake-sanddab-dogfish	.038	Pacific hake	148	.45	.29	.35 - .57
		Pacific sanddab		.12	.78	.04 - .19
		spiny dogfish		.10	1.20	.00 - .19
		English sole		.09	.89	.02 - .15
		rex sole		.07	1.00	.02 - .10
Dover-sablefish-rex-hake	.045	Dover sole	175	.21	.45	.14 - .27
		sablefish		.15	.74	.05 - .23
		rex sole		.11	.97	.03 - .16
		Pacific hake		.10	.87	.03 - .14
		arrowtooth flounder		.07	.95	.01 - .12
		shortspine thornyhead		.06	1.19	.01 - .10
		darkblotched rockfish		.05	1.34	.00 - .08
English-sanddab-rex	.043	English sole	133	.32	.46	.22 - .38
		Pacific sanddab		.26	.52	.15 - .34
		rex sole		.13	.80	.06 - .18
		spiny dogfish		.06	1.58	.00 - .06
		Pacific hake		.06	1.40	.00 - .09
Dover-hake	.036	Dover sole	170	.46	.27	.36 - .52
		Pacific hake		.17	.78	.04 - .29
		rex sole		.09	.86	.03 - .13
		sablefish		.07	.94	.02 - .11
sablefish-hake	.038	sablefish	105	.55	.33	.41 - .64
		Pacific hake		.12	1.07	.02 - .20
		Dover sole		.08	.93	.02 - .10
		arrowtooth flounder		.05	1.58	.00 - .06

(Table 2.4 — continued)

arrowtooth-Dover	.046	arrowtooth flounder	151	.39	.47	.27 - .50
		Dover sole		.10	.87	.03 - .15
		spiny dogfish		.09	1.35	.00 - .14
		sablefish		.07	1.02	.01 - .11
		Pacific hake		.06	1.38	.00 - .09
		rex sole		.05	1.22	.01 - .06
herring	.046	Pacific herring	84	.60	.40	.38 - .82
		spiny dogfish		.07	1.87	.00 - .08
		Pacific sanddab		.06	1.52	.00 - .08
		Pacific hake		.06	1.66	.00 - .10
		English sole		.05	1.70	.00 - .05
sanddab-hake	.034	Pacific sanddab	82	.62	.24	.49 - .71
		Pacific hake		.10	1.28	.00 - .16
		English sole		.08	.76	.03 - .13
		rex sole		.06	.94	.02 - .08
hake-arrowtooth-Dover	.050	Pacific hake	102	.26	.61	.12 - .34
		arrowtooth flounder		.10	.88	.02 - .16
		Dover sole		.10	.97	.02 - .16
		yellowtail rockfish		.08	1.26	.00 - .16
		spiny dogfish		.08	1.21	.02 - .12
		walleye pollock		.08	1.67	.00 - .12
		sablefish		.05	1.26	.00 - .08
sharpchin-redstripe	.062	sharpchin rockfish	67	.28	.97	.04 - .43
		redstripe rockfish		.27	1.03	.01 - .47
		canary rockfish		.05	1.71	.00 - .05
yellowtail	.042	yellowtail rockfish	74	.59	.32	.44 - .75
		Pacific hake		.09	1.48	.00 - .12
stripetail-shortbelly	.061	stripetail rockfish	82	.36	.61	.22 - .52
		shortbelly rockfish		.18	1.71	.00 - .21
		Pacific hake		.09	1.30	.00 - .15
		chilipepper		.09	1.24	.00 - .15
		Dover sole		.07	1.20	.01 - .09
dogfish	.035	spiny dogfish	86	.66	.24	.54 - .77
		Pacific hake		.05	1.78	.00 - .06

(Table 2.4 — continued)

splitnose-Dover-hake	.049	splitnose rockfish	75	.43	.46	.28 - .56
		Dover sole		.15	.89	.03 - .23
		Pacific hake		.11	1.28	.01 - .16
		sablefish		.06	1.42	.00 - .10
		darkblotched rockfish		.06	1.29	.00 - .09
		bank rockfish		.05	2.77	.00 - .00
darkblotched-bocaccio-widow-hake	.066	darkblotched rockfish	62	.22	1.13	.00 - .38
		bocaccio		.13	1.52	.00 - .25
		widow rockfish		.12	1.96	.00 - .03
		Pacific hake		.10	1.23	.01 - .15
		Dover sole		.07	1.11	.01 - .10
		sablefish		.06	1.35	.00 - .08
canary	.045	canary rockfish	64	.53	.41	.34 - .73
		Pacific hake		.07	1.55	.00 - .10
		lingcod		.06	1.35	.00 - .08
lingcod	.048	lingcod	63	.41	.40	.29 - .47
		spiny dogfish		.07	1.47	.00 - .10
		arrowtooth flounder		.07	1.60	.00 - .11
		English sole		.06	1.40	.00 - .12
		Dover sole		.06	1.35	.00 - .08
		Pacific sanddab		.06	1.67	.00 - .09
		Pacific hake		.05	1.75	.00 - .05
		rex sole		.05	1.16	.00 - .07
croaker-hake	.040	white croaker	40	.59	.35	.41 - .76
		Pacific hake		.13	1.09	.03 - .20
		Pacific sanddab		.07	1.38	.01 - .08
		English sole		.06	1.10	.01 - .08
jack-chub-hake	.050	jack mackerel	49	.54	.44	.38 - .72
		chub mackerel		.15	1.29	.00 - .27
		Pacific hake		.12	1.20	.00 - .18
		Pacific sanddab		.05	1.43	.00 - .08
chilipepper	.041	chilipepper	49	.59	.36	.39 - .76
		Pacific hake		.09	1.48	.01 - .13
		stripetail rockfish		.06	1.44	.00 - .12
		Dover sole		.05	1.20	.01 - .07

(Table 2.4 — continued)

Pacific ocean perch	.041	Pacific ocean perch	68	.46	.36	.33 - .59
		Dover sole		.09	.96	.02 - .12
		sablefish		.07	1.28	.01 - .10
		Pacific hake		.07	1.45	.00 - .10
		arrowtooth flounder		.06	.97	.01 - .08
		sharpchin rockfish		.05	1.58	.00 - .08

The mean relative abundance of the single most dominant species in each assemblage (Table 2.4) is similar to a Berger-Parker index of dominance for each assemblage (described in Magurran 1988), which is a measure of within-assemblage diversity where higher dominance indicates lower diversity. The hake assemblage had high species dominance ($\bar{x} = .87$). Other assemblages with moderately high species dominance (\bar{x} greater than about .60) were the herring, sanddab-hake, yellowtail, dogfish, croaker-hake, and chilipepper assemblages. Assemblages with low species dominance (\bar{x} less than about .35) were the Dover-sablefish-rex-hake, English-sanddab-rex, hake-arrowtooth-Dover, sharpchin-redstripe, stripetail-shortbelly, and darkblotched-boccacio-widow-hake assemblages.

Generally, deviations about the mean relative abundance for a given species within an assemblage (Table 2.4) were normally distributed for species with a mean relative abundance of about 10% or greater. However, for species with lower relative abundances, the frequency distribution of observations within an assemblage was right skewed, and was highly skewed in some cases, primarily because of the absence of such species in a large number of hauls. For example, in the English-sanddab-rex assemblage,

the relative abundance of spiny dogfish has a mean that is equal to the 75th percentile, and the mean relative abundance of widow rockfish in the darkblotched-bocaccio-widow-hake assemblage was well above the 75th percentile (Table 2.4). Note also that the within-assemblage relative abundance of some species, even those used to name the assemblage, can be quite variable.

Geographic Range and Incidence of Assemblages

Over the last five surveys combined, the geographic range of assemblages overlapped considerably across latitude and depth (Fig. 2.5), bearing in mind that on a local scale, their range may have been much more restrictive. Most assemblages occurred primarily within the northern region of the study area ($>42^{\circ}$ N, Fig. 2.5a) and over the continental shelf (approximated by areas <200 m deep, Fig. 2.5b), probably partly because these regions form a disproportionately greater portion of the study area. The northern and continental shelf regions compose about 67 and 81% of the study area, respectively (estimates were derived similar to the derivation of assemblage incidence estimates).

The stripetail-shortbelly, croaker-hake, and chilipepper assemblages occurred primarily to the south ($<42^{\circ}$ N, Fig. 4a). The hake-sanddab-dogfish, English-sanddab-rex, herring, sanddab-hake, croaker-hake, and jack-chub-hake assemblages occurred primarily over the shallow portion of the continental shelf (<125 m), whereas the splitnose-Dover-hake and Pacific ocean perch assemblages occurred primarily over the

Fig. 2.5. The 5th, 25th, 50th, 75th, and 95th percentiles of the estimated incidence of each assemblage for the last five surveys combined (a) across latitude and (b) across depth.

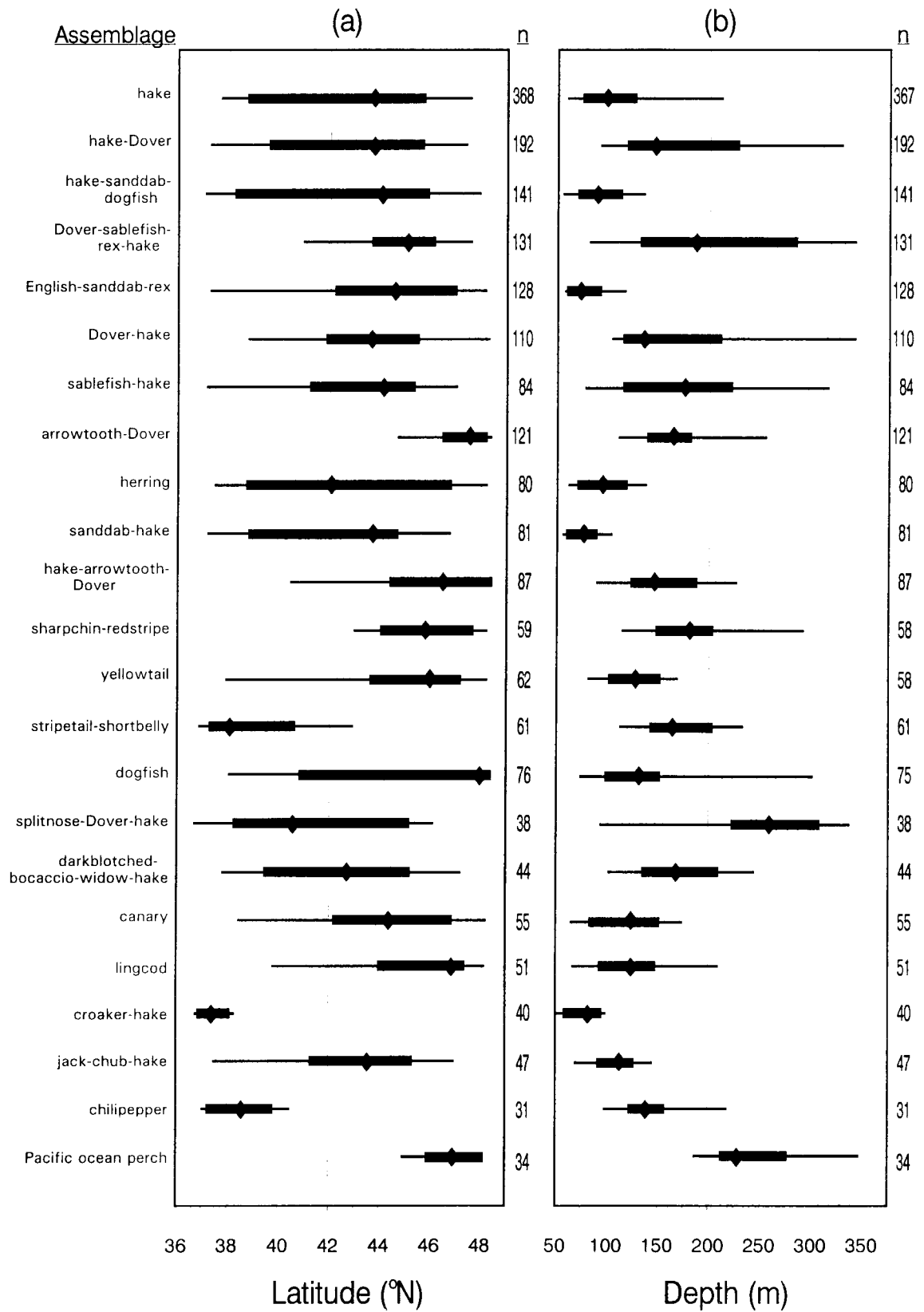


FIGURE 2.5

upper continental slope (>200 m, Fig. 4b). Some assemblages were distributed very widely across latitude or depth. Assemblages were distributed much more widely across latitude than comparable distances across depth, indicating the potential existence of sharper environmental gradients across depth than latitude.

Most assemblages were encountered over the entire study period (Table 2.5), though many occurred relatively infrequently. The croaker-hake and jack-chub-hake assemblages were not encountered in 1977 and 1980, respectively. The hake assemblage occurred more frequently than any other assemblage. Because the sampling unit, for statistical analyses, is a unit of area, the estimated incidence of an assemblage can be interpreted as an estimate of the proportion of the study area that was occupied by the assemblage. The four hake-dominated assemblages together occurred, on average across the 1980 to 1992 surveys, over about 39% of the total study area.

The hake assemblage had about twice the incidence within the southern region in 1980 and 1986 than in the same region of other years (Fig. 2.6). These differences are not apparent from incidence estimates for the entire study area (Table 2.5). The hake assemblage had a higher incidence in the south than in the north in 1980 and 1986, but in 1989 and 1992, the reverse is indicated. The assemblage occurred over the continental shelf more than over the upper slope from 1977 to 1986 (Fig. 2.7), although there is no evidence that this occurred in 1989 and 1992 (also see Fig. 2.8).

Table 2.5. Estimated incidence (\hat{I}) of bottom-trawl fish assemblages identified from the NMFS 1977 to 1992 triennial surveys. Total sample size for each year is 444, 322, 470, 501, 418, and 410; $\pm = 2 \times$ standard error. Those incidence estimates whose $\pm 2SE$ range did not include the 1980-92 mean are in bold.

Assemblage		Year						1980-92 \bar{x}
		*1977	1980	1983	1986	1989	1992	
hake	\hat{I}	.15	.25	.15	.22	.18	.18	.20
	\pm	.04	.06	.04	.04	.04	.04	
hake-Dover	\hat{I}	.09	.03	.10	.08	.12	.10	.09
	\pm	.03	.02	.03	.03	.03	.03	
hake-sanddab-dogfish	\hat{I}	.02	.02	.08	.06	.08	.10	.07
	\pm	.02	.02	.03	.03	.03	.03	
Dover-sablefish- rex-hake	\hat{I}	.09	.06	.09	.10	.06	.03	.07
	\pm	.03	.03	.03	.03	.02	.02	
English-sanddab-rex	\hat{I}	.02	.05	.05	.05	.07	.08	.06
	\pm	.02	.03	.03	.02	.03	.03	
Dover-hake	\hat{I}	.10	.06	.05	.09	.03	.02	.05
	\pm	.03	.02	.02	.03	.02	.02	
sablefish-hake	\hat{I}	.05	.08	.04	.05	.03	.04	.05
	\pm	.02	.04	.02	.02	.02	.02	
arrowtooth-Dover	\hat{I}	.07	.03	.02	.06	.06	.01	.04
	\pm	.02	.02	.01	.02	.02	.01	
herring	\hat{I}	.01	.03	.02	.00	.04	.12	.04
	\pm	.01	.02	.01	.01	.02	.03	
sanddab-hake	\hat{I}	.00	.01	.03	.03	.07	.05	.04
	\pm	.00	.01	.02	.02	.02	.02	
hake-arrowtooth- Dover	\hat{I}	.04	.02	.05	.03	.03	.02	.03
	\pm	.02	.02	.02	.01	.02	.02	
sharpchin-redstripe	\hat{I}	.02	.03	.03	.02	.02	.03	.03
	\pm	.02	.02	.01	.01	.01	.02	

(Table 2.5 — continued)

yellowtail	\hat{I}	.04	.07	.03	.03	.02	.01	.03
	\pm	.03	.03	.02	.02	.01	.01	
stripetail-shortbelly	\hat{I}	.03	.05	.03	.03	.02	.04	.03
	\pm	.02	.03	.02	.02	.01	.02	
dogfish	\hat{I}	.03	.03	.06	.01	.03	.03	.03
	\pm	.02	.02	.02	.01	.02	.02	
splitnose-Dover-hake	\hat{I}	.04	.04	.01	.03	.01	.01	.02
	\pm	.01	.02	.01	.02	.01	.01	
darkblotched-bocaccio- widow-hake	\hat{I}	.04	.04	.03	.02	.01	.01	.02
	\pm	.02	.03	.01	.02	.01	.01	
canary	\hat{I}	.03	.02	.05	.02	.01	.00	.02
	\pm	.02	.02	.02	.01	.01	.01	
lingcod	\hat{I}	.05	.03	.02	.02	.01	.01	.02
	\pm	.03	.02	.01	.01	.01	.01	
croaker-hake	\hat{I}	**	.01	.01	.01	.01	.06	.02
	\pm	**	.01	.01	.01	.01	.02	
jack-chub-hake	\hat{I}	.01	**	.01	.01	.06	.04	.02
	\pm	.01	**	.01	.01	.02	.02	
chilipepper	\hat{I}	.03	.02	.02	.01	.03	.01	.02
	\pm	.02	.02	.02	.01	.02	.01	
Pacific ocean perch	\hat{I}	.05	.02	.02	.01	.01	.01	.01
	\pm	.02	.02	.01	.01	.01	.01	

*1977 covered a slightly deeper depth range than subsequent surveys.

**assemblage was not encountered.

Fig. 2.6. Estimates of regional incidence ($\pm 2SE$) from 1977 to 1992 for assemblages that showed significant differences in incidence between the regions north (N) and south (S) of 42° N.

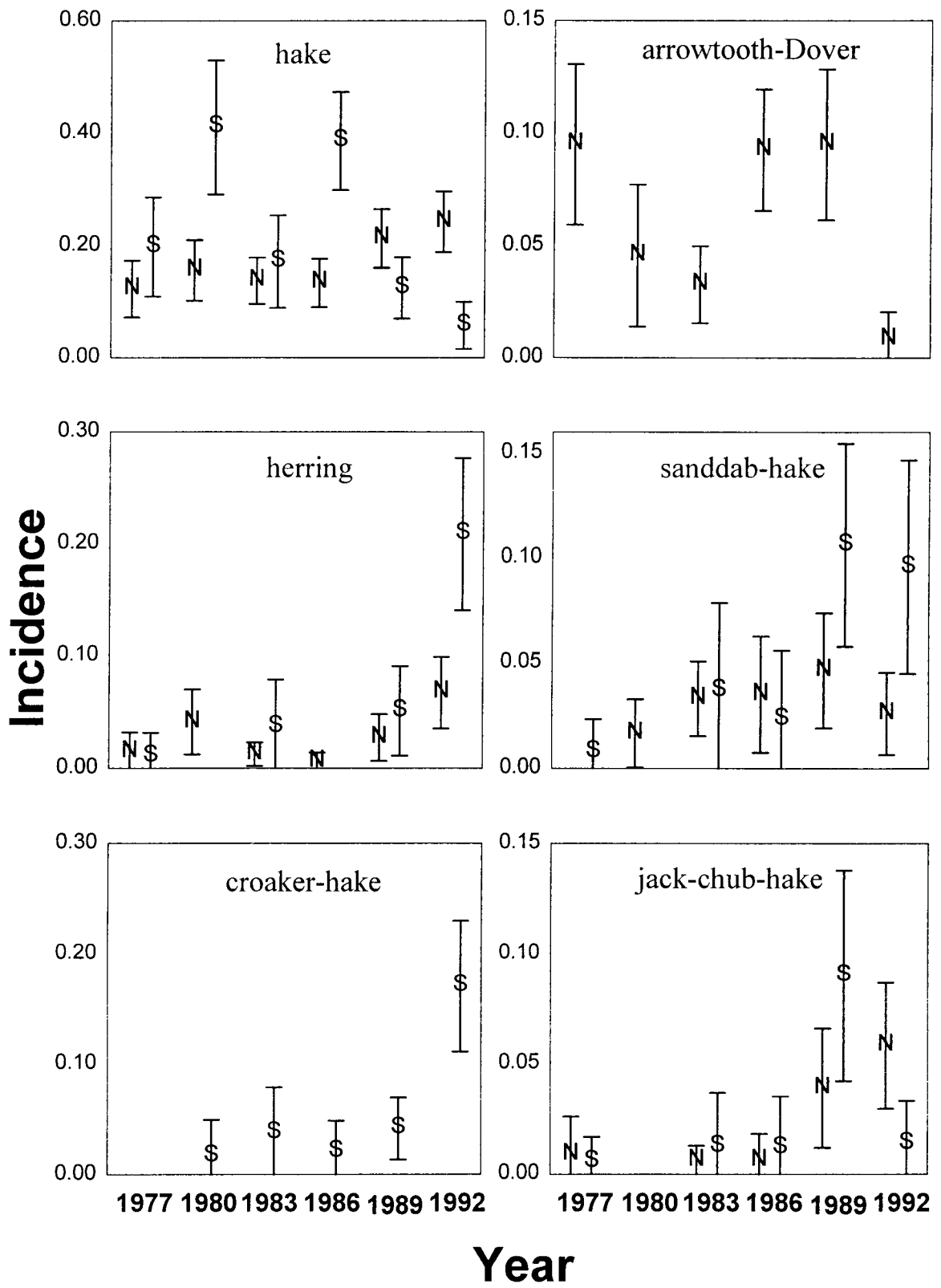


FIGURE 2.6

Fig. 2.7. Estimates of regional incidence ($\pm 2SE$) from 1977 to 1992 for assemblages that showed significant differences in incidence between the continental shelf (H) and upper slope (L).

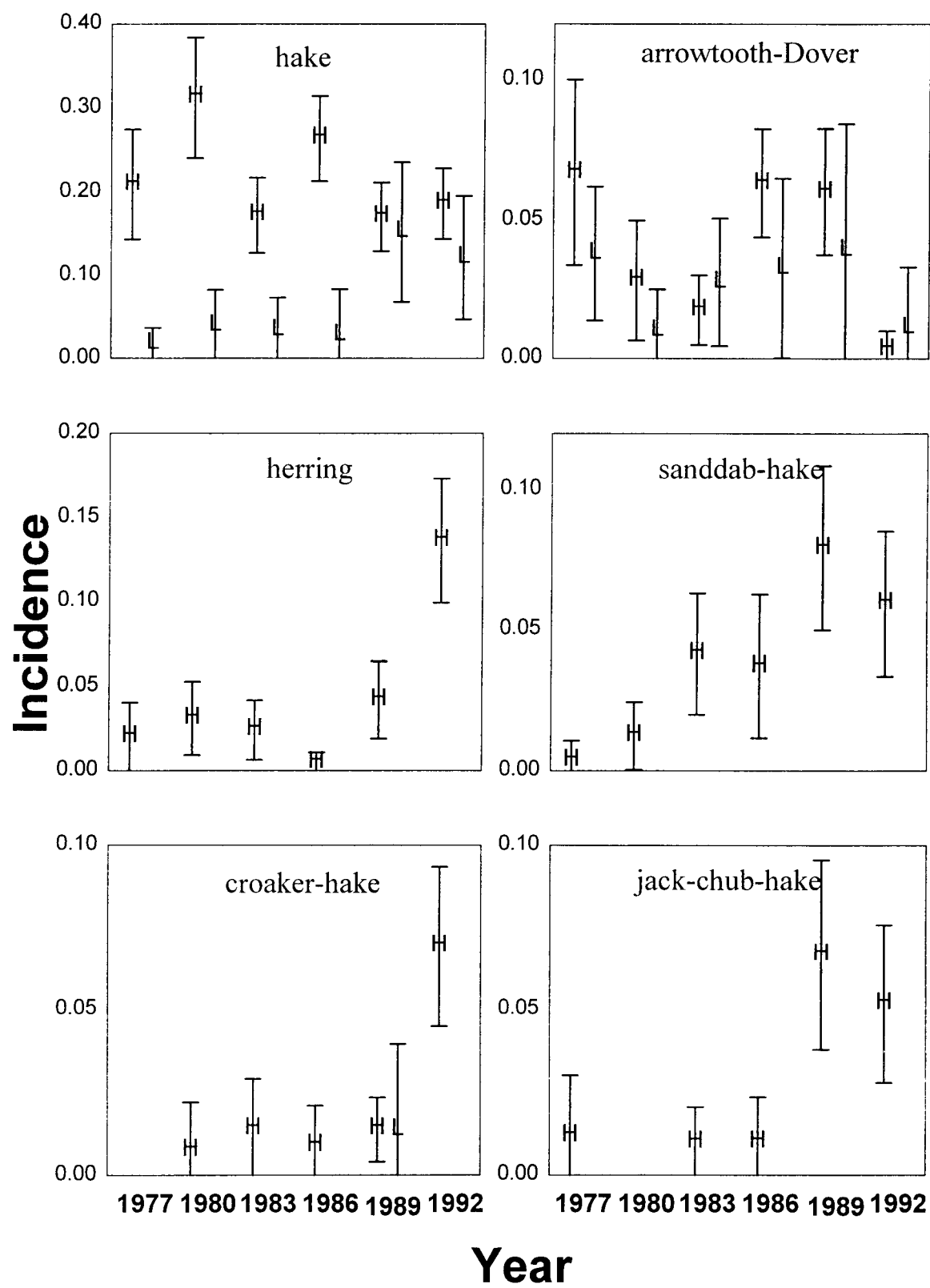


FIGURE 2.7

Fig. 2.8. Location of assemblages within the study area from 1977 to 1992 (50- and 250-m isobaths are shown).

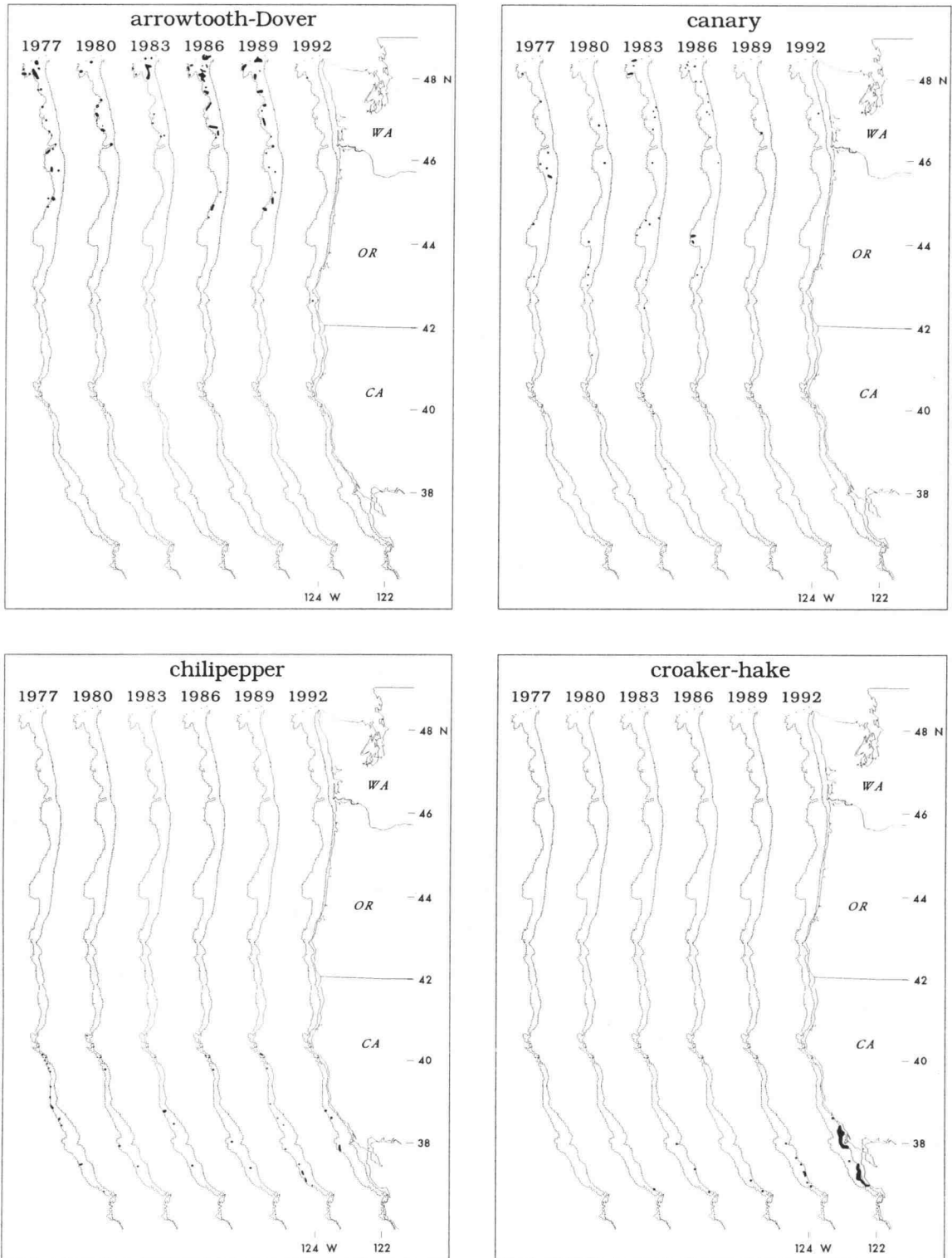


FIGURE 2.8

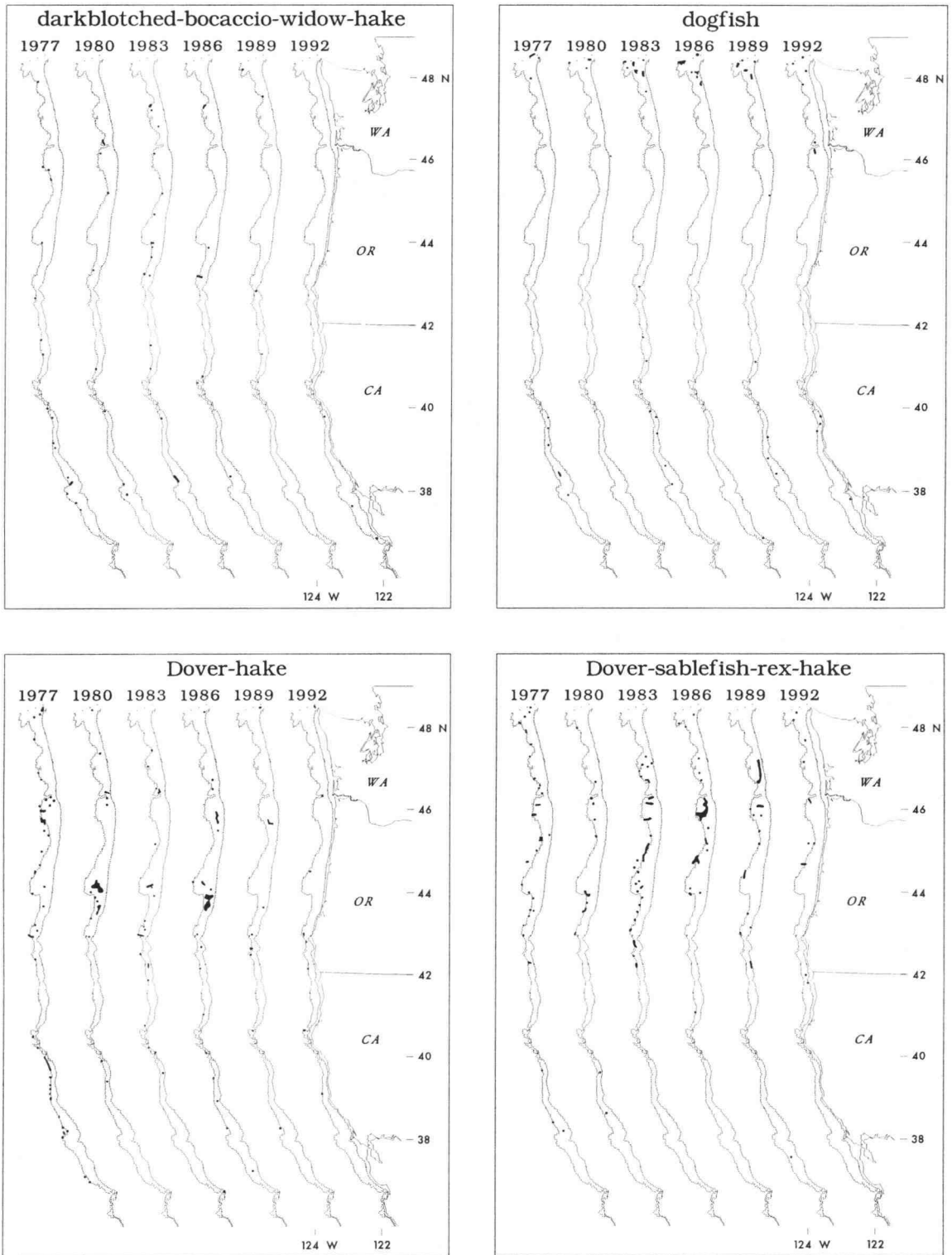


FIGURE 2.8 (Continued)

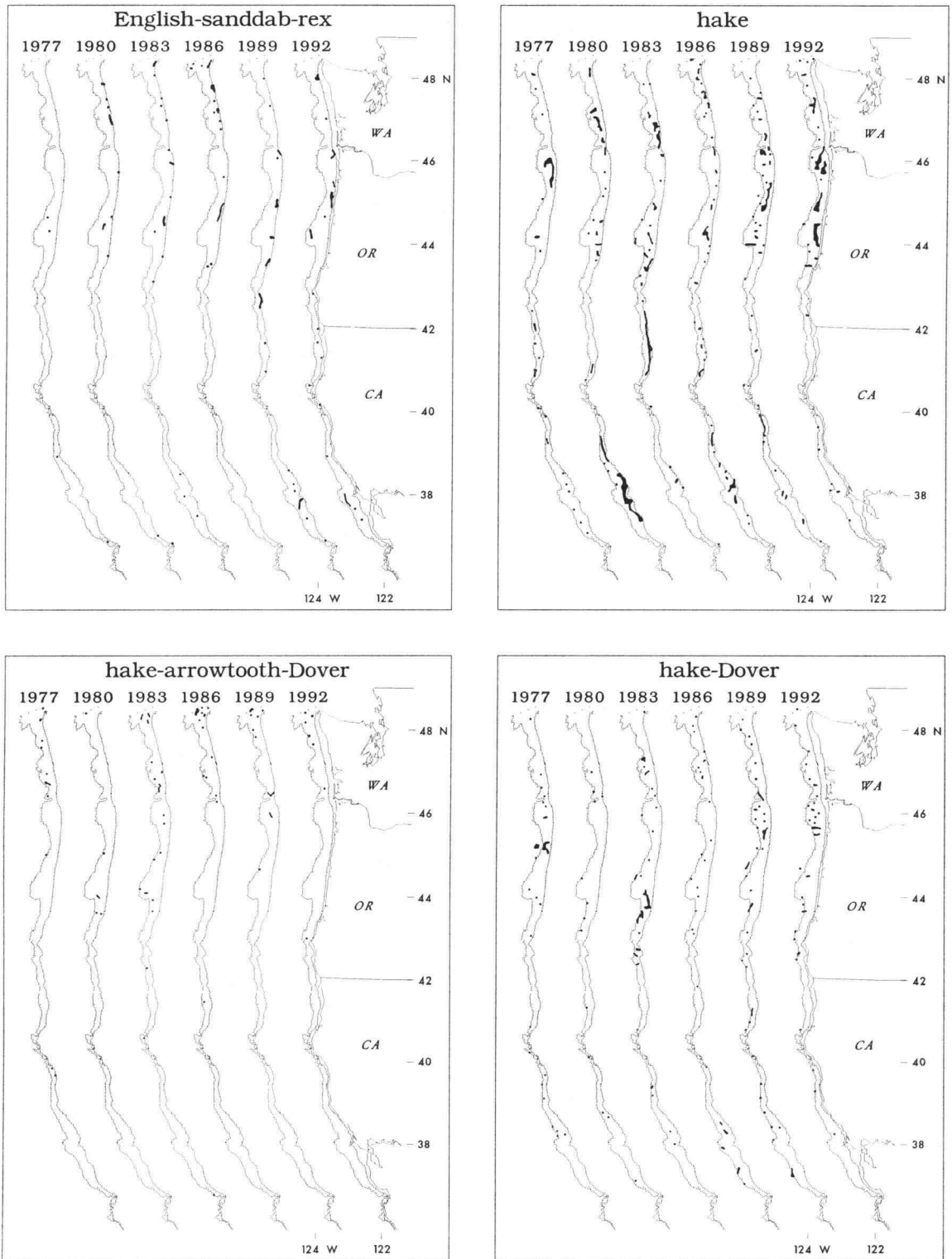


FIGURE 2.8 (Continued)

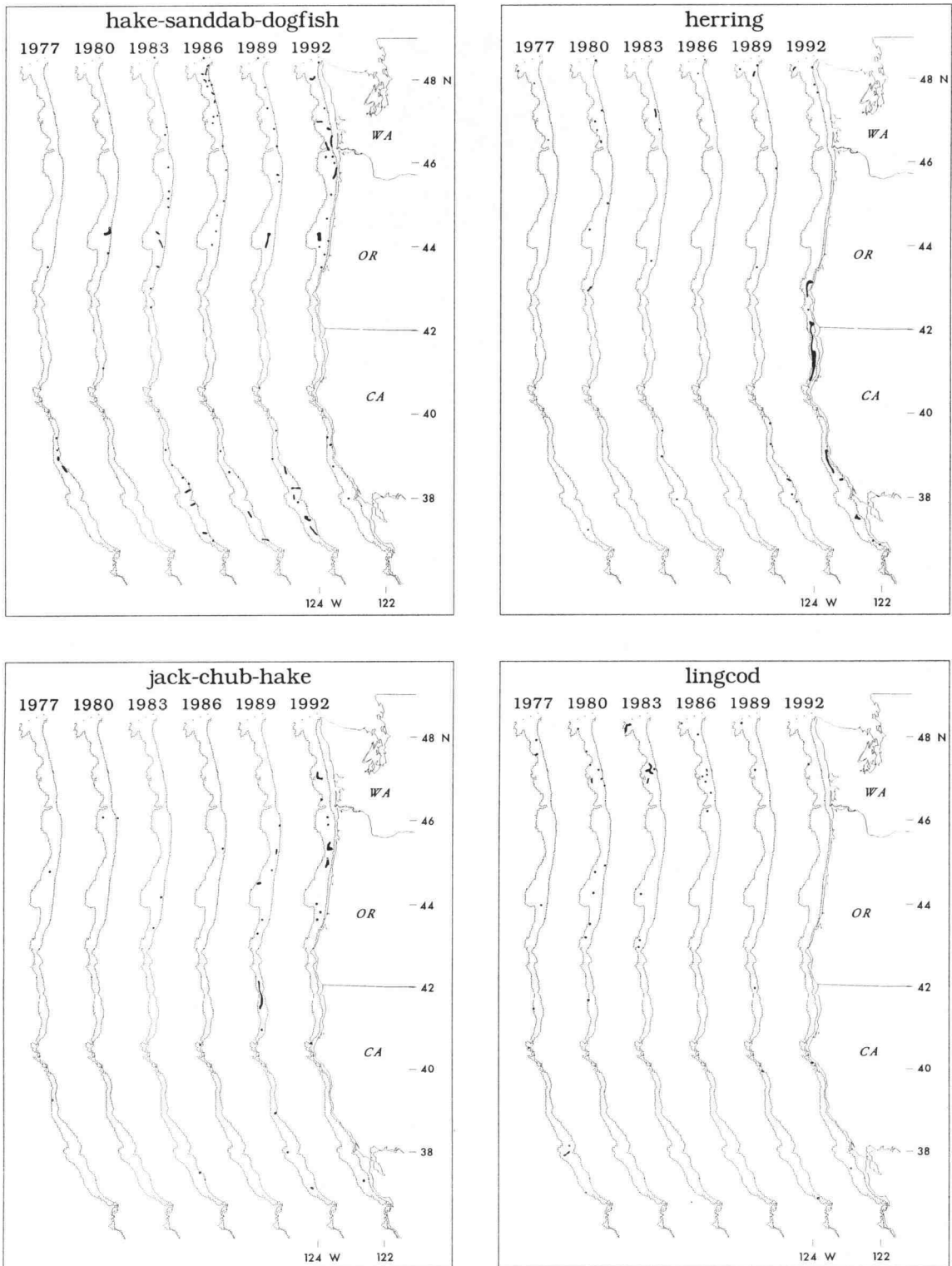


FIGURE 2.8 (Continued)

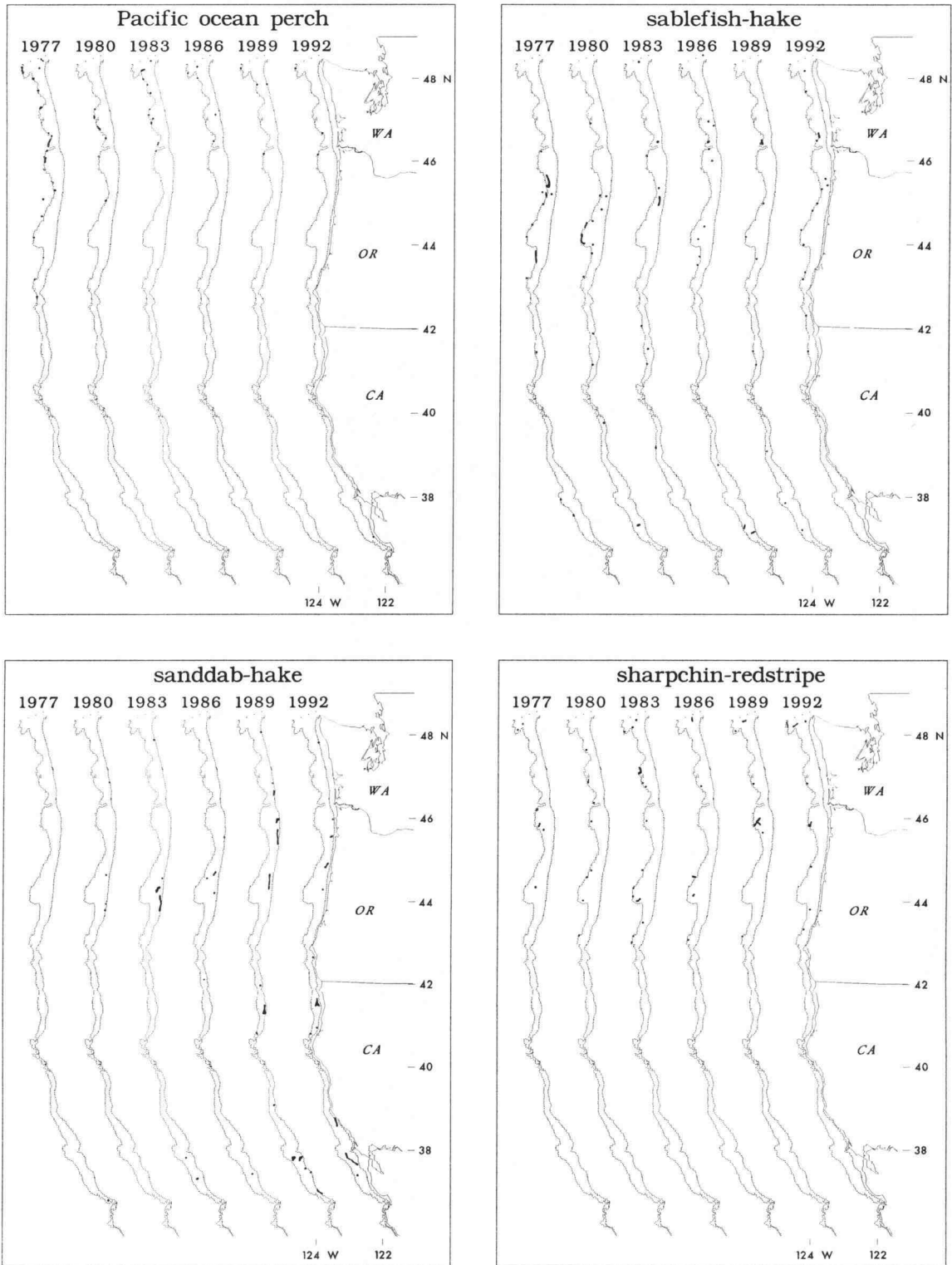


FIGURE 2.8 (Continued)

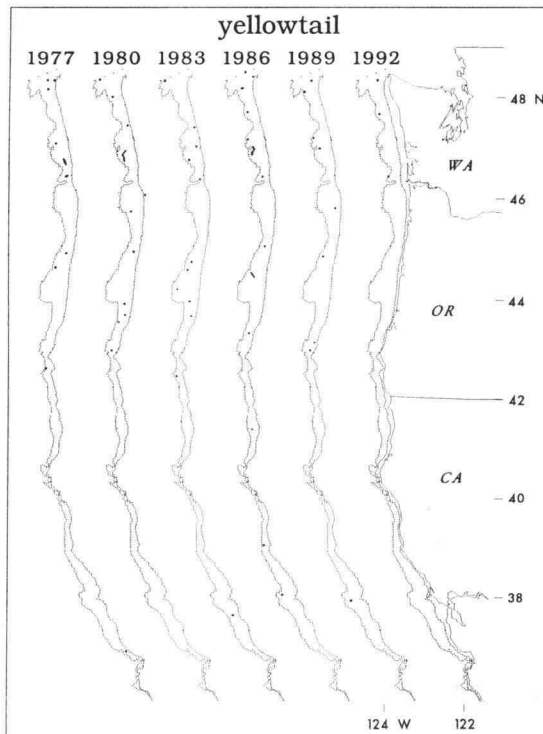
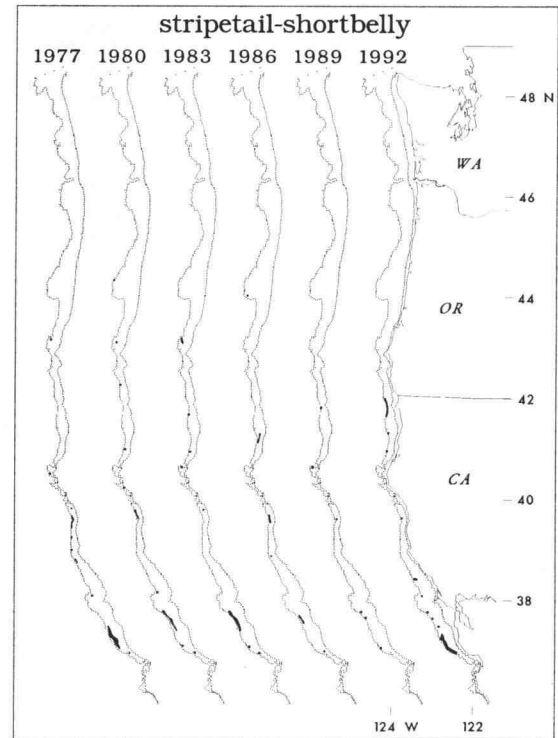
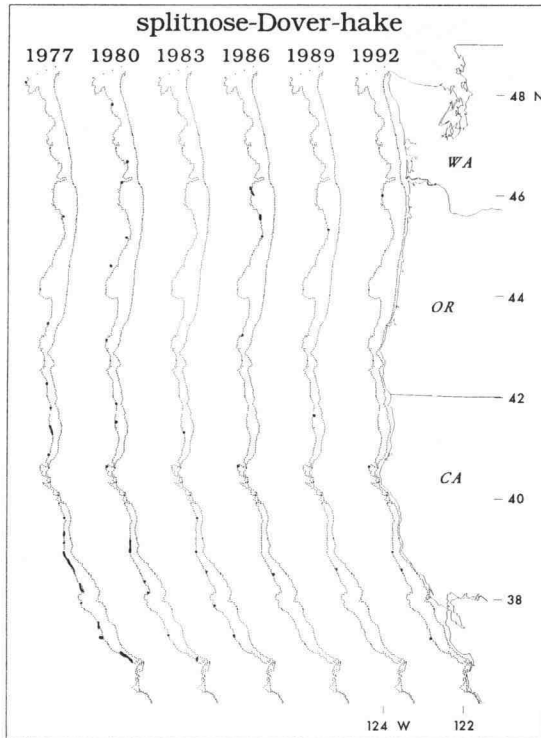


FIGURE 2.8 (Continued)

The arrowtooth-Dover assemblage occurred in the northern region only (Figs. 2.5a and 2.6). Estimates of the incidence of the arrowtooth-Dover assemblage for 1977, 1986, and 1989 are at least twice as high as estimates for other years, and its incidence in 1992 was very low (Table 2.5, Fig. 2.6). Years with high incidence were accompanied by high incidence over the shelf. Imprecise estimates over the upper slope preclude detection of significant differences in incidence within the upper slope region across years.

The estimated incidence of the herring assemblage in 1992 was threefold of similar estimates for previous years (Table 2.5). This increase was apparently due primarily to increases in its occurrence within the southern region (Fig. 2.6) over the continental shelf (Figs. 2.7 and 2.8).

The sanddab-hake assemblage was encountered rarely in 1977 (possibly because the 1977 survey covered a slightly deeper area than subsequent surveys), and occurred infrequently in 1980, but occurred over about 7% of the study area in 1989 (Table 2.5). Its increased occurrence in 1989 can be ascribed to increases in its incidence within the southern region over the continental shelf (Figs. 2.6-2.8).

The croaker-hake assemblage had an incidence of 1% or less in all but the 1992 survey when its incidence was about 6% (Table 2.5). Its increased occurrence in 1992 can be ascribed solely to increases in its occurrence within the southern region and

primarily within the region of the continental shelf (Figs. 2.6 and 2.7) in shallow waters near San Francisco Bay (Fig. 2.8).

The jack-chub-hake assemblage had an incidence of 1% or less in the first four surveys, but occurred over about 6% and 4% of the study area in 1989 and 1992 (Table 2.5), and occurred entirely within the continental shelf region (Fig. 2.7). Increases in its incidence were apparently due to increases in its occurrence within both the northern and southern regions in 1989, but primarily to increases within the northern region in 1992 (Figs. 2.6 and 2.8).

Maps of the distribution of assemblages reveal that they generally occurred within broad geographic boundaries, but their distributions were largely discontinuous (Fig. 2.8). However, these maps should be interpreted cautiously, because the density of hauls varies among areas, and haul locations are not constant between surveys. Also, one should keep in mind that areas indicating homogeneous species compositions would invariably include heterogeneity at a higher sampling density.

Differentiating Assemblages Across Environmental Variables

The highest correlation between any two variables were only moderate negative correlations between bottom temperature and latitude and between bottom temperature and depth (total-sample correlation coefficients, Table 2.6). The first and second canonical functions captured 64% and 28% of the total variation among all observations

Table 2.6. Results of discriminant analysis of 19 assemblages using five environmental discriminating variables in the northern region ($>42^{\circ}$ N) of the study area (number of observations = 1,525).

Total-Sample Correlation Coefficients					
Variable	Latitude	Depth	Substrate	Surface temp.	Bottom temp.
Latitude	1.00				
Depth	-.07	1.00			
Substrate	.04	-.20	1.00		
Surface temp.	.20	.16	-.12	1.00	
Bottom temp.	-.31	-.34	.08	.10	1.00

Canonical function	Cumulative eigenvalue	Squared canonical correlation
1	.64	.40
2	.92	.22
3	.96	.04
4	.98	.02
5	1.00	.02

Total Canonical Structure					
Variable	Canonical function				
	1	2	3	4	5
Latitude	-.068	.975	.204	-.046	-.015
Depth	.980	.034	-.182	.005	.071
Substrate	-.260	.140	-.390	.806	-.333
Surface temp.	.305	.074	.842	.409	.157
Bottom temp.	-.398	-.315	-.026	.340	.792

(cumulative eigenvalue = 92%, Table 2.6). Canonical correlation coefficients express the degree of association between the groups (assemblages) and the canonical functions (Klecka 1980). The squared canonical correlation coefficient can be interpreted as the proportion of the variation in the canonical function explained by the assemblages. Accordingly, the assemblages explained only 40% and 22% of the variation of the first and second canonical variates, respectively (squared canonical correlation, Table 2.6). Total canonical structure coefficients are correlations between each discriminating variable and the discriminant functions (Klecka 1980). The first and second functions were highly correlated with depth and latitude, respectively (total canonical structure, Table 2.6). In short, relatively little discrimination among groups was achieved by the five environmental variables, and the discrimination that was achieved was obtained primarily from depth, and secondly from latitude.

Concomitantly, classification functions that were derived from the five environmental variables did not accurately classify assemblage membership. The apparent error rate indicated a misclassification rate of about 77% (a holdout validation procedure to estimate error rates gave similar results). Correct classification by chance alone, without adjusting prior probabilities by assemblage incidence, is 1 out of 19 (19 assemblages), or about 5%, so the correct classification rate of 23% was substantially better than chance alone, but nevertheless indicates low predictive power. Some assemblages were more accurately classified than others. About 76% of the hauls belonging to the Pacific ocean perch assemblage were classified correctly from the classification functions, followed by a correct classification rate of 63% for the dogfish

assemblage, 59% for the sanddab-hake assemblage, 44% for the arrowtooth-Dover assemblage, and 36% for the Dover-hake assemblage. Most other assemblages had a correct classification rate of much less than 30%.

Discussion

Problems in Comparing Assemblages Among Studies

Difficulties in comparing assemblages among studies arise from differences in the methods and criteria used to delineate assemblages, and the accepted levels of within-assemblage variation. Cluster analysis is commonly used to identify fish assemblages from trawl survey data (Gabriel and Tyler 1980, Colvocoresses and Musick 1984, Overholtz and Tyler 1985, Fargo and Tyler 1991, Weinberg 1994), and has been used in the analysis of commercial landing data (Leaman and Nagtegaal 1987) and observer data from commercial catches (Rogers and Pikitch 1992). Cluster analysis groups entities according to their similarities in a set of attributes. There are many different clustering methods, but common to most methods, is the calculation of resemblance measures indicating similarities between every possible pair of entities. Some fish assemblage studies use measures of the *absolute* abundance of species in each haul in the formation of the resemblance matrix (e.g. Overholtz and Tyler 1985, Weinberg 1994), where the matrix reflects differences in total catch weights among hauls, while other studies use *relative* abundance which results in the assignment of hauls to clusters based solely on species composition, regardless of the size of the catch (e.g. Gabriel and Tyler 1980,

present study). The existence of numerous clustering methods, resemblance measures, and criteria for determining the fusion of clusters (fusion strategy), results in a diverse array of potential methods of analysis.

A difficulty with cluster analysis is in deciding on the appropriate number of meaningful clusters that are present in the data (Everitt 1980). Agglomerative clustering begins with each haul in its own cluster and proceeds to fuse two clusters, step by step, until all hauls are contained in a single cluster. As clustering proceeds, the amount of within-cluster variance increases and between-cluster variance decreases. The fewer clusters derived, the greater the resultant within-cluster variation. Beyond testing for significant differences between clusters, the amount of “acceptable” within-cluster variance is somewhat subjective, and should be recognized in the interpretation of clustering results. The number and kinds of assemblages that are identified from cluster analysis will depend to some extent on the amount of accepted within-assemblage variation. Gleason (1926) commented long ago that a difficulty in comparing plant associations across studies is that “we have no general agreement of opinion as to how much variation may be permitted within the scope of a single association”. The same can be said regarding studies of fish associations. I started at the point in the clustering process where 80% of the total variation in species composition among hauls was explained by the clusters (52 clusters), and subsequently fused clusters based on two practical criteria. The 23 clusters I derived accounted for about 70% of the total variation among 2,565 hauls.

Because of differences in the analysis of fish assemblages among studies, it seems particularly important to provide measures of the amount of variation that exists in the assemblages that are identified, a step that is often overlooked. I provided three measures of variation to evaluate how “tightly” the hauls were grouped and the variability that exists in species composition within the designated assemblages: (1) estimates of variance associated with the estimated mean relative abundance of each species within each assemblage (Table 2.4); (2) a multivariate measure of within-assemblage deviation (SD_m , Table 2.4); and (3) a measure of the proportion of the total variation in species composition among hauls that is accounted for by the designated assemblages (70%). It should be recognized that even though a cluster contains hauls that are “most similar” in species composition, the variation in the abundance of any single species within the cluster can be high.

Comparisons of Assemblage Composition Among Studies

Gabriel (1982) identified 32 assemblages from the 1977 survey data. Like the present study, Gabriel used species' *relative abundance* in the clustering process. However, in contrast to my study, Gabriel used over 60 species to identify assemblages (versus 33 species used here), and used the Bray-Curtis resemblance measure and group average fusion strategy. Perhaps the greatest difference in analysis between Gabriel's (1982) study and mine, was Gabriel's regrouping of the data into clumps of three spatially adjacent hauls prior to clustering to reduce computations and skewness in the frequency distribution of species abundance. Moreover, some hauls were assigned to

more than one clump. Clumping hauls would change the species composition from reflecting the average species abundance over the towed area at one haul location to a species composition reflecting the abundance of species averaged over three separate locations. Also, Gabriel noted that the inclusion of hauls in more than one clump probably artificially increased the similarity of adjacent clumps.

Gabriel (1982) identified nine more assemblages from the 1977 survey than the number of assemblages that I identified in all six surveys combined. Estimates of within-assemblage variation in species composition were not given. In the present study, within-assemblage variation in species relative abundance indicates that hauls were grouped reasonably tightly for species making up 5% or more of the biomass of a given assemblage (Table 2.4). Many of the assemblages that Gabriel identified are not directly comparable to the assemblages I identified. Contrary to Gabriel's study, I identified the occurrence in 1977 of one assemblage dominated by herring, one assemblage dominated by jack mackerel, and one assemblage dominated by lingcod.

Weinberg (1994) identified rockfish (Scorpaenidae) assemblages within the northern region of the study area ($>42^{\circ}$ N) from the same data I used. Instead of grouping *hauls* with similar species relative abundances, as I did, Weinberg grouped *species* with similar abundances among hauls, consequently making inferences to the spatial distribution of assemblages difficult. Nevertheless, Weinberg identified three rockfish assemblages within the northern region that persisted throughout the study period. One of the rockfish assemblages (Weinberg's redstripe-rosethorn-sharpchin

assemblage) is similar in composition to the sharpchin-redstripe assemblage I identified. I identified six rockfish-dominated assemblages that persisted within the area of Weinberg's study: sharpchin-redstripe, yellowtail, splitnose-Dover-hake, darkblotched-bocaccio-widow-hake, canary, and Pacific ocean perch assemblages (Figs. 2.5a and 2.8); albeit they occurred infrequently in some years (Table 2.5).

Comparisons of Assemblage Incidence Among Studies

Gabriel (1982) and Gabriel and Tyler (1980) mapped the boundaries of assemblages they identified from the 1977 survey data. Their assemblages have very continuous boundaries that are delimited by depth, whereas I found much more disjunct assemblage boundaries across depth and latitude (Fig. 2.8). Some of these discrepancies may be due to differing methods of clustering, particularly from their clumping of adjacent hauls prior to their analysis, and the way they delineated assemblage boundaries. Apparently, they considered assemblage boundaries justifiable only if they were contiguous on a map, and forced boundaries to follow depth contours (Gabriel 1982).

Stable assemblage boundaries have been indicated in areas of the northeast Pacific coast over years spanning about five years (Gabriel and Tyler 1980, Fargo and Tyler 1991), and off the northwest Atlantic coast over about a 15-yr period during the 1960's and 70's (Colvocoresses and Musick 1984, Overholtz and Tyler 1985). A more recent study shows that substantial shifts in assemblage boundaries in the northwest Atlantic have occurred after 1987 in association with severe declines in the abundance of many

species from exploitation and possibly large-scale environmental changes (Gomes et al. 1995). My study, on the west coast of the U.S., indicates changes in assemblage boundaries over the 1977-92 study period, which is consistent with submersible observations of significant changes in species composition over rocky banks off Oregon between 1988 and 1990 (Hixon et al. 1991). The perception of boundary stability among studies is undoubtedly related to methods of analysis and interpretation, including the level of resolution at which assemblages are identified.

It is unknown whether changes in the incidence of some assemblages were due primarily to environmental variability or impacts from fishing. However, the persistence of assemblages, although varying in incidence among surveys, suggests that fishing practices over the last 15 years had no *drastic* impact on the existence of summertime bottom-trawl fish assemblages. The observed persistence also implies that the El Niño event of 1983, heralded as the largest this century (Norton et al. 1985, Mysak 1986), had no recognizable impact on the existence of assemblages that I identified. This does not imply that changes in fish assemblages have not occurred prior to 1977, or that more subtle and therefore undetectable changes have not been occurring. Also, changes in the relative abundance of rarer species and other attributes of community organization would not be detected in the present study. Increased fishing intensity usually leads to a decrease in the average size of fish landed (Dickie and Kerr 1982). More detailed analyses could incorporate age or size specific information. Moreover, impacts from fishing or the 1983 El Niño event may produce delayed responses. Note that the increase in the herring, croaker-hake, and jack-chub-hake assemblages occurred in the 1989 and

1992 surveys (Table 2.5). Percy and Schoener (1987) observed a drastic increase in the abundance of jack mackerel and chub mackerel in pelagic waters within the northern region of the present study area in 1983 and 1984.

It may be useful to classify future survey hauls from the classification functions derived herein (Appendix 2) to monitor the persistence of bottom-trawl assemblages. However, because future hauls would be classified into the predefined assemblages that they most closely resemble, regardless of how different they may be in species composition, a minimum level of probability of group membership would have to be stated in the classification procedure so that potentially “new” assemblages might be detected.

Hake-dominated assemblages together covered on average about 39% of the study area from 1980 to 1992. The preponderance of hake-dominated assemblages over the 15-yr study period, suggests that Pacific hake may play a large role in the dynamics of demersal fish communities off the west coast of the United States. The potential of dramatically altering trophic dynamics within the California Current System from severe reductions in Pacific hake stock(s) should be recognized in setting harvest levels.

Differentiating Assemblages Across Environmental Variables

Results from discriminant analysis suggests that assemblage membership from a randomly drawn haul would be difficult to predict from environmental variables alone.

The small predictive power that was achieved came mostly from knowing the haul's depth and secondly its latitude, which is consistent with Gabriel's (1982) analysis of the 1977 survey data. The distribution of assemblages across latitude and depth (Fig. 2.5a and b) indicates greater segregation of assemblages across depth than comparable distances across latitude, probably reflecting sharper environmental gradients across depth than latitude.

The low discriminating power of environmental variables in my study is consistent with findings from Overholtz and Tyler (1985), who used canonical correlation analysis to determine the strength of a linear relationship between *species* abundance and a set of six environmental variables (latitude, longitude, depth, bottom temperature, bottom oxygen, and bottom salinity) on the east coast of the United States. Their environmental variables accounted for only a small amount (<33%) of the total variation in species distribution, and similar to my study, depth and latitude accounted for most of the variability.

Assemblage membership may be more predictable from commercial hauls where fishing locations are not selected randomly and other factors are considered from previous fishing experience in selecting a fishing location. Rogers and Pikitch (1992) investigated how well five predefined fishing strategies, which were based on fishing gear, fishing depth, and the species targeted, corresponded to the assemblage that was actually caught, which was identified after fishing. Three of the fishing strategies used bottom-trawl gear. Of these three, they found that the assemblage of fish that was caught,

generally matched their predefined fishing strategy. Furthermore, from inspection of the species composition in each of their designated assemblages (Rogers and Pikitch 1992: Table 3) it appears that the assemblages were dominated by only a few species, suggesting that small groups of species may be targeted fairly well.

Chapter 3

CORRESPONDENCE BETWEEN ENVIRONMENTAL VARIABILITY AND VARIABILITY IN SPECIES COMPOSITION, AND POTENTIAL FACTORS AFFECTING THE DISTRIBUTION OF FISH ASSEMBLAGES

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Introduction

The application of a single-species management approach to a mixed species fishery, such as the trawl fishery, is inadequate and alternative management approaches are needed (Mercer 1982, Pikitch 1988). In order to discuss potential management alternatives that embrace the inherent spatial complexity of co-occurring species, it would be useful to understand relationships between species abundance, distribution, and the prevalence of fish assemblages. Clearly, species exist at various levels of abundance and spatial distributions. Relationships between distributional responses of fish stocks to variations in overall abundance have only recently been explored (Murawski and Finn 1988, Crecco and Overholtz 1990, Swain and Wade 1993, Swain and Sinclair 1994, Marshall and Frank 1994, 1995). Moreover, the mechanisms involved in forming the mosaic of overlapping fish distributions that occur at various spatial scales and the extent to which these mosaics change are poorly understood.

On the West Coast of the United States, the National Marine Fisheries Service (NMFS) has conducted triennial standardized bottom-trawl surveys over the continental shelf and upper slope off California, Oregon, and Washington since 1977. NMFS routinely produces a tabulation of abundance estimates and a description of the areal distribution of various species based on catch-per-unit-effort data from each survey (Gunderson and Sample 1980, Weinberg et al. 1984, Coleman 1986, 1988, and Weinberg et al. 1994). Dark and Wilkins (1994) give a detailed account of trends in the abundance

and distribution of 11 commercially important species based on data from the first four surveys.

Using data from the NMFS triennial surveys, I examine a few of the multitude of potential factors associated with the occurrence and distribution of fish assemblages. In my view, the composition of species that are observed in the bottom-trawl surveys are a result of interactions between the developing physical environment and concurring developing biological systems (Fig. 3.1). The physical environment, within which biological systems develop, determines the potential for fish recruitment, population growth, and the development of habitable environments, which are reflected in fish abundance and distribution. Changes in abundance may further impact the distribution of individuals through density-dependent mechanisms.

The study area and species considered here are the same as those in Chapter 2. First, I establish some general features regarding the abundance, density, and spatial distribution of the 33 dominant species. Because incidence was correlated with biomass in five of the six flatfish species, I examine differences in their occupation among substrate types in association with changes in their incidence.

Second, if environment serves as a foundation within which biological systems develop, then environmental variation may foster variation in species composition by inducing changes in species abundance and distribution. I examine regional environmental variation as indicated by upwelling intensity and surface and bottom water

Fig. 3.1. Diagram of some of the components associated with the occurrence and distribution of fish assemblages.

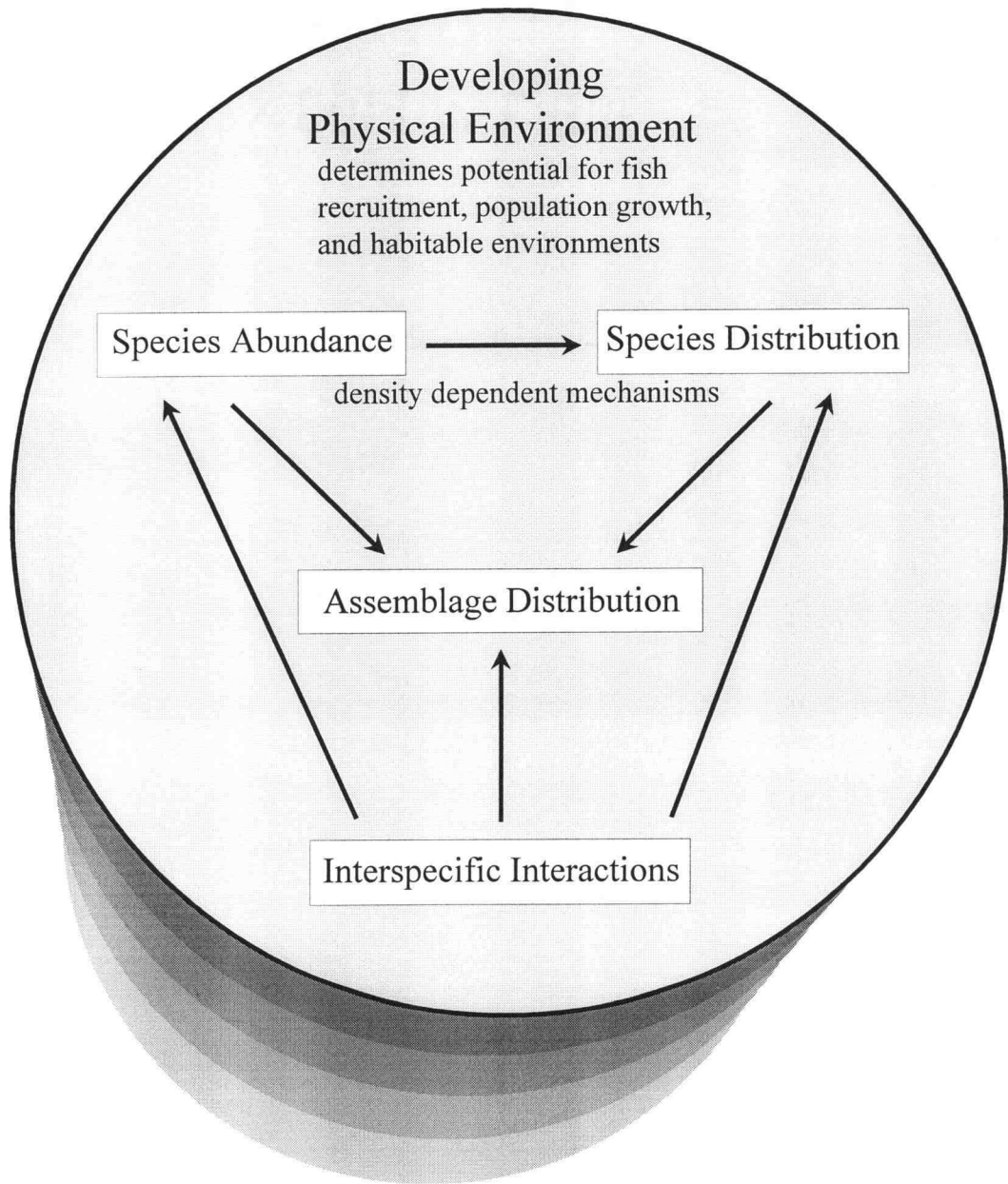


FIGURE 3.1

temperatures, and compare them to variation in species composition in similar regions to explore potential correspondence between environment and species composition.

Lastly, I consider a simple conceptual model predicting possible changes in regional species composition under different scenarios of change in a single species' abundance, incidence, and density. Interspecific interactions such as predation (including fishing), predator avoidance, attraction to prey, and competition, also affect species distribution, but are not considered here.

As in Chapter 2, I define "incidence" as the estimated proportion of sampling units that are occupied by a species. Because, in the present study, the sampling unit was a unit of area, incidence can be interpreted as the estimated proportion of a specified area that was occupied by a species.

Part 1. Species Abundance and Distribution

Methods

Species Biomass

I estimated the biomass of each of the 33 dominant species (see Table 2.3 for a list of species), and total fish biomass, within the entire study area in each survey using the estimator of the population total for stratified random sampling (Cochran 1977,

Gunderson and Sample 1980). The number of sampling units in a stratum was the stratum's area (km^2) and the number of sample observations from the stratum was the number of satisfactorily completed hauls. The measurement in each haul was the catch weight (kg) of each species (or combination of species) adjusted to a "standardized" sampling unit of 1- km^2 of seafloor (CPUE) (see Chapter 2 for a description of the sampling design). I calculated similar estimates for smaller regions within the study area by multiplying the CPUE of each haul by the inverse of its stratum's sampling fraction. In doing so, the number of sampling units within the region (km^2) is estimated implicitly rather than measured from a map.

It was necessary to calculate estimates of species biomass independently from published estimates, because I investigated variations in biomass at various spatial scales at which estimates were not available. Furthermore, biomass estimates from the 1992 survey were not available when the present study was initiated.

Species Distribution

The geographic range of each species in the 1980 to 1992 surveys combined was determined by plotting the 25th, 50th, and 75th percentiles of their estimated incidence across latitude and depth. The 1977 survey was not included, because it covered a slightly deeper area than subsequent surveys. Each observation was assigned a frequency equal to the inverse of the sampling fraction of its corresponding stratum to account for differences in sampling effort among strata.

Characteristics of each species' occurrence within the study area was summarized by calculating their average incidence, biomass, and density over the last five surveys. Incidence for each survey year was estimated using the estimator of the population proportion for stratified random sampling (Scheaffer et al. 1990). The density of a given species within areas of its occurrence, was calculated by dividing its average estimated biomass by the product of its average estimated incidence and the area of the entire study area (approximately 39,687 km²).

Correlations Between Species Biomass and Incidence, and the Occupation of Substrate Types by Flatfish

To identify species that have distributions that may be affected by abundance, Pearson coefficients of correlation between estimates of incidence and biomass were calculated for each of the 33 species (each survey provided one observation, $n = 6$). Because incidence was correlated with biomass in five of the six flatfish species, I compared their occupation among substrate types in association with changes in their incidence. Substrate data were available for the northern portion ($>42^{\circ}$ N) of the study area. As in Chapter 2, surficial substrate at each haul location was categorized into "mud", "sand", "shell-gravel", or "rock" from a digitized map of the distribution of offshore deposits on the continental shelf and upper slope off Oregon and Washington (Moore and Luken 1979). Mud and sand is much more prevalent within the study area (39% and 48%, respectively) than shell-gravel and rock (6% and 8%, respectively) (see Chapter 2). Mud generally occurs in deeper water than do other substrates.

Within each substrate type and survey year, the area of substrate occupied by a given flatfish species was estimated by summing the inverse of the sampling density (haul/km²) over all hauls in which at least one specimen occurred. To investigate the potential of differential use of sand and mud substrate with increasing overall incidence within the northern part of the study area, the ratio of the estimated area of sand to area of mud that was occupied by each flatfish species was regressed on the estimate of the species' overall incidence. The overall incidence of each species within the northern area was estimated by dividing the area occupied in all substrate categories combined by an estimate of the total (occupied and unoccupied) area of all substrate categories combined.

Results and Discussion

Species Biomass

The combined biomass of the 33 dominant species composed at least 95% of the total fish biomass in each survey. Spiny dogfish, Pacific hake, and sablefish were consistently among the top three most abundant species, and together composed from 53-63% of the fish biomass in each of the last five surveys (Table 3.1, Fig. 3.2). Pacific hake was very abundant, composing from 29-47% of the fish biomass (Fig. 3.2).

Estimates of biomass for individual flatfish species (Bothidae and Pleuronectidae) were 2-3 times as precise as those for rockfish (Scorpaenidae) (Table 3.1). The average coefficients of variation of the mean for flatfish and rockfish biomass estimates over all

Table 3.1. Estimated biomass (\hat{B} ; tons) of each of the 33 dominant species from the NMFS triennial surveys from 1977 to 1992. Total sample size for each year is 525, 474, 513, 533, 431, and 420; CV = standard error / estimate.

Species		Year						1980-92 x̄
		*1977	1980	1983	1986	1989	1992	
Squalidae								
spiny dogfish	B̂	32,994	34,655	74,714	23,635	78,680	40,935	50,524
	CV	.36	.48	.48	.34	.41	.25	
Clupeidae								
American shad	B̂	557	192	3,252	1,216	4,963	2,633	2,451
	CV	.31	.41	.40	.18	.51	.21	
Pacific herring	B̂	7,031	12,231	4,193	2,086	11,712	19,994	10,043
	CV	.83	.76	.55	.63	.55	.19	
Gadidae								
Pacific cod	B̂	5,107	1,963	1,449	1,356	1,479	1,244	1,498
	CV	.51	.57	.35	.12	.18	.21	
Pacific hake	B̂	69,341	203,624	129,437	238,336	339,653	299,155	242,041
	CV	.15	.23	.15	.12	.14	.12	
walleye pollock	B̂	931	977	581	1,402	3,262	572	1,359
	CV	.62	.81	.32	.22	.41	.42	
Carangidae								
jack mackerel	B̂	2,674	108	5,062	2,079	48,574	43,736	19,912
	CV	.60	.63	.57	.66	.34	.29	
Sciaenidae								
white croaker	B̂	11	1,810	2,241	3,391	5,977	8,322	4,348
	CV	.80	.77	.33	.38	.46	.37	

(Table 3.1 — continued)

Scombridae

chub mackerel	\hat{B}	0	0	9	27	8,478	21,179	5,938
	CV	.	.	.51	.72	.43	.29	

Scorpaenidae

Pacific ocean perch	\hat{B}	14,794	7,711	6,144	3,255	5,114	3,171	5,079
	CV	.35	.28	.26	.38	.53	.35	

silvergray rockfish	\hat{B}	14,580	1,340	3,829	619	1,168	167	1,425
	CV	.91	.43	.66	.51	.51	.42	

darkblotched rockfish	\hat{B}	4,231	4,017	8,763	8,425	3,347	6,570	6,224
	CV	.18	.25	.28	.31	.17	.45	

splitnose rockfish	\hat{B}	8,255	12,547	5,028	6,442	5,617	5,364	7,000
	CV	.18	.51	.21	.24	.23	.26	

widow rockfish	\hat{B}	3,629	1,254	3,826	5,356	9,269	12,821	6,505
	CV	.65	.38	.62	.61	.61	.87	

yellowtail rockfish	\hat{B}	24,599	15,311	15,353	11,545	22,212	11,106	15,105
	CV	.33	.31	.41	.25	.55	.33	

chilipepper	\hat{B}	9,047	11,926	8,468	10,946	17,381	22,624	14,269
	CV	.25	.49	.47	.31	.29	.73	

shortbelly rockfish	\hat{B}	27,666	1,202	2,412	12,458	10,240	21,112	9,485
	CV	.47	.52	.58	.86	.47	.55	

bocaccio	\hat{B}	7,377	5,873	7,245	8,150	23,041	595	8,981
	CV	.31	.25	.53	.71	.96	.43	

canary rockfish	\hat{B}	26,884	7,986	20,150	10,700	10,405	1,665	10,181
	CV	.73	.36	.28	.29	.41	.42	

(Table 3.1 — continued)

redstripe rockfish	\hat{B} CV	5,662 .49	8,012 .45	8,384 .43	5,239 .62	7,084 .39	13,039 .44	8,352
yellowmouth rockfish	\hat{B} CV	292 .74	1,593 .87	680 .62	371 .86	19 .53	371 .95	607
bank rockfish	\hat{B} CV	495 .46	3,103 .81	144 .53	3,519 .67	3 .71	303 .74	1,414
stripetail rockfish	\hat{B} CV	5,687 .25	16,815 .41	10,357 .40	7,619 .26	10,735 .28	6,794 .33	10,464
sharpchin rockfish	\hat{B} CV	2,800 .30	2,893 .26	10,209 .37	6,112 .47	4,289 .27	19,604 .55	8,622
shortspine thornyhead	\hat{B} CV	2,524 .09	1,551 .18	2,497 .13	2,590 .17	1,831 .15	2,144 .16	2,123
Anoplopomatidae								
sablefish	\hat{B} CV	13,033 .13	46,750 .38	30,864 .31	28,002 .27	38,406 .41	58,023 .26	40,409
Hexagrammidae								
lingcod	\hat{B} CV	16,349 .65	12,450 .58	7,994 .14	3,748 .12	7,982 .23	4,250 .54	7,285
Bothidae								
Pacific sanddab	\hat{B} CV	965 .18	1,980 .15	7,582 .12	11,262 .12	30,011 .35	17,616 .11	13,690
Pleuronectidae								
arrowtooth flounder	\hat{B} CV	15,969 .26	7,327 .27	5,392 .10	9,950 .07	18,592 .33	5,173 .09	9,287
rex sole	\hat{B} CV	3,836 .07	3,503 .11	9,264 .07	12,626 .07	12,623 .07	12,048 .08	10,013

(Table 3.1 — continued)

Pacific halibut	\hat{B}	296	260	1,428	4,534	4,875	5,779	3,375
	CV	.60	.57	.17	.12	.16	.19	
Dover sole	\hat{B}	18,851	11,249	19,356	25,903	16,872	14,147	17,505
	CV	.06	.09	.07	.08	.08	.11	
English sole	\hat{B}	1,792	2,847	7,068	7,442	12,372	9,879	7,922
	CV	.18	.18	.09	.07	.11	.09	
Biomass Totals**:								
33 dominant species combined	\hat{B}	348,257	445,062	423,373	480,343	776,267	692,137	
	CV	.13	.13	.11	.08	.10	.08	
All bottom-trawl fish combined	\hat{B}	362,214	455,847	441,187	503,899	804,896	722,874	
	CV	.13	.13	.10	.08	.09	.08	

*1977 survey covered a slightly deeper depth range than subsequent surveys.

**Biomass totals were estimated separately from individual species estimates.

six surveys were .16 and .45, respectively. The relatively high precision attained in estimating flatfish biomass from trawl surveys has been noted by others (Dark and Wilkins 1994), and is probably related, in part, to the widespread occurrence of flatfish (fewer zero values among hauls).

I compared my species biomass estimates for the entire study area to published estimates that were based on the same data source (Table 3.2). Published estimates were available for comparison to mine for at least eight species in each of the first five surveys; most came from survey reports that were published by National Marine Fisheries Service (Gunderson and Sample 1980, Weinberg et al. 1984, Coleman 1986, 1988, and Weinberg

Fig. 3.2. Percentage of the total fish biomass comprising a given species or group of species in each of the triennial surveys from 1977 to 1992.

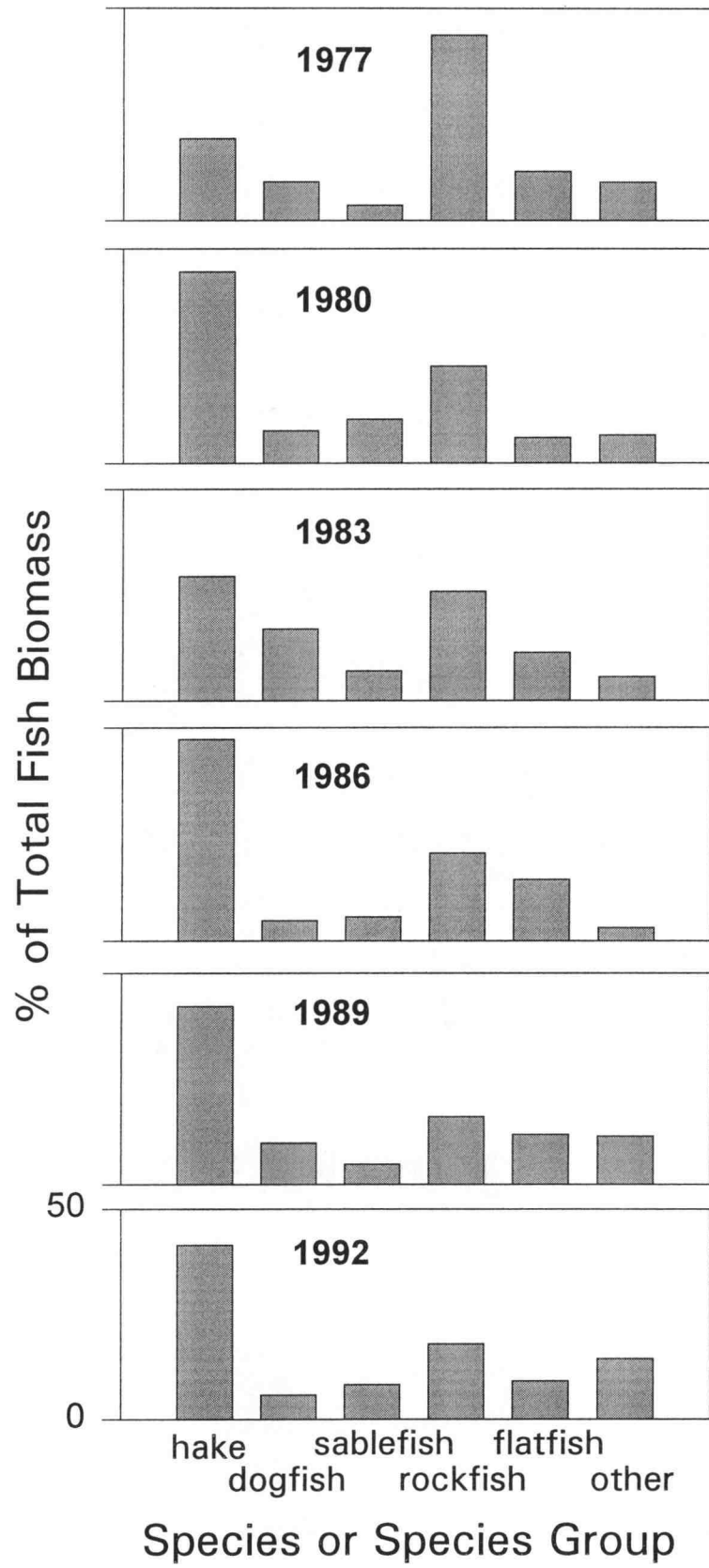


FIGURE 3.2

Table 3.2. Biomass estimates from the present study (\hat{B} ; tons) compared to published estimates (publ. est.). Published estimates for 1977 and 1989 include an area from 35°30'-36°48' which was not included in my estimates. $\% = (\hat{B} / \text{publ. est.}) \times 100$.

Species		Year					
		1977	1980	1983	1986	1989	1992
spiny dogfish	\hat{B}	32,994	34,655	74,714	23,635	78,680	40,935
	publ. est.					97,836	
	%					80%	
Pacific hake	\hat{B}	69,341	203,624	129,437	238,336	339,653	299,155
	publ. est.	69,640	183,914	127,457	239,153	355,684	
	%	100%	111%	102%	100%	95%	
Pacific ocean perch	\hat{B}	14,794	7,711	6,144	3,255	5,114	3,171
	publ. est.	15,050	6,802		3,169	9,506	
	%	98%	113%		103%	54%	
silvergray rockfish	\hat{B}	14,580	1,340	3,829	619	1,168	167
	publ. est.	3,650				1,062	
	%	400%				110%	
darkblotched rockfish	\hat{B}	4,231	4,017	8,763	8,425	3,347	6,570
	publ. est.	4,240				3,107	
	%	100%				108%	
splitnose rockfish	\hat{B}	8,255	12,547	5,028	6,442	5,617	5,364
	publ. est.	9,190				5,920	
	%	90%				95%	
widow rockfish	\hat{B}	3,629	1,254	3,826	5,356	9,269	12,821
	publ. est.	3,370	1,287		5,409	7,372	
	%	108%	97%		99%	126%	
yellowtail rockfish	\hat{B}	24,599	15,311	15,353	11,545	22,212	11,106
	publ. est.	24,720	10,979	13,650	11,655	17,762	
	%	100%	139%	112%	99%	125%	

(Table 3.2 — continued)

chilipepper	\hat{B}	9,047	11,926	8,468	10,946	17,381	22,624
	publ. est.	9,590	10,449	9,425	10,945	17,466	
	%	94%	114%	90%	100%	100%	
shortbelly rockfish	\hat{B}	27,666	1,202	2,412	12,458	10,240	21,112
	publ. est.	24,950				10,987	
	%	111%				93%	
bocaccio	\hat{B}	7,377	5,873	7,245	8,150	23,041	595
	publ. est.	8,390	5,186	7,710	8,162	16,442	
	%	88%	113%	94%	100%	140%	
canary rockfish	\hat{B}	26,884	7,986	20,150	10,700	10,405	1,665
	publ. est.	26,940	6,965	18,820	10,998	8,308	
	%	100%	115%	107%	97%	125%	
redstripe rockfish	\hat{B}	5,662	8,012	8,384	5,239	7,084	13,039
	publ. est.	5,770				5,548	
	%	98%				128%	
stripetail rockfish	\hat{B}	5,687	16,815	10,357	7,619	10,735	6,794
	publ. est.	7,830				10,378	
	%	73%				103%	
sharpchin rockfish	\hat{B}	2,800	2,893	10,209	6,112	4,289	19,604
	publ. est.	2,770				4,790	
	%	101%				90%	
shortspine thornyhead	\hat{B}	2,524	1,551	2,497	2,590	1,831	2,144
	publ. est.	2,640				1,741	
	%	96%				105%	
sablefish	\hat{B}	13,033	46,750	30,864	28,002	38,406	58,023
	publ. est.		41,752	30,557	27,925	38,082	
	%		112%	101%	100%	101%	
lingcod	\hat{B}	16,349	12,450	7,994	3,748	7,982	4,250
	publ. est.		11,195	7,788	3,826	8,161	
	%		111%	103%	98%	98%	
Pacific sanddab	\hat{B}	965	1,980	7,582	11,262	30,011	17,616
	publ. est.					32,088	
	%					94%	
arrowtooth flounder	\hat{B}	15,969	7,327	5,392	9,950	18,592	5,173
	publ. est.		7,052		9,812	17,517	
	%		104%		101%	106%	

(Table 3.2 — continued)

rex sole	\hat{B} publ. est. %	3,836	3,503	9,264	12,626	12,623 12,678 100%	12,048
Pacific halibut	\hat{B} publ. est. %	296	260	1,428	4,534	4,875 4,645 105%	5,779
Dover sole	\hat{B} publ. est. %	18,851	11,249 10,698 105%	19,356 19,242 101%	25,903 25,121 103%	16,872 16,456 102%	14,147
English sole	\hat{B} publ. est. %	1,792	2,847 2,598 110%	7,068	7,442 7,313 102%	12,372 12,495 99%	9,879

Source of published estimates: Dark et al. 1980, Gunderson and Sample 1980, Weinberg et al. 1984, Coleman 1986, 1988, and Weinberg et al. 1994.

et al. 1994). Most of my estimates (86%) were within 15% of published estimates.

Disparate estimates did not appear to be associated with particular species or surveys; except my 1980 estimates across species tended to be higher than published estimates (on average 112% of published estimates, $n = 12$, see Table 3.2). Discrepancies between my estimates and published estimates may be caused, in part, by differences in data screening prior to estimation. Of note, I excluded 26 hauls from the 1980 survey data set, because they contained incomplete catch information. On average, my estimates were 97%, 101%, 100%, and 106% of published estimates for the 1977, 1983, 1986, and 1989 surveys, respectively ($n = 14, 8, 12$, and 23).

I examined the potential cause of four large discrepancies between published estimates and mine: the 1977 silvergray rockfish estimate, the 1989 Pacific ocean perch

estimate, the 1980 yellowtail rockfish estimate, and the 1989 bocaccio estimate (see Table 3.2). In 1977, silvergray rockfish occurred in a small number of hauls. My much greater biomass estimate for this species in 1977 than the published estimate (Gunderson and Sample 1980) is due to my large estimated biomass for this species in the far northern region of the study area (Vancouver area). The exclusion or inclusion of a single haul can sometimes make a large difference in a given estimate. One particular haul had a very large catch of silvergray rockfish; if the haul was excluded from my biomass estimate, my total estimate would become 1,392 t, rather than 14,580 t (however, my estimate would then be only 38% of the published estimate). I suspect that my 14,580 estimate is too high due to an error in the recorded catch for this species in the aforementioned haul.

My much smaller biomass estimate for Pacific ocean perch in 1989 than the published estimate (Weinberg et al. 1994) is due to Weinberg et al.'s larger estimated biomass for this species in strata within the far northern region of the study area (Vancouver area). Weinberg et al. (1994) incorporated hauls within Canadian waters (where Pacific ocean perch is typically abundant) into their CPUE estimates for two northern U.S. strata (pers. comm. M. Wilkins, NMFS, Seattle), which biases their total biomass estimate, and may account for their comparably higher estimate. The discrepancy in the 1989 bocaccio estimate may have resulted for the same reason as that for Pacific ocean perch. I was unable to resolve the discrepancy in the 1983 yellowtail rockfish estimate. Because large discrepancies apparently occurred infrequently (see Table 3.2), I used my estimates for subsequent analyses.

Species Distribution

Although some species were relatively localized in distribution, others were widespread and overlapped considerably with other species across latitude and depth (Fig. 3.3). Across latitude, white croaker, chilipepper, shortbelly rockfish, bocaccio, bank rockfish, and stripetail rockfish had centers of their range (50th percentile) in the southern region of the study area (<42°N). Across depth, Pacific ocean perch, splitnose rockfish, yellowmouth rockfish, bank rockfish, and shortspine thornyhead had centers of their range over the upper slope (approximated by areas >200 m deep).

The depiction of the average geographic range of each species (Fig. 3.3) should be viewed cautiously. It would appear that several species, such as white croaker and bank rockfish, occurred in isolation to other species. However, species are patchily distributed within their geographic range and their centers of distribution vary over time, so considerable overlap can occur. For example, white croaker dominated an assemblage in the 1992 survey (croaker-hake assemblage, Table 2.4 in Chapter 2), but approximately 40% of the assemblage's biomass was composed of the remaining 33 dominant species, primarily Pacific hake, Pacific sanddab, and English sole.

The average species' incidence ranged from .01 (bank rockfish) to .88 (rex sole) (Fig. 3.4, Table 3.3). Spiny dogfish, Pacific hake, sablefish, and all flatfish species, except Pacific halibut, were widely distributed and occurred on average over an aggregated area of more than 48% of the study area. The most ubiquitous flatfish species

Fig. 3.3. The range from the 25th to 75th percentiles of the estimated incidence of each of the 33 dominant species across latitude and depth over the last five surveys combined. The intersection of the ranges (dot) for a given species indicates the 50th percentile.

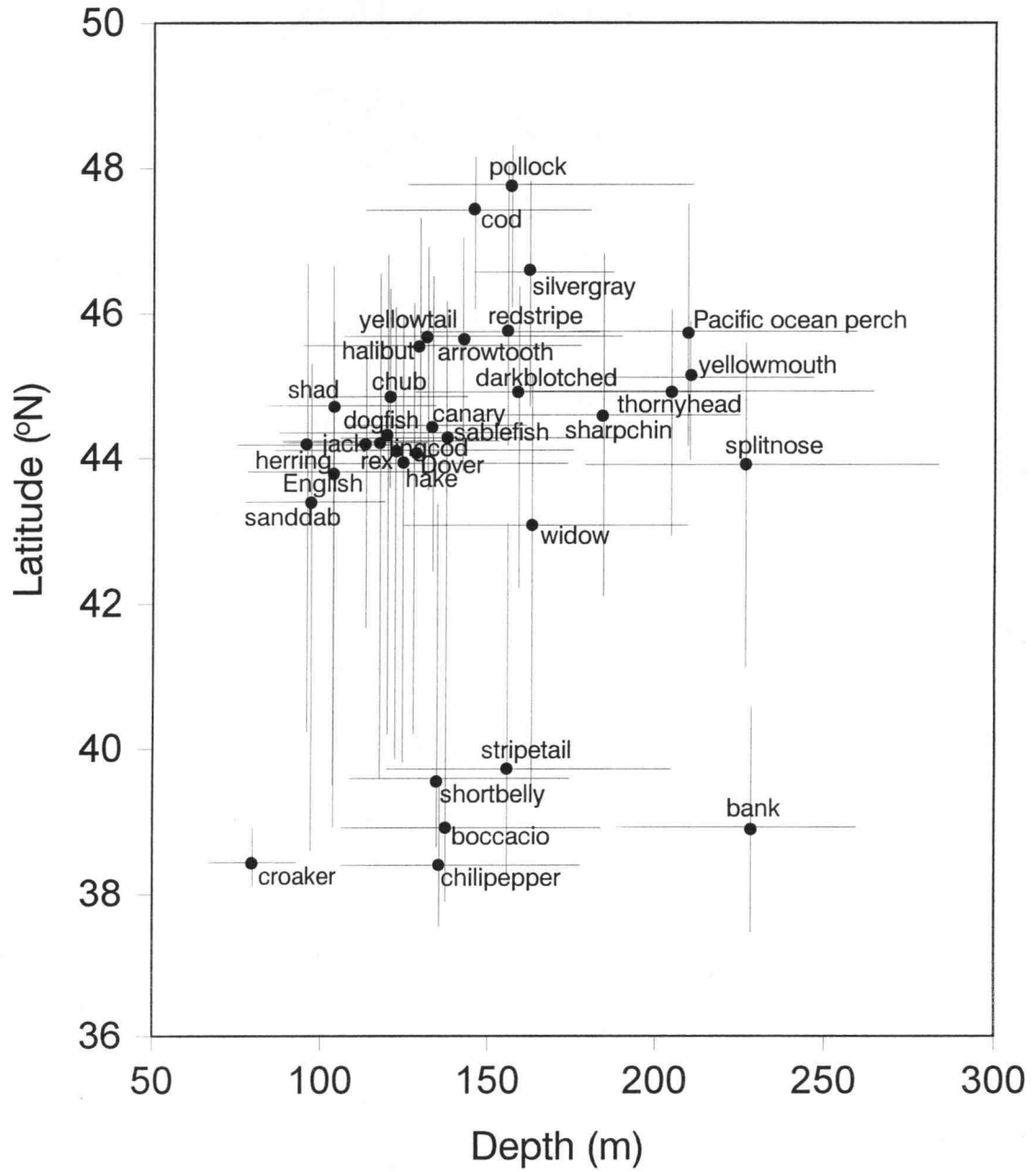


FIGURE 3.3

Fig. 3.4. Plot of mean incidence on $\log_{10}(\text{mean biomass})$ for each of the 33 dominant species over the survey years 1980-1992. The area of the circle is proportional to the average density of a given species within areas of its occurrence (filled = flatfish species, cross-hatched = rockfish species).

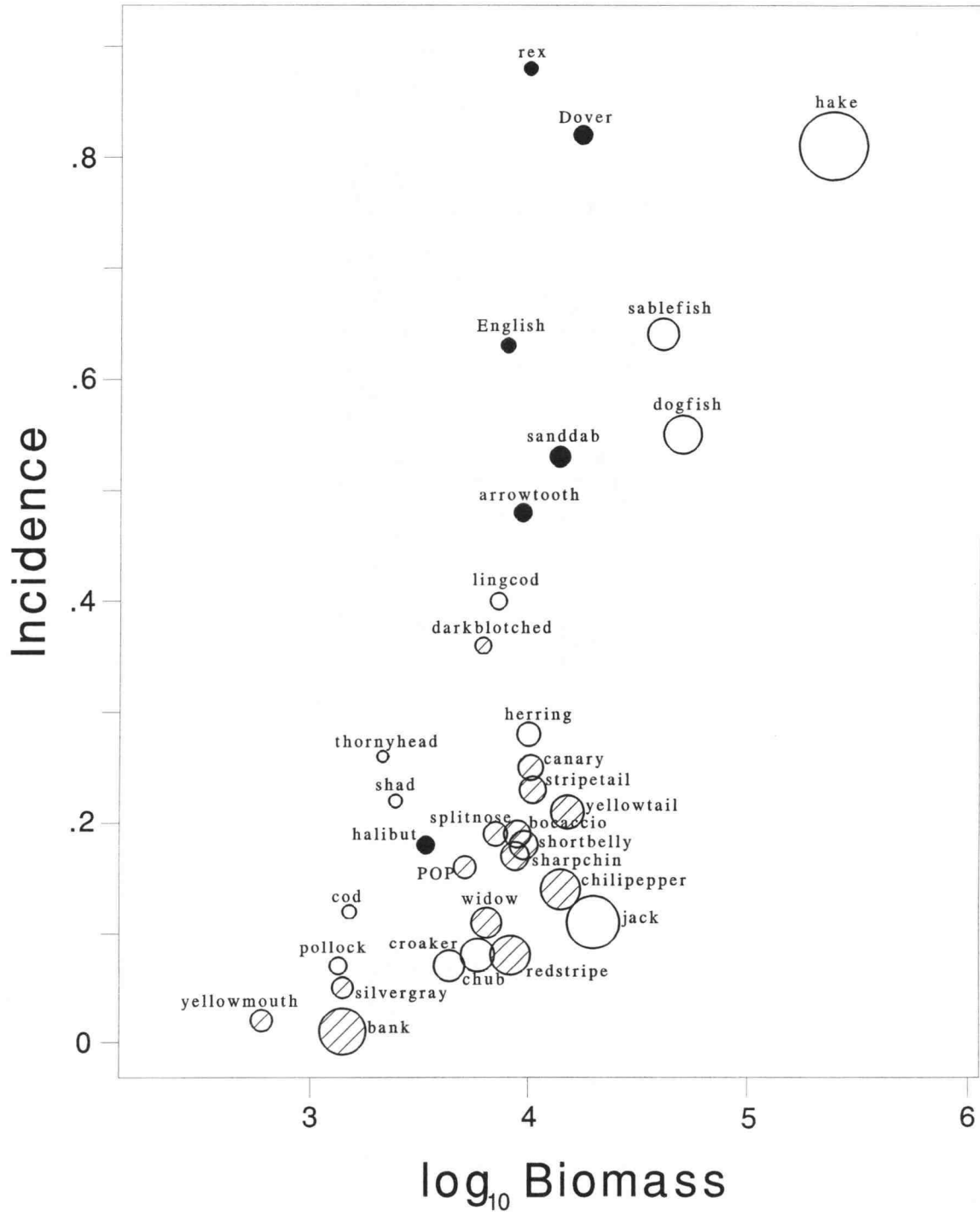


FIGURE 3.4

Table 3.3. Estimated incidence (\hat{I}) of each of the 33 dominant species from the NMFS triennial surveys from 1977 to 1992. Total sample size for each year is 525, 474, 513, 533, 431, and 420; CV = standard error / estimate.

Species		Year						1980-92 \bar{x}
		*1977	1980	1983	1986	1989	1992	
spiny dogfish	\hat{I}	.45	.44	.56	.49	.61	.67	.55
	CV	.05	.05	.04	.05	.03	.03	
American shad	\hat{I}	.12	.05	.24	.25	.19	.37	.22
	CV	.14	.24	.09	.09	.10	.06	
Pacific herring	\hat{I}	.09	.16	.20	.18	.22	.62	.28
	CV	.17	.12	.10	.10	.08	.03	
Pacific cod	\hat{I}	.20	.07	.10	.15	.14	.12	.12
	CV	.08	.20	.11	.09	.11	.12	
Pacific hake	\hat{I}	.79	.67	.83	.89	.81	.87	.81
	CV	.03	.04	.02	.02	.02	.02	
walleye pollock	\hat{I}	.06	.04	.10	.07	.07	.05	.07
	CV	.13	.25	.12	.13	.17	.22	
jack mackerel	\hat{I}	.02	.01	.08	.02	.14	.30	.11
	CV	.43	.54	.17	.36	.12	.07	
white croaker	\hat{I}	.01	.02	.07	.08	.06	.10	.07
	CV	.71	.43	.19	.17	.15	.11	
chub mackerel	\hat{I}	0	0	.01	.01	.09	.30	.08
	CV	.	.	.49	.70	.16	.07	
Pacific ocean perch	\hat{I}	.27	.16	.17	.16	.12	.18	.16
	CV	.05	.10	.08	.09	.10	.09	
silvergray rockfish	\hat{I}	.06	.06	.08	.04	.03	.02	.05
	CV	.18	.22	.15	.23	.30	.34	
darkblotched rockfish	\hat{I}	.41	.26	.40	.40	.42	.32	.36
	CV	.05	.08	.06	.05	.06	.06	

(Table 3.3 — continued)

splitnose	\hat{I}	.27	.16	.23	.21	.20	.15	.19
rockfish	CV	.05	.11	.07	.06	.08	.08	
widow rockfish	\hat{I}	.12	.13	.13	.10	.09	.12	.11
	CV	.12	.15	.13	.15	.17	.13	
yellowtail	\hat{I}	.27	.21	.31	.25	.14	.16	.21
rockfish	CV	.07	.10	.07	.08	.12	.11	
chilipepper	\hat{I}	.12	.13	.11	.18	.16	.14	.14
	CV	.10	.14	.14	.10	.08	.10	
shortbelly	\hat{I}	.09	.19	.12	.28	.17	.14	.18
rockfish	CV	.14	.11	.13	.08	.10	.10	
bocaccio	\hat{I}	.22	.30	.21	.25	.12	.05	.19
	CV	.08	.07	.10	.08	.12	.20	
canary rockfish	\hat{I}	.22	.21	.36	.31	.21	.16	.25
	CV	.09	.11	.07	.07	.10	.12	
redstripe	\hat{I}	.07	.07	.08	.08	.09	.08	.08
rockfish	CV	.19	.2	.15	.15	.15	.18	
yellowmouth	\hat{I}	.01	.01	.02	.02	.01	.02	.02
rockfish	CV	.37	.52	.32	.43	.52	.33	
bank rockfish	\hat{I}	.02	.02	.02	.01	.00	.01	.01
	CV	.19	.31	.37	.56	.71	.44	
stripetail	\hat{I}	.19	.20	.31	.27	.27	.22	.23
rockfish	CV	.09	.10	.09	.08	.07	.08	
sharpchin	\hat{I}	.14	.13	.14	.18	.18	.20	.16
rockfish	CV	.11	.14	.10	.11	.10	.09	
shortspine	\hat{I}	.37	.23	.29	.34	.26	.20	.26
thornyhead	CV	.05	.08	.06	.05	.06	.05	
sablefish	\hat{I}	.60	.47	.62	.81	.66	.66	.64
	CV	.04	.06	.04	.02	.04	.03	
lingcod	\hat{I}	.27	.32	.47	.40	.44	.37	.40
	CV	.08	.08	.05	.06	.06	.06	
Pacific sanddab	\hat{I}	.21	.32	.58	.62	.53	.62	.53
	CV	.09	.07	.03	.03	.04	.03	

(Table 3.3 — continued)

arrowtooth	\hat{I}	.57	.33	.44	.53	.52	.58	.48
flounder	CV	.04	.07	.05	.04	.04	.03	
rex sole	\hat{I}	.81	.73	.89	.95	.90	.94	.88
	CV	.03	.03	.02	.01	.02	.01	
Pacific halibut	\hat{I}	.01	.02	.11	.31	.25	.21	.18
	CV	.42	.44	.12	.07	.08	.09	
Dover sole	\hat{I}	.87	.66	.81	.94	.88	.81	.82
	CV	.02	.04	.02	.01	.02	.02	
English sole	\hat{I}	.3	.45	.66	.66	.64	.72	.62
	CV	.07	.06	.03	.03	.03	.03	

*1977 survey covered a slightly deeper depth range than subsequent surveys.

were rex and Dover soles. In areas of a given species' occurrence, flatfish occurred less densely than did other species. In areas of their occurrence, the ten most densely occurring species, in order of decreasing density, were Pacific hake, jack mackerel, bank rockfish, redstripe rockfish, chilipepper, spiny dogfish, chub mackerel, yellowtail rockfish, sablefish, and white croaker.

Those species with high incidence (Pacific hake, spiny dogfish, sablefish, and flatfish), but not necessarily high density (e.g. flatfish), "overlapped" a greater number of the fish assemblages that were identified in Chapter 2 than did species with lower incidence (Fig. 3.5). The number of assemblages that were overlapped by a given species was defined as the number of assemblages where the species composed an average of at least 5% of the assemblage's biomass (see Table 2.4 in Chapter 2).

Fig. 3.5. For each of the 33 dominant species, the number of assemblages where the species composed >5% of the assemblage's biomass. "Other" are those species that overlapped three or fewer assemblages.

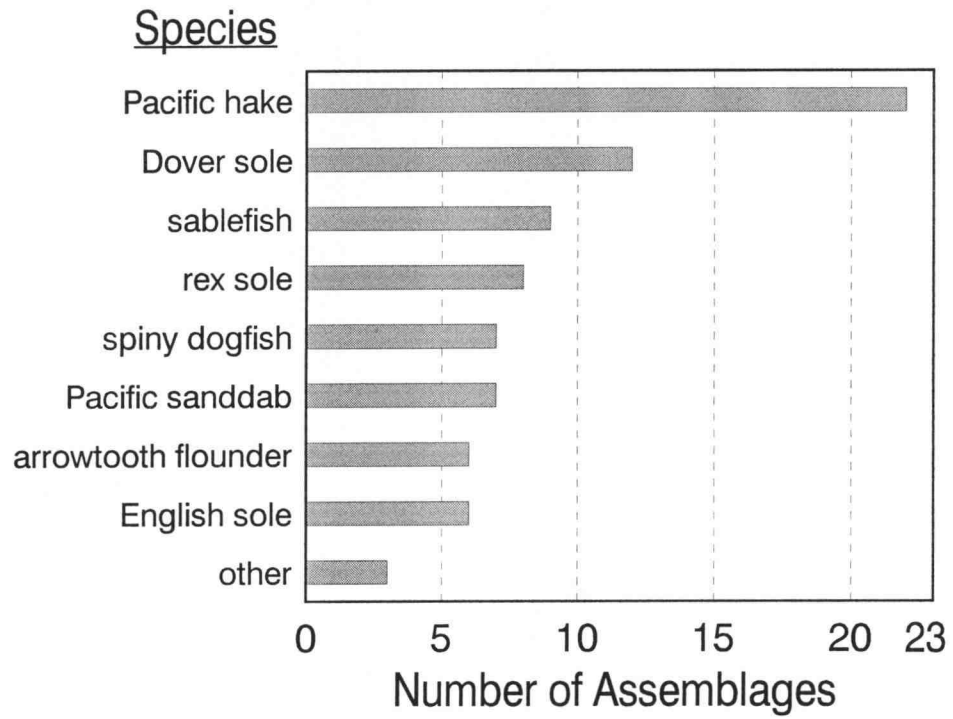


FIGURE 3.5

Rockfish as a group were consistently more abundant (Fig. 3.2) and occurred in higher density within a smaller aggregated area than that of flatfish (Fig. 3.4). The clumped, and often wide ranging distribution of rockfish has been widely observed (Dark and Wilkins 1994). It appears that much of the species composition in the bottom-trawl surveys reflects the widespread distribution of flatfish, Pacific hake, sablefish, and spiny dogfish punctuated by dense patches of rockfish.

Correlation Between Species Biomass and Incidence, and the Occupation of Substrate Types by Flatfish

Correlations between species biomass and incidence (which were best fit with a \log_{10} -transform of biomass) were significant ($p < .05$) in five of the six flatfish species (Table 3.4, Fig. 3.6), suggesting that the spatial distribution of flatfish may be affected by abundance (density-dependent distribution). Such a relationship is exhibited in small shoaling pelagic fishes (Csirke 1988), and may be a feature of marine fish populations in general (Winters and Wheeler 1985). A positive relationship between distribution and abundance among other animal species is common and found at various spatial scales, but is not universal (Gaston and Lawton 1990). In the present study, imprecise estimates of the abundance and incidence of some species (Tables 3.1 and 3.3), and sampling by the bottom trawl of probably only a small proportion of the total population of some pelagic species, may have precluded the detection of a similar correlation in other species. Furthermore, significant correlations may exist within age-classes, but be obscured when they are analyzed in aggregation (Marshall and Frank 1994).

Table 3.4. Pearson coefficients of correlation between estimates of species incidence and biomass (r), and incidence and log-transformed biomass (r_{10}) with their associated p -values. Each triennial survey provided one observation ($n = 6$).

Species	r	r_{10}	p
English sole	.84	.95	.004
rex sole	.94	.95	.004
Pacific halibut	.91	.94	.005
Dover sole	.86	.90	.016
Pacific sanddab	.60	.88	.020
chub mackerel	*.99	*.82	*.179
white croaker	.78	.80	.055
jack mackerel	.85	.78	.069
silvergray rockfish	.45	.74	.095
American shad	.46	.72	.105
shortspine thornyhead	.73	.71	.117
Pacific ocean perch	.83	.70	.123
canary rockfish	.47	.61	.198
bank rockfish	.16	.61	.198
spiny dogfish	.54	.56	.243
Pacific herring	.76	.55	.262
Pacific cod	.63	.54	.264
sharpchin rockfish	.54	.54	.266
bocaccio	-.08	.46	.356
chilipepper	.36	.44	.381
arrowtooth flounder	.36	.32	.542
Pacific hake	.26	.22	.669
yellowmouth rockfish	-.17	.17	.749
darkblotched rockfish	.18	.12	.818
redstripe rockfish	.07	.06	.913
stripetail rockfish	-.11	.00	.999
yellowtail rockfish	-.03	-.01	.992
walleye pollock	.09	-.02	.975
sablefish	-.20	-.12	.814
splitnose rockfish	-.22	-.14	.785
shortbelly rockfish	-.37	-.16	.759
lingcod	-.68	-.54	.269
widow rockfish	-.51	-.58	.226

*chub mackerel was not encountered in 1977 and 1980 ($n=4$).

Fig. 3.6. Correlation between estimated incidence and $\log_{10}(\text{biomass})$ for each of five flatfish species where each point represents an estimate from one of the six triennial surveys.

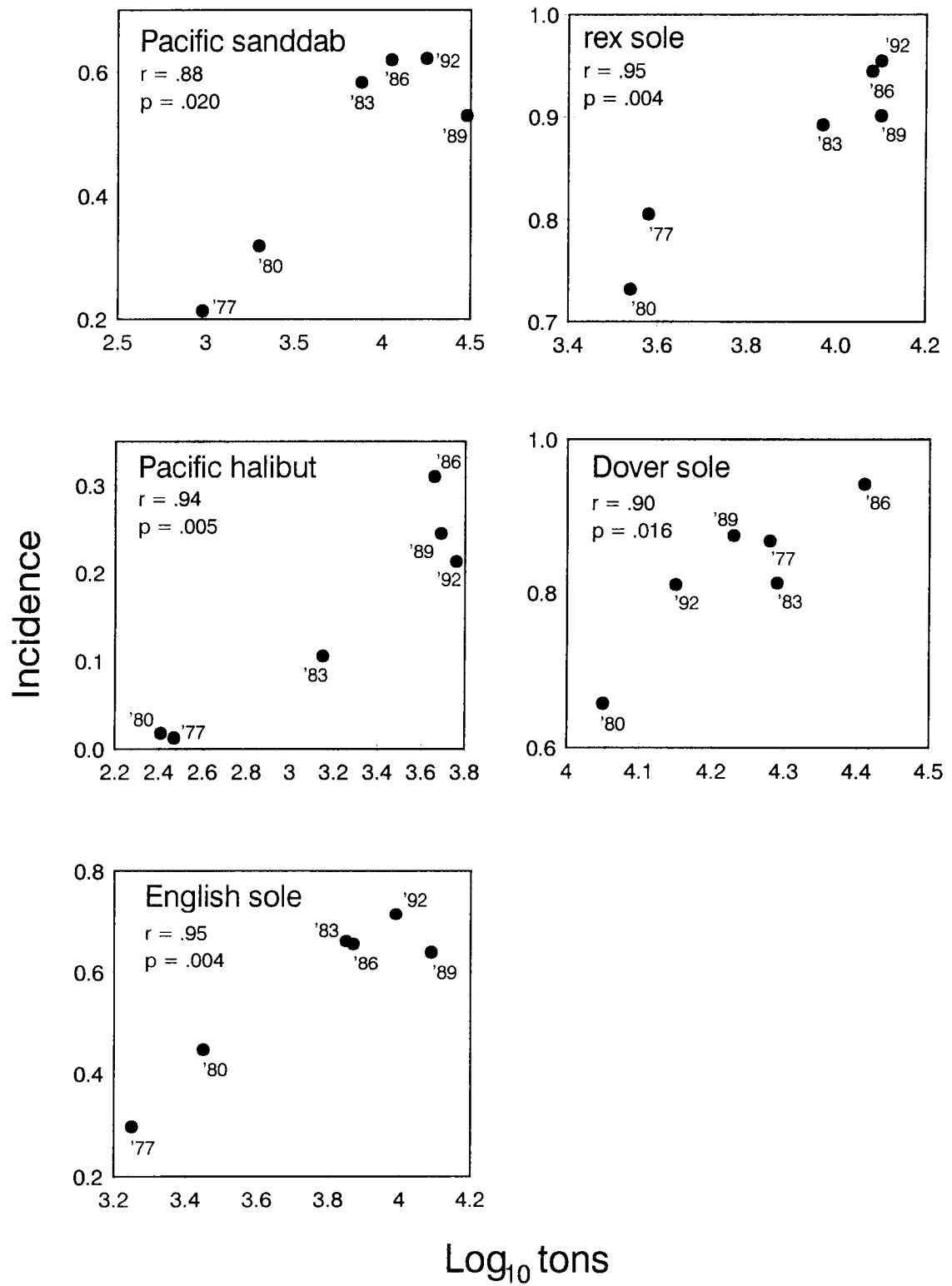


FIGURE 3.6

In some cases, positive correlations between incidence and abundance may be a sampling artifact, because as individuals become less abundant, they are more difficult to detect under a constant level of sampling effort (Gaston and Lawton 1990, Hanski et al. 1993). Furthermore, if individuals are randomly distributed, then a correlation between incidence and abundance is expected (Wright 1991). A positive relationship between incidence and abundance does not imply that the “geographic range” of a fish stock increases with increases in abundance (Murawski and Finn 1988, Marshall and Frank 1994), rather it simply suggests that an increase in biomass is accompanied by an increase in occupied space. Nevertheless, investigating such relationships may be useful for exploratory purposes and lead to hypotheses that can be tested under perhaps more rigorous conditions.

Of the five flatfish species that showed a significant correlation between incidence and abundance (Pacific sanddab, rex sole, Pacific halibut, Dover sole, and English sole), rex and Dover soles occupied more of the available area within each substrate category than the other flatfish species (Fig. 3.7), coinciding with their high incidence within the study area (Table 3.3).

Pacific sanddab and English sole occupied a higher ratio of sand to mud substrate over the last five surveys (Fig. 3.8) than did rex sole, Pacific halibut, and Dover sole, which may be associated with Pacific sanddab and English sole occupying a slightly shallower depth range (see Fig. 3.3) where sand may be more prevalent (Moore and Luken 1979) than the depth range of the other three flatfish species. Of course, substrate

Fig. 3.7. Area occupied by five flatfish species in four substrate types within the northern portion of the study area for each triennial survey. For each species, the survey years are presented in order of increasing incidence within the northern region.

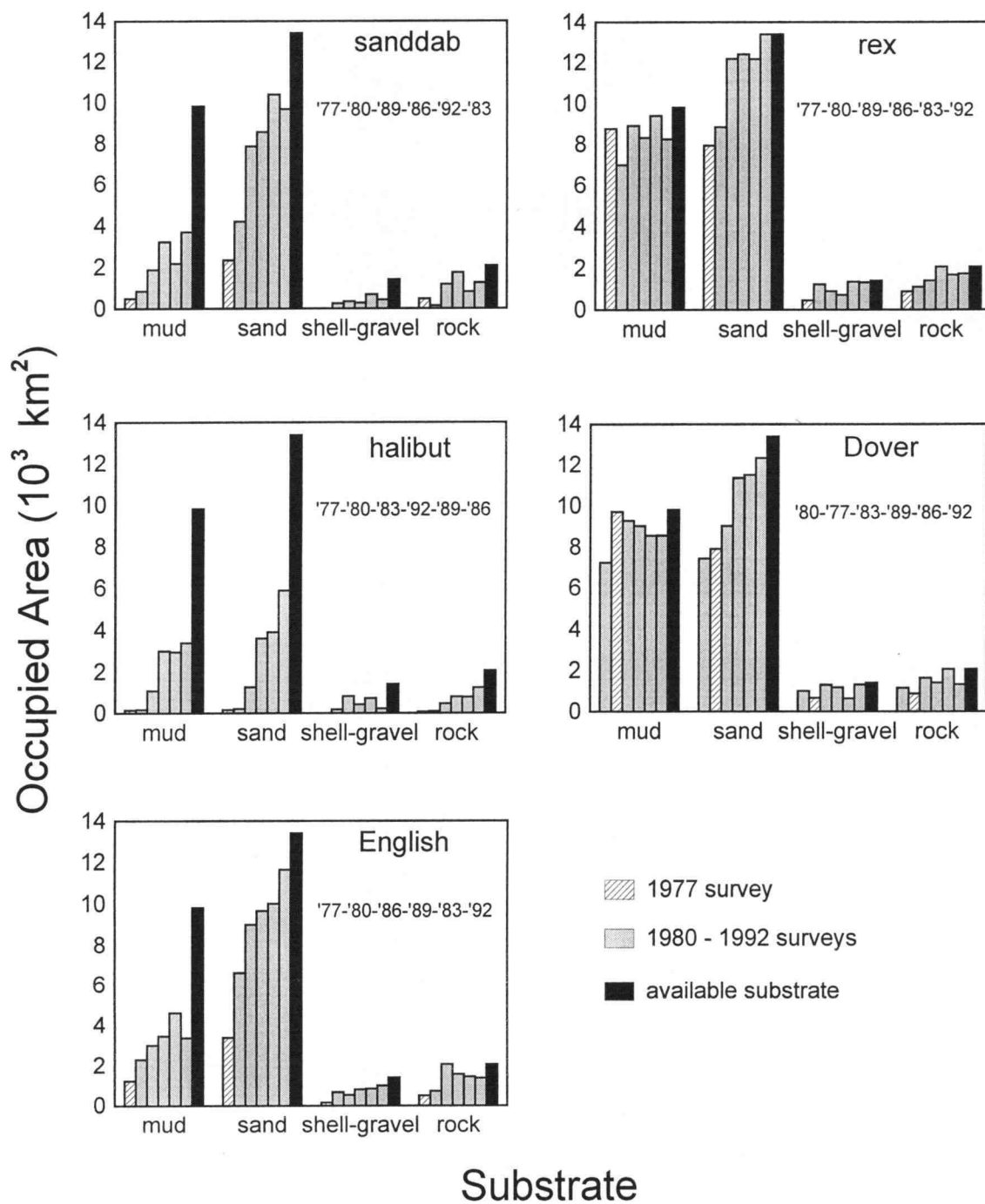


FIGURE 3.7

Fig. 3.8. Regression of the ratio of the area occupied in sand to the area occupied in mud for each of five flatfish within the northern portion of the study area for the 1980-1992 surveys.

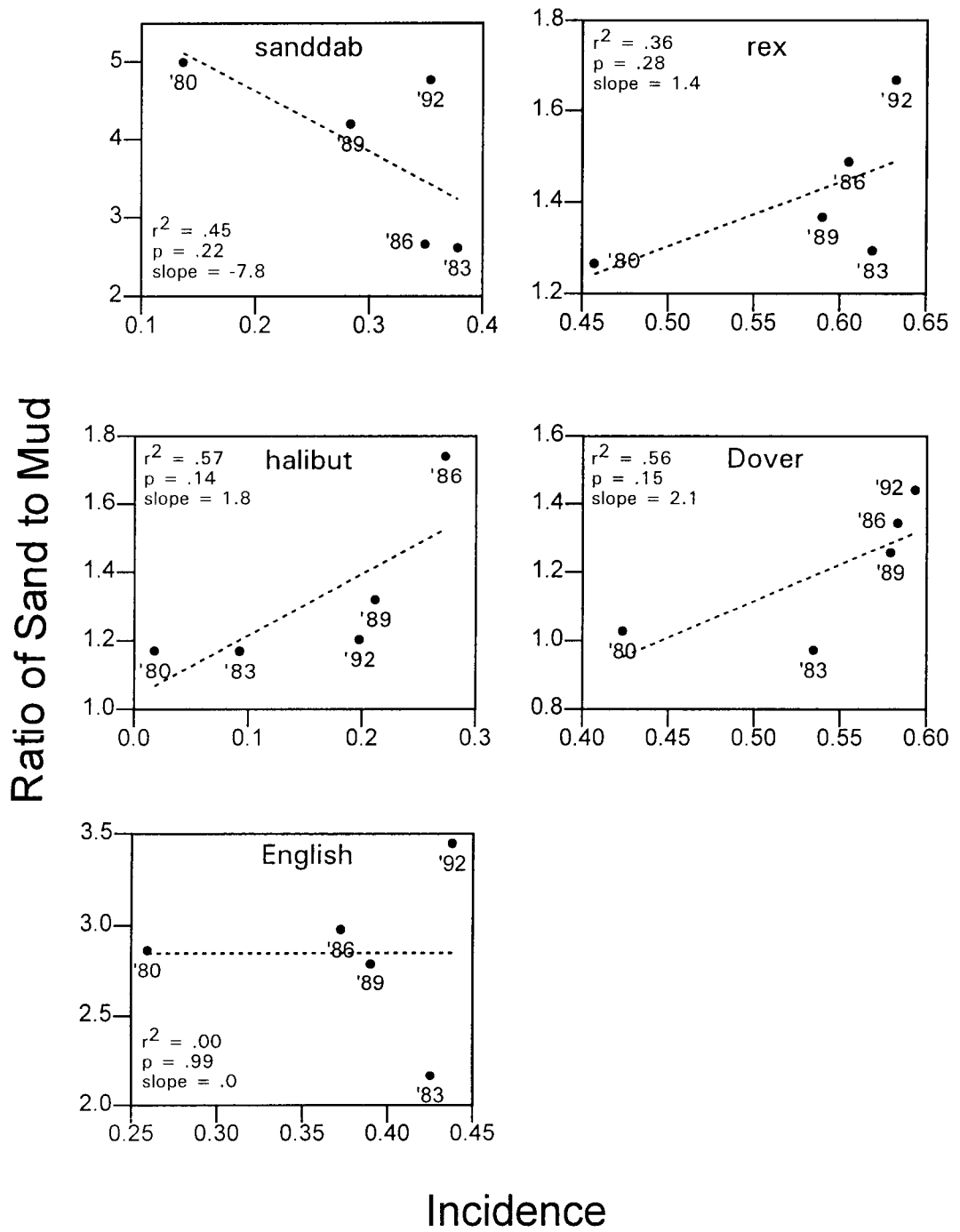


FIGURE 3.8

may be associated other physical or biological characteristics (e.g. temperature, distribution of preferred prey, and refuge from predators or competition) that more directly determine the distribution of flatfish.

Although inconclusive (because of the poor fit) the sand:mud ratio regressed on incidence (Fig. 3.8) suggests that sand was occupied at a greater rate than mud as incidence increased in the slightly deeper-ranging flatfish species (rex sole, Pacific halibut, and Dover sole). For example, the regression slope for Dover sole (2.1), indicates that increases in overall incidence of 10% were accompanied with an increase in the occupation of sand of .21 times more than the occupation of mud. Conversely, for Pacific sanddab, mud was occupied at a greater rate than sand with increasing overall incidence.

Part 2. Intersurvey Environmental Variation and Variation in Species Composition

Methods

Environmental Variation

Sampling effort limited the resolution to which environmental variation and variation in species composition could be examined across the study area. Eight regions were delineated from four latitudinal (<40°00', 40°00'-42°50', 42°50'-46°15', >46°15') and two depth intervals (<125 m and >125 m). Environmental variation within regions

was assessed from annual variation in monthly upwelling indices, and intersurvey variation in surface and bottom water temperature measurements that were taken during trawling.

Latitudinal boundaries were selected on the basis of physiographic characteristics of the study area (Deimling 1990). Perhaps the most prominent latitudinal boundary is near Cape Blanco ($42^{\circ}50'$) (Fig. 3.9). To the south, the coastline is rugged, and the continental shelf is narrow and receives little freshwater input. To the north, the coastline is relatively smooth, and the shelf is broad and receives significant freshwater input, primarily from the Columbia River (Shepard and Wanless 1971, Landry and Hickey 1989).

Within the southern area, the latitudinal division at Delgada Canyon ($40^{\circ}00'$), adjacent to Cape Mendocino, marks the position of the Gorda Escarpment and the southern extent of the Juan de Fuca tectonic plate. The northwesterly-trending coastline to the south has weaker onshore transport during winter and stronger offshore transport during summer than the northerly-trending coastline to the north (Parrish et al. 1981).

Within the northern area, the latitudinal division at Astoria Canyon (about $46^{\circ}15'$), at the entrance of the Columbia River, separates the canyon-excised coast off Washington to the north, from the Oregon coast to the south. It also marks generally the southernmost extent of shell and gravel surficial substrate (Moore and Luken 1979).

Fig. 3.9. Eight regions of the study area that were delineated to compare intersurvey environmental variability and variability in species composition.

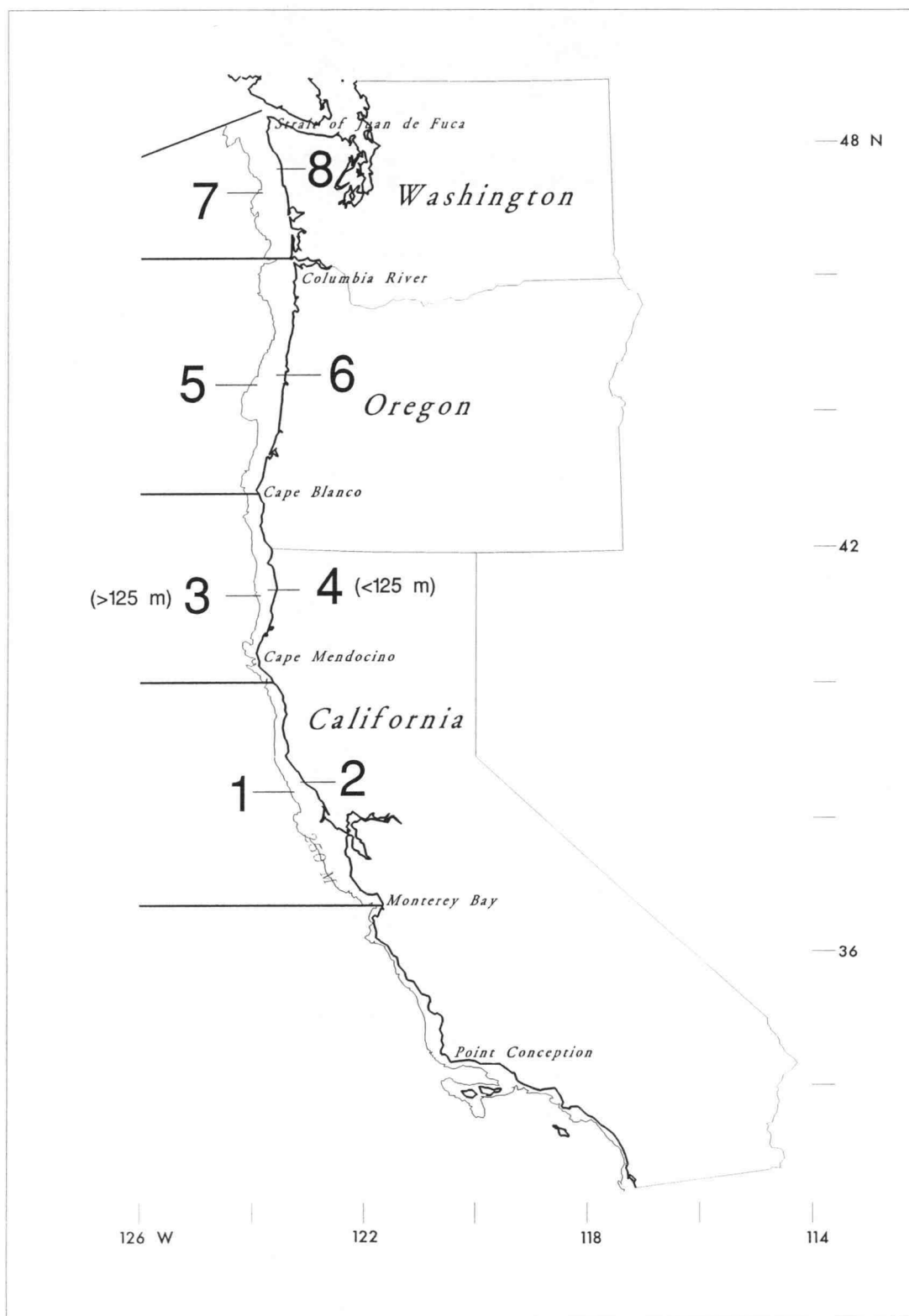


FIGURE 3.9

Off Oregon, the depth where wave actions are effective in moving bottom sediments vary from about 95 m in summer to 200 m during winter (Kulm et al. 1975). I chose the 125-m depth contour to approximate the boundary between the outer shelf and deep upper slope waters from the shallow shelf. Deep water has properties influenced predominately by internal processes such as advection and diffusion; whereas the shallow shelf water is influenced largely by external processes such as seasonal heating and cooling, precipitation, evaporation, wind mixing, freshwater runoff, and wave-induced sediment transport.

Positive values of the upwelling index is an estimate of the amount of bottom water that is upwelled to the surface to replace water that has been transported *offshore* from wind stress (Ekman transport) (Bakun 1973). Negative values indicate *onshore* transport of surface water causing the reverse of upwelling (downwelling). The upwelling index is indicative of large-scale water movement over hundreds of kilometers off shore and index values are available for only distinct latitudes, five of which are along the coast within the present study area. Therefore, upwelling was evaluated by latitudinal trends, rather than within the designated regions of the present study. Monthly indices were available for latitudes 36°, 39°, 42°, 45°, and 48° N. I calculated the mean and standard deviation of the monthly upwelling index for each month over the years spanning the trawl surveys. 1977 to 1992 ($n = 16$).

Surface temperature was measured at 66% of the haul locations in 1980 and at more than 95% of the haul locations in the remaining four surveys. Bottom temperature

was measured less consistently than surface temperature; at only 9% of the haul locations in 1983, but 89% of the haul locations in 1992 (see details on the collection of temperature measurements in Chapter 2). For each region, I averaged temperature measurements across hauls, then calculated the standard deviation of these averages over survey years ($n = 6$).

Variation in Species Composition

Within each region in a given year, species composition can be represented by a single point in 33-dimensional space (33 species), where the coordinates of each point are specified by the relative abundance of each species. As a measure of variation in species composition within each region, I calculated the deviation (multivariate standard deviation) of these points, measured in Euclidean distance, from their five-year 1980-92 mean (“root-mean-square standard deviation”, FASTCLUS, SAS Institute Inc. 1988). The 1977 survey was not included in the calculations, because it covered a slightly deeper depth range than subsequent surveys.

Results and Discussion

It is recognized that upwelling is strongest during summer, and that southern latitudes (about $<42^{\circ}$ N) experience upwelling for most of the year, while northern latitudes experience moderate to low upwelling during the summer and downwelling during winter (Bakun 1973, Parrish et al. 1981; also Fig. 3.10). Within the study area, interannual variation in the monthly upwelling index was greatest during the summer in

the south, and greatest in the winter in the north (Fig. 3.11). In general, upwelling variation during the trawl surveys in summer decreased with latitude. Variation in surface water temperature was generally higher in the northern regions ($>42^{\circ}$ N, Fig. 3.12a). There appeared to be no consistent pattern in the variation in regional bottom water temperature across latitude or depth regions (Fig. 3.12b).

Measures of deviations in species composition among the last five surveys (SD_m , Fig. 3.13) indicate that the greatest amount of variation occurred within the shallow shelf area off California (region 2) and within both the shallow shelf and deep areas between Cape Mendocino and Cape Blanco (regions 3 and 4, see Fig. 3.9). The region of least variation occurred in the shallow shelf area off northern Washington (region 8). It should be recognized that the multivariate standard deviation can be affected greatly by large variations in the relative abundance of only a single species, and therefore does not necessarily indicate substantial shifts in the biomass of *all* species.

If environment determines the potential for species abundance and distribution (Fig. 3.1), then the regions with the greatest intersurvey environmental variation might be expected to contain the greatest amount of intersurvey variation in species composition. Consistent with this, the regions with high variation in species composition (regions 2-4) corresponded to areas of greatest intensity and interannual variation in upwelling during the summer (approximately $\leq 42^{\circ}$ N, Fig. 3.11). Although general seasonal characteristics of upwelling within the California Current System (CCS) are maintained

Fig. 3.10. Mean of the monthly upwelling index over the years spanning the triennial surveys (1977-1992, $n = 16$) for latitudes 36° , 39° , 42° , 45° , and 48° N.

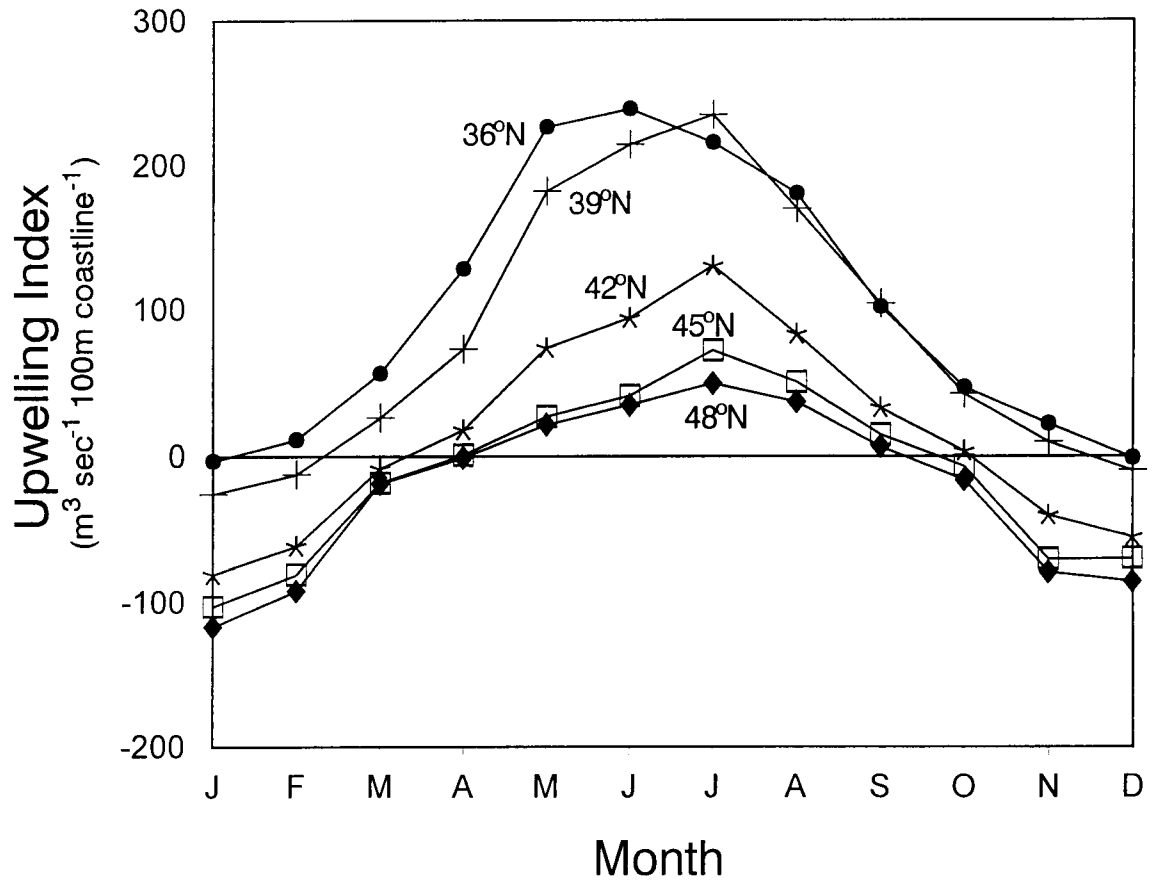


FIGURE 3.10

Fig. 3.11. Standard deviation of the monthly upwelling index over the years spanning the triennial surveys (1977-1992, $n = 16$) for latitudes 36° , 39° , 42° , 45° , and 48° N.

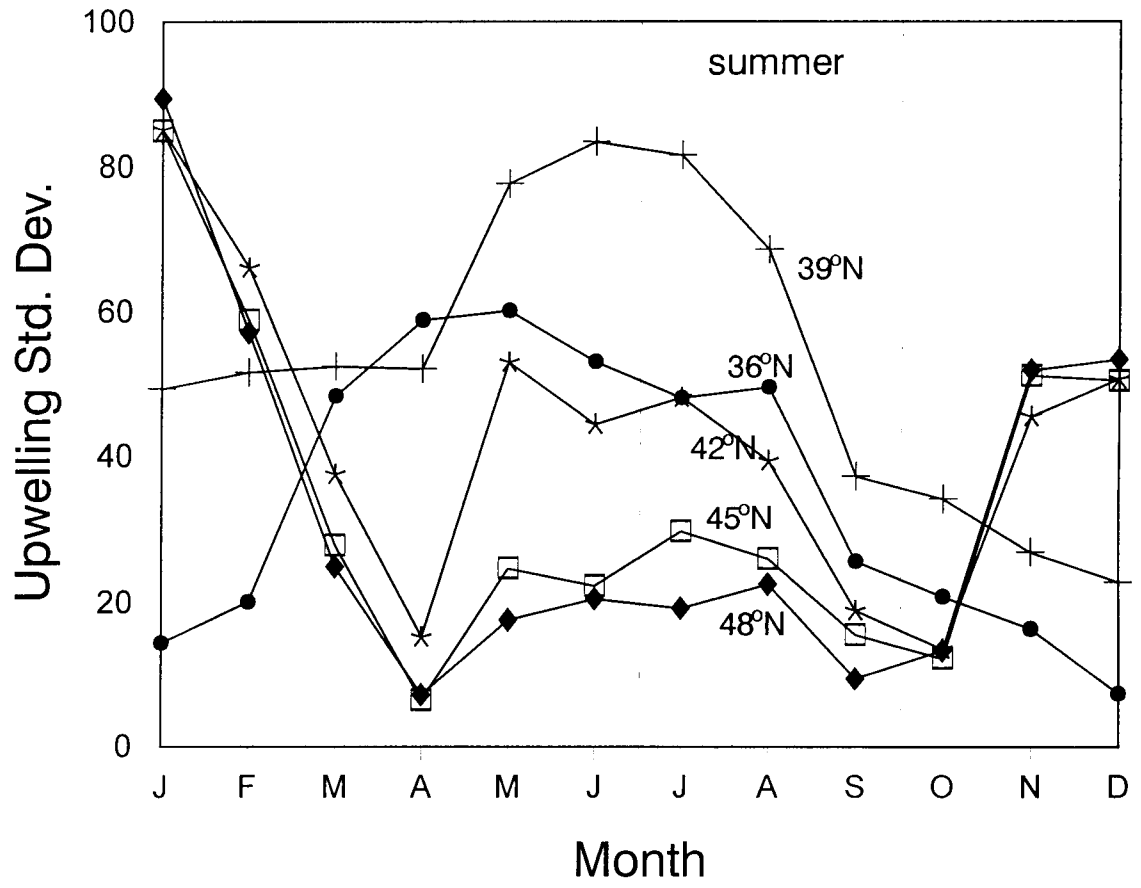


FIGURE 3.11

Fig. 3.12. Intersurvey variation (std. dev., $n = 6$) in (a) surface and (b) bottom temperature from averaged temperature measurements across hauls within each of eight regions (see Fig. 3.9).

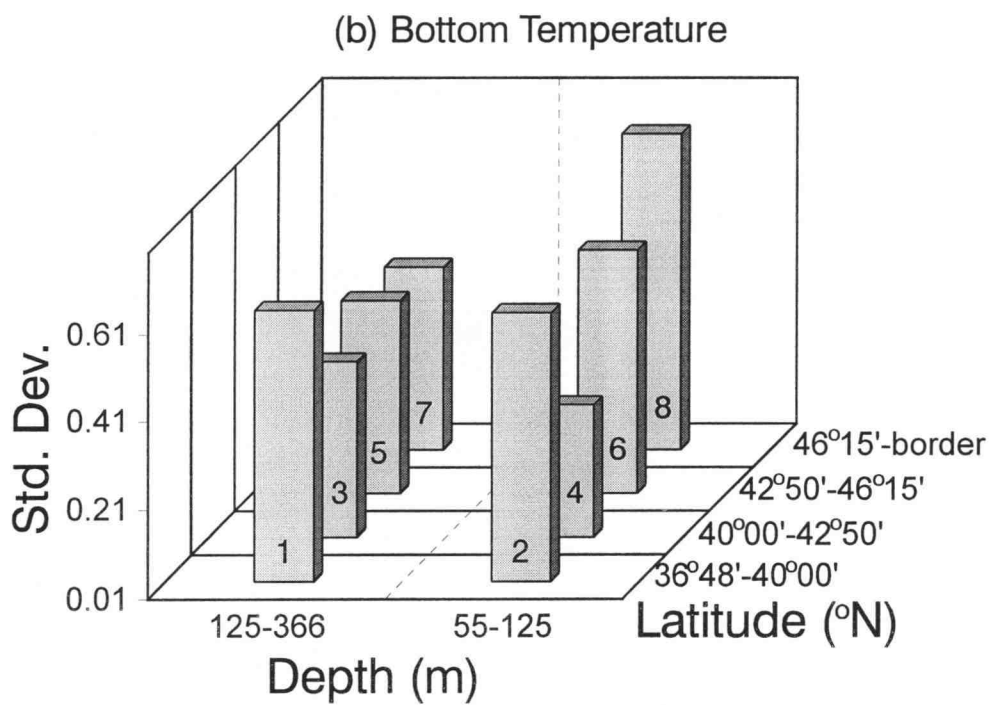
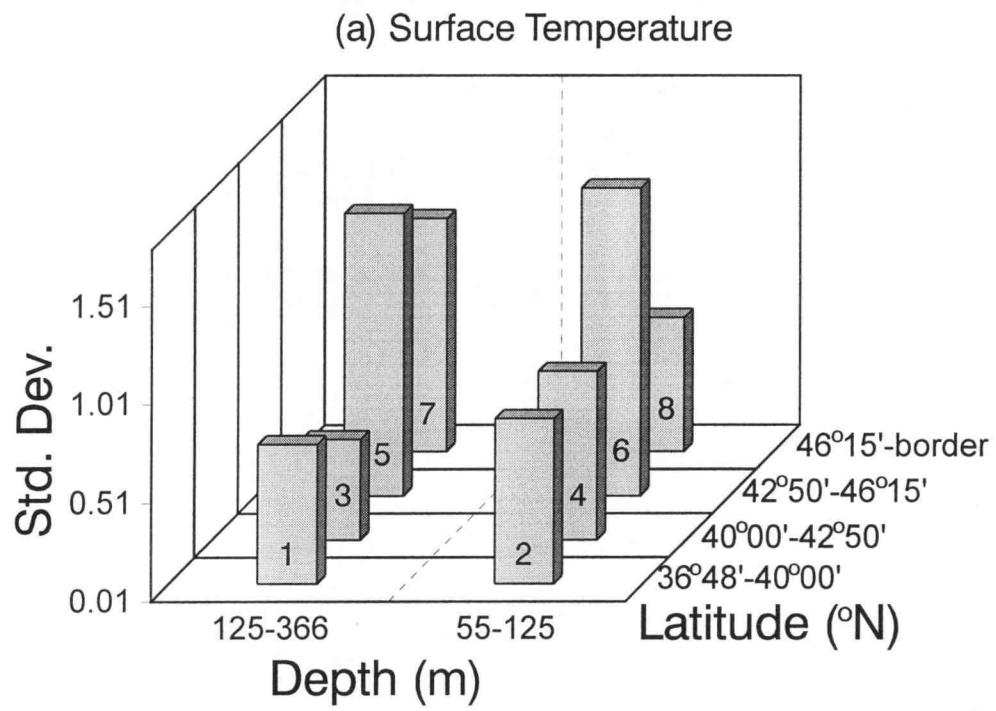


FIGURE 3.12

Fig. 3.13. Variation in species composition, indicated by the multivariate standard deviation (SD_m , $n = 5$, 1980-1992 surveys), within eight regions of the study area (see Fig. 3.9).

interannually, large interannual differences in seasonal onset, intensity, duration, and properties of short-scale fluctuations in upwelling occur (Parrish et al. 1981).

Compared to the north, the southern portion of the study area (approximately south of Cape Blanco, Fig. 3.9) is recognized as having more persistent, but variable upwelling during the year. The regions between Cape Blanco and Cape Mendocino (regions 3 and 4), which had high variation in species composition, have particularly strong pulses (2 days to several weeks) of offshore water transport during summer. Capes such as these tend to be upwelling ‘centers’ which generate narrow (~40 km) offshore surface (0-200 m) jets, carrying filaments of coastal water several hundred kilometers offshore (Parrish et al. 1981, Huyer 1990).

Contrary to upwelling, variation in species composition (Fig. 3.13) did not appear to correspond to intersurvey variation in surface temperature (Figs. 3.12a). Temperature at the surface may be too far removed from processes substantially affecting the distribution of bottom-trawl fish, whereas bottom temperature may directly impact the distribution of bottom-fish and may also be more closely indicative of processes of near-bottom circulation. However, there was an unanticipated *negative* correspondence between variation in bottom temperature and variation in species composition (Figs. 3.12b and 3.13). Pearson coefficients of correlation and associated p-values for variation in species composition, surface temperature, and bottom temperature were: -.20 ($p = .64$) for variation in surface temperature and variation in species composition; -.72 ($p = .04$)

for variation in bottom temperature and variation in species composition; and -0.13 ($p = 0.75$) for variation in surface temperature and variation in bottom temperature.

The species most responsible for intersurvey variation in species composition within the regions of high variation (regions 2-4) were spiny dogfish, Pacific herring, Pacific hake, jack mackerel, white croaker, chub mackerel, splitnose rockfish, chilipepper, shortbelly rockfish, bocaccio, sharpchin rockfish, sablefish, and Dover sole (Table 3.5). Of these, Pacific hake had the greatest affect on variation, and in fact greatly affected variation in all regions, because of its usually high and variable within-region abundance, particularly in the shallow regions of the shelf (Fig. 3.14). For example, its estimated biomass within region 2 in 1980 was 60 times its 1992 region 2 biomass (although the estimated biomass within the entire study area in 1980 was only 85% of 1992's, Table 3.1).

Jack mackerel affected species composition within five of the eight regions (mainly shallow regions, Table 3.5) primarily from its high level of abundance in the latter two surveys (Table 3.1). Species such as Pacific herring, white croaker, chub mackerel, shortbelly rockfish, and Pacific sanddab, affected species composition within fewer regions (Table 3.5); and similar to jack mackerel, mostly from high levels of abundance during only one or two surveys (Table 3.1).

Upwelling is linked to increased primary production by pumping cold, nutrient-rich water to the surface. It may also affect the vertical and horizontal structure of the

Table 3.5. Species that contributed substantially to variation in species composition among survey years within eight regions of the study area (see Fig. 3.9). A species is not listed or ranked if it did not reach a relative abundance of at least 5% in a given region over the last five surveys. Within each region, species were ranked in order (high to low) of variability (std. dev., $n=5$) relative to the 1980-92 mean biomass of all 33 species combined. Shaded columns refer to the deep regions.

Species	Region							
	1	2	3	4	5	6	7	8
spiny dogfish	3	2	1				3	2
Pacific herring		5		5		6		
Pacific hake	1	1	2	1	1	1	1	1
jack mackerel		4		2	3	3		3
white croaker		6						
chub mackerel				6		4		
splitnose rockfish			4					
widow rockfish	6						8	
yellowtail rockfish							6	
chilipepper	4		6					
shortbelly rockfish	2			3				
bocaccio	8		5				2	
canary rockfish	9						9	
redstripe rockfish							7	
stripetail rockfish	7							
sharpchin rockfish			7		4			
sablefish	5	3	3	4	2		4	
lingcod						5		
Pacific sanddab						2		
arrowtooth flounder							5	
Dover sole			8					

Fig. 3.14. Estimated biomass of each of the 33 dominant species indicating species composition within each of eight regions of the study area (see Fig. 3.9).

FIGURE 3.14

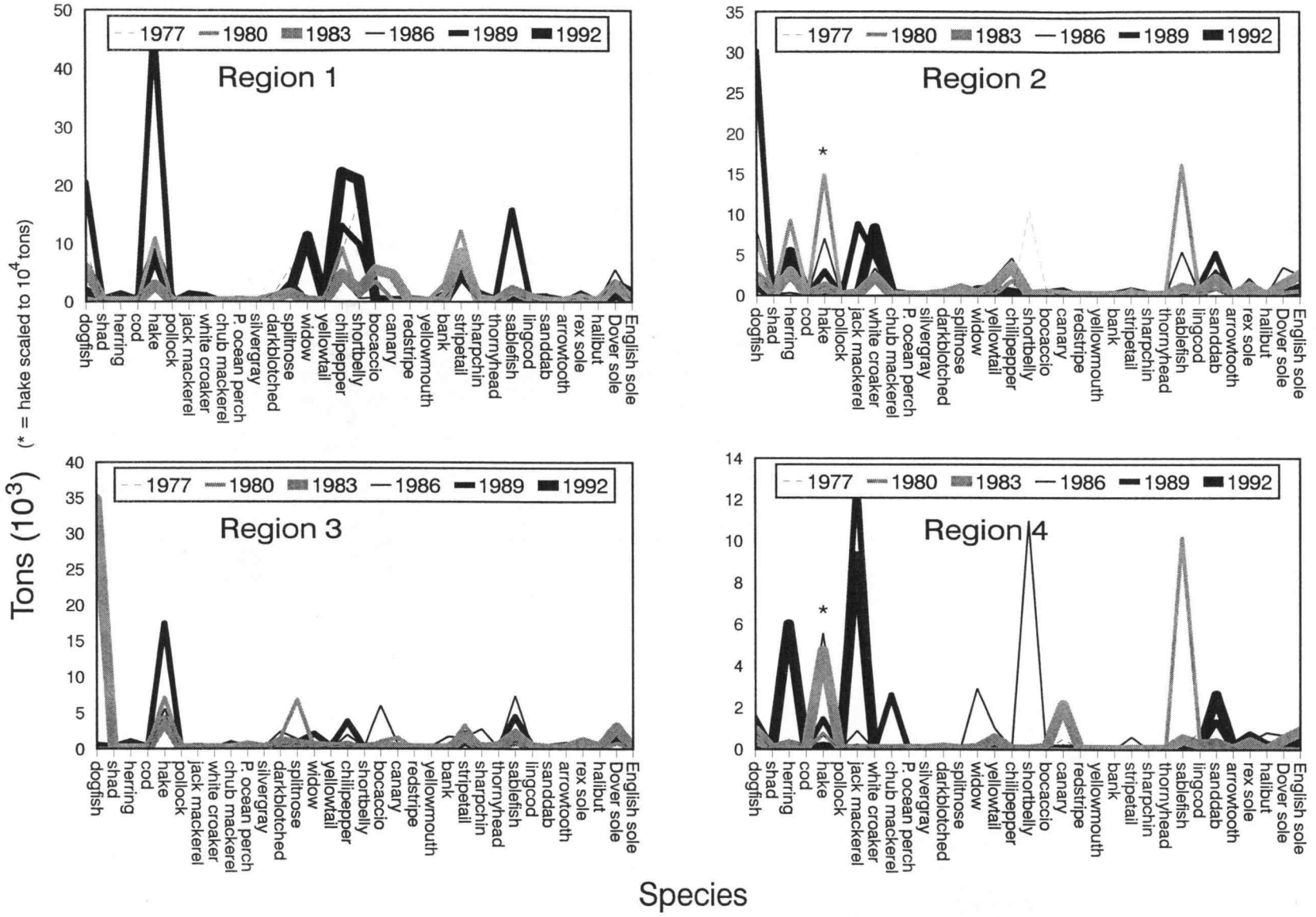
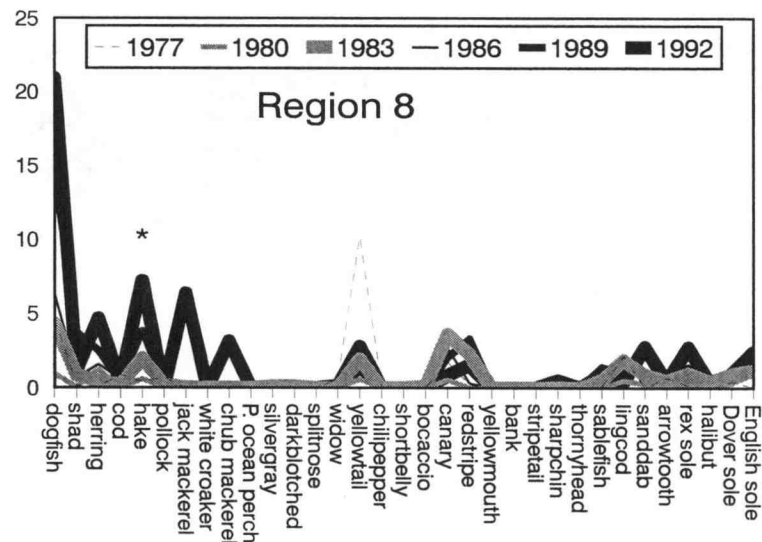
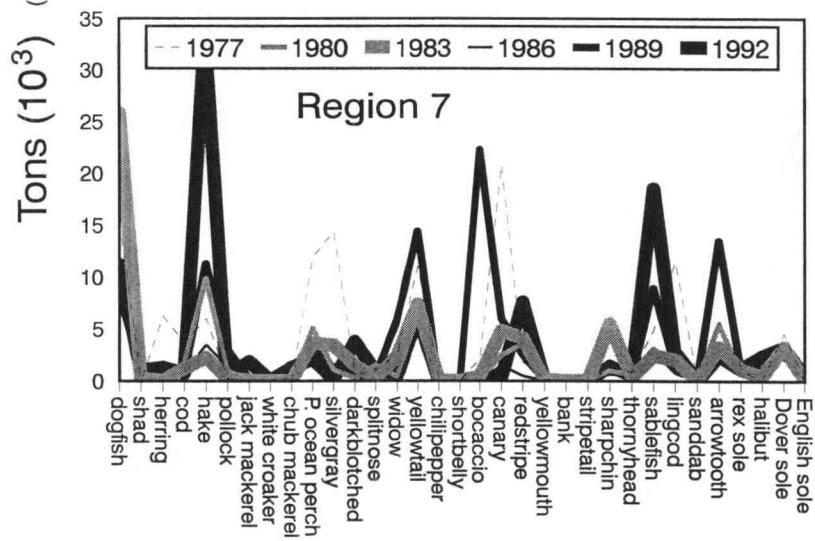
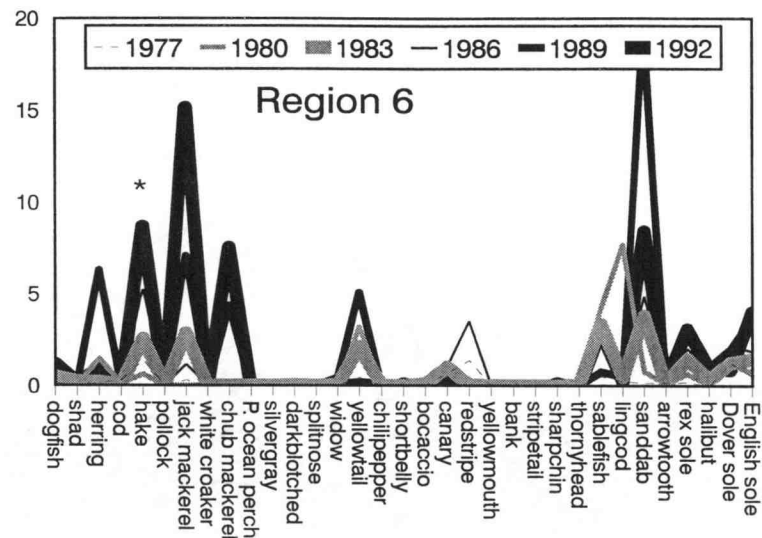
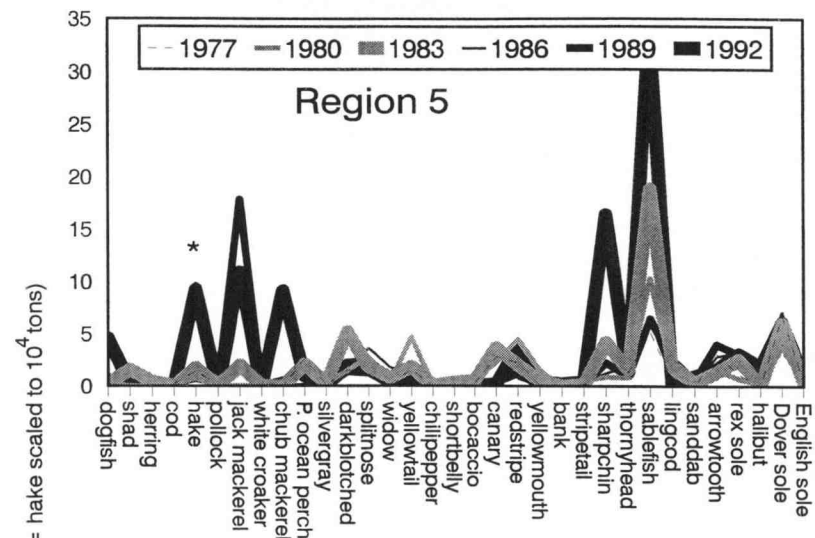


FIGURE 3.14 (Continued)



water column. For example, in the case of stratified water, upwelling may bend isotherms, isohalines, and isopycnals upward to the point of intersecting the surface near the coast (Huyer 1990). Therefore, interannual variation in upwelling may not only contribute to variation in species composition by causing variation in food production and availability, but also by altering the vertical and horizontal structure of the water column.

The distribution of pelagic¹ fish near the bottom may reflect their midwater distributions associated with their responses to stimuli within the upper water column. Fish respond to changes in the environment through vertical and horizontal movements. Laevastu and Hayes (1981) suggest that pelagic fish respond to short-term changes (<3 days) primarily by moving vertically. Moreover, most pelagic species undergo additional vertical movements to varying extent in concert with the diel vertical movements of their prey. Generally, these fish move upward before sunset and are more dispersed in the water column at night, and move downward at sunrise and are less dispersed in deeper water during the day. The thermocline may form a barrier to the vertical movement of some fish (Laevastu and Hayes 1981).

Consequently, seasonal changes in the thermal structure of the water column may affect the vertical distribution of fish, particularly epipelagic fish, such as Pacific herring, jack mackerel, and chub mackerel. The increased abundance of these latter three species

For clarity, I have adopted the following definitions: "Demersal" fish as adults live and feed predominately near the bottom at most times, and are contrasted to "pelagic" fish which live predominately within the water column, but can also occur in large quantities near the bottom. The pelagic environment includes the "epipelagic" zone (0-200m deep) and the "mesopelagic" zone (200-1000m deep).

in the bottom-trawl surveys (Table 3.1), and the corresponding increase in incidence of assemblages they dominated (see Table 2.5, Chapter 2), occurred in the latter two surveys, and may reflect an anomaly in the vertical structure of the water column, such as a weaker or deeper thermocline. Of note, in a 7-yr seining study, jack and chub mackerel showed a dramatic increase in abundance in the upper water layers off Oregon and Washington in the summer of 1983 and 1984 in association with the 1983 El Niño event (Pearcy and Schoener 1987); however, both these species were in low abundance near the bottom in 1983 according to data from the bottom-trawl surveys (Table 3.1), but instead exhibited peak abundances in the 1989 and 1992 surveys.

Fish move horizontally generally in response to gradual (several days to months) changes in the environment which often occur over large areas (Laevastu and Hayes 1981). Over the course of a year, fish may migrate across great horizontal distances between spawning, wintering, and feeding grounds (Harden Jones 1968). Most of the 33 dominant species in the present study are outside their spawning period during the summer (Hart 1973, Bailey et al. 1982, Eschmeyer et al. 1983, Love et al. 1990), so their horizontal movements are probably driven by requirements for feeding while maintaining themselves within physiologically suitable habitats.

Adult Pacific hake migrate throughout the entire study area to feed, starting from southern California during spring and ending in northern Washington and Vancouver, Canada in fall. The rate of their northward migration varies and its timing is probably linked to the development of the California Undercurrent (Bailey et al. 1982). The

distribution of Pacific hake within the California Current System during the summer can vary substantially among years (Figs. 3.14), and because of Pacific hake's immense abundance, it has a considerable impact on species composition, particularly over the shallow portion of the shelf. The distribution of Pacific hake is also influenced greatly by wide variations in year-class strength (Dark and Wilkins 1994).

Pacific ocean perch, sablefish, and Dover sole migrate across a large depth range from deeper off-shelf waters in the winter to shelf waters in the summer, apparently with the shelfward intrusion of cold water (Alverson et al. 1964). The onset of cold water intrusion can vary from year to year, and with it, variable timing in the migration of these species onto the shelf, introducing another potential source of intersurvey variation in species composition.

Part 3. Relating Species Abundance, Incidence, and Density to Changes in Species Composition

Methods

Conceptual Model

Models that mathematically relate spatial area to fish density have only recently been developed (MacCall 1990, Swain and Sinclair 1994, Marshall and Frank 1995). Their application include an examination of the effects of density-dependent distribution on the catchability of a fish stock (Swain and Sinclair 1994), and investigating evidence

of density-dependent habitat selection by examining the dynamics between local density and increases in overall abundance (Marshall and Frank 1995). Herein, I developed a simple conceptual model to explore the relationship between regional changes in a species' biomass, incidence, and density, and their potential affect on species composition (Fig. 3.15).

Each rectangular box in the model (Fig. 3.15) represents the potential geographic range of a given species across geographic sites over a specified period of time. Two smaller areas are indicated within the geographic range — the area of occupied sites are indicated by solid boundary lines and unoccupied sites by dashed lines. Within a species potential geographic range, from time t_1 to t_2 , the biomass of a species may increase, decrease, or remain constant. Similarly, the area it occupies may increase, decrease, or remain constant.

The model assumes that in scenarios with constant or increasing incidence (1, 2, 4, 5, 7, and 8), the geographic sites occupied in time t_1 are occupied in time t_2 . Similarly, in scenarios with decreasing incidence (3, 6, and 9), no sites become newly occupied in time t_2 . Thus, from time t_1 to t_2 , one of nine different scenarios involving the change (or lack of change) in biomass, incidence, and density can occur. In scenario 1, unchanging density from time t_1 to t_2 within the continuously occupied area is possible only if total incidence increases proportionally to total biomass and the continuously and newly occupied areas incur equal densities, or if incidence does not increase proportionally to biomass and occupied areas incur unequal densities. Also, in

Fig. 3.15. Conceptual model of the relationship between changes in a species' biomass ($b+$ = increase, $b0$ = no change, $b-$ = decrease), incidence (i), and density (d) from time $t1$ to $t2$. Regional changes in fish density may affect species composition.

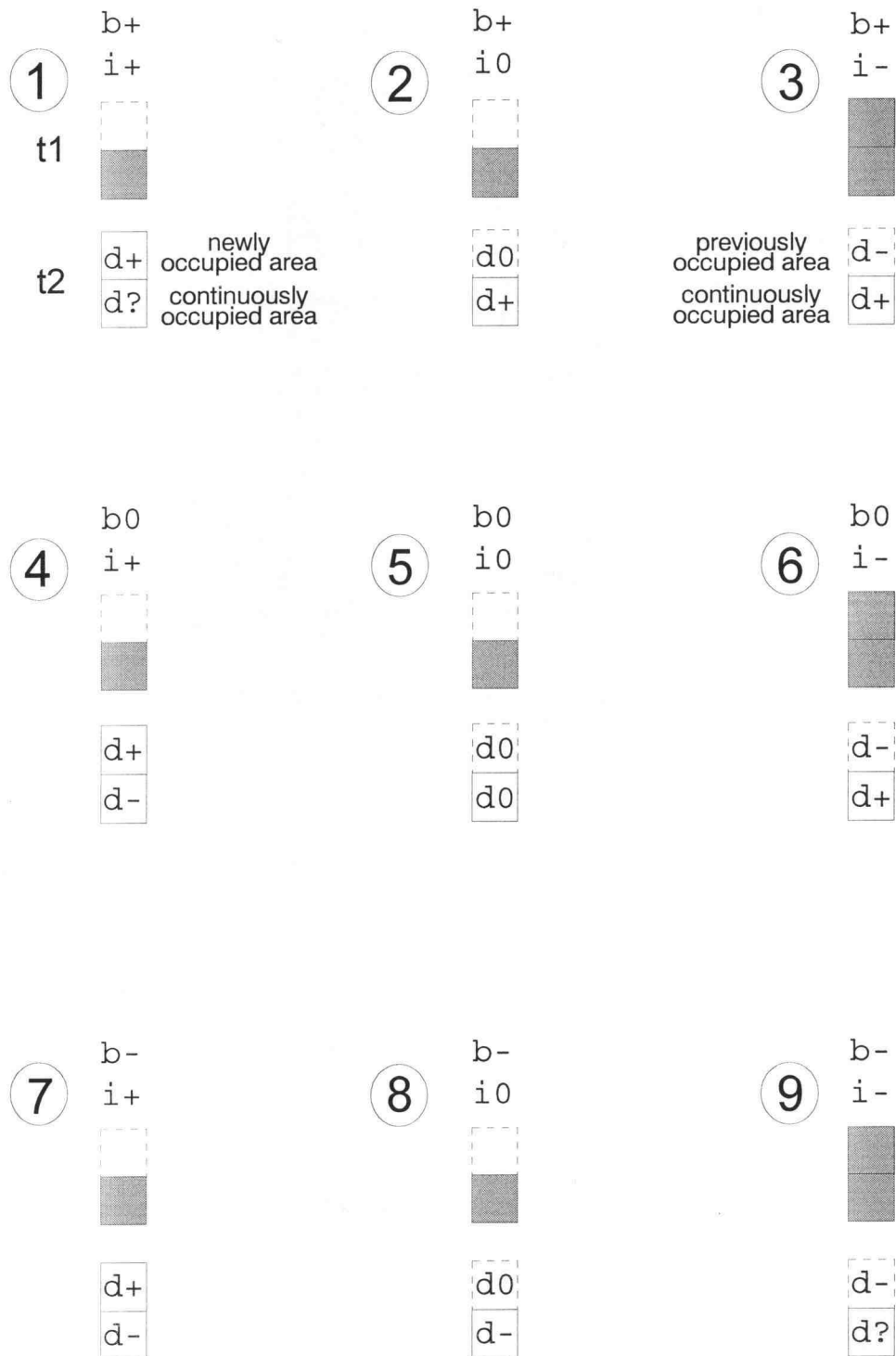


FIGURE 3.15

scenario 9, unchanging density within the continuously occupied area is possible only if incidence decreases proportionally to biomass.

I use the term “species composition” to refer to a group of species and their relative abundance. If a given species’ density changes within an area, then species composition within that region will be affected if the density of co-occurring species remains constant. The magnitude of the effect will depend upon the magnitude of change in density relative to the density of co-occurring species.

Numerous mechanisms may be involved in producing a given scenario. For example, scenarios 1 and 9 may occur from a population maintaining a constant density through density-dependent mechanisms such as competition for food or space, or territorial behavior. Scenario 3 may occur if the amount of habitable environment decreases (including the possibility of a decrease in the area occupied by prey), forcing a coincidental increase in fish biomass to occupy a smaller area, resulting in higher fish density. Scenario 7 may occur from an increase in the amount of habitable environment and a coincidental decrease in biomass (opposite of scenario 3). Scenario 6 may occur for the same reason as scenario 3, but because biomass does not change, a correlation between biomass and incidence would not be expected and fish density should be lower than in scenario 3. No change in incidence (scenarios 2, 5, and 8) may occur if the amount of habitable environment remains constant.

Empirical Examination of the Conceptual Model

I used the NMFS research catch data to investigate whether changes in density of a given species and its affect on species composition were consistent with expectations from the conceptual model (Fig. 3.15). Because some estimates of biomass and incidence were imprecise (see Tables 3.1 and 3.3), I investigated only those cases with large changes in biomass or incidence. Data from the 1977 survey were omitted, because this survey was conducted over a slightly greater depth range than subsequent surveys. Furthermore, predictions from the model could be tested only from data that met the assumptions of the model (i.e. area category 1 in Fig. 3.16 was small; see assumptions above).

Because there was an unmanageable number of cases to examine for meeting the assumptions of the model ($33 \text{ species} \times 4 \text{ successive year combinations} = 132 \text{ cases}$), I sought to limit the scope of potential cases to investigate. Therefore, of those species that exhibited substantial variation in *both* incidence and biomass, I examined only those that showed a consistency in scenarios among successive years (i.e. changes in biomass and incidence were correlated). Thus, I examined those species that exhibited invariance in biomass only or in incidence only, and those that showed a positive or negative correlation in biomass and incidence. To identify which species showed one of these characteristics, I assigned each of the 33 species to one of four categories according to their degree of variation in total biomass and incidence among surveys: (1) those that exhibited little change in both biomass and incidence; (2) those that exhibited little

Fig. 3.16. An example of the area categories that each latitude/longitude grid cell was assigned. A grid was overlaid over the entire study area for each survey year; each cell had a dimension of .10 degree of latitude by .20 degree of longitude. Area categories are: (1) cell occupied in the first year only; (2) cell occupied in both years; (3) cell occupied in the second year only; and (4) cell was not sampled in both years.

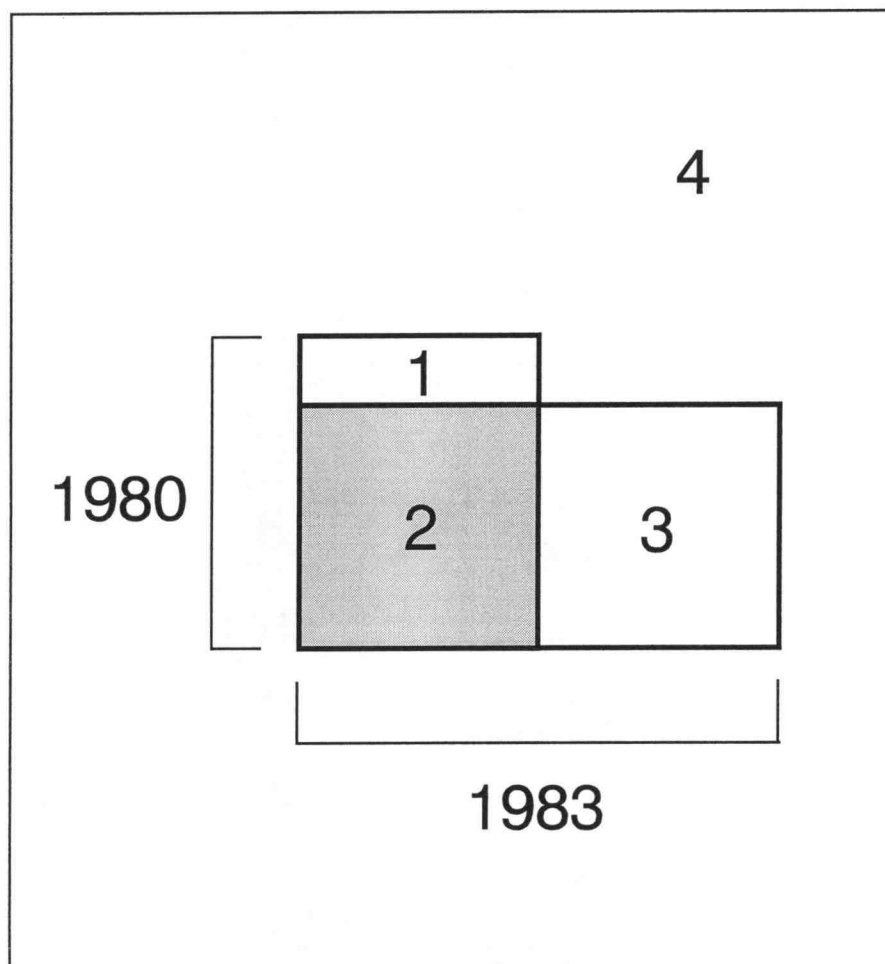


FIGURE 3.16

change in biomass, but a change in incidence; (3) those that exhibited a change in biomass, but little change in incidence; and (4) those that exhibited a change in both biomass and incidence.

Variation in biomass and incidence were measured by the difference in the maximum and minimum estimates among the latter five surveys (see Tables 3.1 and 3.3); for biomass, this difference was evaluated relative to the mean of the five estimates. Those species that were assigned to the first three variation categories and only those in variation category 4 that exhibited a positive or negative correlation in biomass and incidence were chosen for further examination. I recognized that there is a continuum in the degree to which species exhibit change. Distinguishing between species that exhibit change from those that exhibit little change is somewhat subjective. Furthermore, imprecise estimates for a given species may suggest greater variation in biomass and incidence among surveys than actually exist (McArdle and Gaston 1993).

To determine which species and year combinations met the assumptions of the model, and to evaluate changes in density within area categories (see Fig. 3.16), the entire study area was overlaid with a grid of cells consisting of .10 degree of latitude by .20 degree of longitude. For a given species and two survey years, each cell was classified into one of the area categories: (1) occupied in the first year only; (2) occupied in both years (continuously occupied); (3) occupied in the second year only (newly occupied); or (4) was not sampled in both years (Fig. 3.16). The species' average density (CPUE) across hauls in each cell was calculated and subsequently averaged across cells within

each area category, then compared between the two years. As an indicator of the effect of a given species on species composition in the continuously and newly occupied areas, I calculated the abundance of the species relative to the abundance of a set of select species.

Results and Discussion

No fish were assigned to variation category 1 (Table 3.6). Six species were assigned among categories 2 and 3, and the remainder of the 33 species were assigned to variation category 4. Of those species assigned to category 4, only the flatfish species Pacific sanddab, rex sole, Pacific halibut, Dover sole, and English sole showed a significant ($p < .05$) correlation between biomass and incidence (see Table 3.4 and Fig. 3.6). Therefore, these flatfish species and the species assigned to variation categories 2 and 3 were evaluated for meeting the assumptions of the model. Of these, only three species/year cases met the assumptions of the model sufficiently, Pacific sanddab and English sole between 1980 and 1983, and Pacific cod between 1980 and 1986.

In the context of species composition, changes in the density of a given species are meaningful only if viewed in reference to the density of co-occurring species. I chose to reference changes in the density of Pacific sanddab, English sole, and Pacific cod to the abundance of the six dominant flatfish species for two reasons. First, I needed to reduce the number of reference species, otherwise changes in the density of the subject species would be obscured from species with high abundance (e.g. Pacific hake); and

Table 3.6. Species categorized by whether they did (\pm) or did not (0) exhibit substantial variation in biomass or incidence among the last five triennial surveys.

Variation category	Biomass	Incidence	Species	Potential scenario (see Fig. 3.15)
1	0	0	<i>none</i>	5
2	0	\pm	Pacific cod, shortspine thornyhead	4, 6
3	\pm	0	yellowmouth rockfish, bank rockfish, redstripe rockfish, widow rockfish	2, 8
4	\pm	\pm	all remaining 33 species	1, 3, 7, or 9 if correlation between biomass and incidence exists; otherwise any combination of scenarios among years.

second, Pacific sanddab, English sole, and Pacific cod are true demersal species, and therefore, it seems most appropriate to compare their abundance to other demersal species.

From 1980 to 1983, Pacific sanddab had about a four-fold increase in biomass and increased its incidence by .26 within the study area (Tables 3.1 and 3.3). According to scenario 1 (Fig. 3.15), species composition should be affected within Pacific sanddab's newly occupied area from an increase in Pacific sanddab density (providing the density of co-occurring species does not increase at a greater rate). Whether Pacific sanddab increased, decreased, or maintained a constant density within its continuously occupied area would depend upon whether it maintained a homogeneous density within its newly occupied and continuously occupied areas and whether its total incidence increased

proportionally to biomass. If its total incidence increased at a lower rate than its biomass, then its overall density would increase.

There was about a three-fold increase in the density of Pacific sanddab within its continuously occupied area (\bar{x} CPUE in area category 2, Table 3.7). Furthermore, although Pacific sanddab's density within its newly occupied area (category 3) in 1983 was relatively high, it was only about one-half the density within the continuously occupied area in the same year (Table 3.7). It appears that newly occupied sites may be occupied at a lower density than continuously occupied sites with increases in biomass. The abundance of Pacific sanddab relative to the abundance of the other five flatfish increased within both continuously and newly occupied areas, even though the density of the other five flatfish combined increased two- to three-fold. Pacific sanddab's relative abundance within its continuously occupied area increased from 31% in 1980 to 53% in 1983, and reached 22% within the newly occupied area.

From 1980 to 1983, English sole increased its biomass by about 2.5 times and increased its incidence by .21 (Tables 3.1 and 3.3). English sole exhibited changes in density similar to Pacific sanddab. It increased its density within its continuously occupied area about two-fold (although Pacific sanddab increased three-fold) and had a density within its newly occupied area in 1983 of about one-half its density within its continuously occupied area in the same year (Table 3.7). In context to an over two-fold increase in density of the other flatfish within both English sole's continuously and newly occupied areas, unlike Pacific sanddab, English sole's relative abundance among other

Table 3.7. Density estimates (CPUE) within area categories calculated from a grid of cells covering the entire study area. Cell dimensions were .10 degree of latitude by .20 degree of longitude. The number of hauls and cells that were assigned to a given area category are indicated. The categories are: 1 = cell occupied in the first year only; 2 = cell occupied in both years; 3 = cell occupied in the second year only; and 4 = cell was not sampled in both years.

	Area category	Year	# of hauls	# of cells	\bar{x} CPUE (kg/km ²)	All six flatfish \bar{x} CPUE (kg/km ²)
Pacific sanddab	1	'80	11	6	23	884
		'83	11	6	0	1992
	2	'80	206	74	140	594
		'83	179	74	444	1276
	3	'80	116	47	0	385
		'83	122	47	226	1244
	4	'80	33	21	76	692
		'83	89	57	90	1104
English sole	1	'80	41	15	20	872
		'83	30	15	0	1726
	2	'80	289	103	118	719
		'83	263	103	220	1357
	3	'80	82	44	0	637
		'83	100	44	117	1692
	4	'80	33	21	139	692
		'83	89	57	197	1104
Pacific cod	1	'80	12	3	143	1036
		'86	7	3	0	2452
	2	'80	50	16	535	1324
		'86	75	16	171	2052
	3	'80	80	27	0	629
		'86	102	27	54	2100
	4	'80	102	57	8	981
		'86	186	74	72	1699

flatfish within its continuously occupied area remained about the same in both years (about 20%). Within its newly occupied area, English sole reached a relative abundance of 7%.

The incidence of Pacific cod increased .08 between 1980 and 1986, which was not accompanied by an increase in biomass (Tables 3.1 and 3.3). According to scenario 4 (Fig. 3.15), species composition may be affected within Pacific cod's continuously occupied area from a decrease in the density of Pacific cod and affected within Pacific cod's newly occupied area from an increase in cod density. Accordingly, within Pacific cod's continuously occupied area from 1980 to 1986 (area category 2, Table 3.7), Pacific cod decreased its density by about one-third, and its relative abundance among flatfish decreased from 40% in 1980 to 8% in 1986. However, Pacific cod's decrease in relative abundance was spurred by a concomitant one and one-half-fold increase in flatfish density. Within Pacific cod's newly occupied area in 1986 (area category 3), the increase in density of Pacific cod was met with an increase in its relative abundance among flatfish from 0% to only 3%; however, the density of flatfish within the same area increased over three-fold (if flatfish density remained the same, then the relative abundance of Pacific cod would have increased to 8%). Although Pacific cod increased its spatial occurrence, it did so at a density of only 32% of its density within its continuously occupied area in the same year.

The positive linear relationship between incidence and log-transformed biomass in flatfish (Fig. 3.6) is consistent with density-dependent habitat selection which occurs

when habitats are differentially selected as incidence changes in response to changes in population abundance (MacCall 1990, Swain and Wade 1993, Marshall and Frank 1995). As a population expands spatially in response to increases in abundance, individuals may increasingly inhabit less desirable habitats. However, incidence and biomass may not increase proportionally nor have a linear relationship. The decreasing rate of increase in incidence with increasing biomass in five of the six flatfish of the present study (Fig. 3.6) indicates that the overall density of these flatfish increases with biomass.

Species' density is often heterogeneous among geographic spaces. Continuously occupied sites, over a specified period of time, may represent areas of preferred habitat. With increasing overall density, individuals may distribute across sites such that they continue to fill high-density preferred or "optimal" habitats, but at a lower rate than their occupation of previously unoccupied "marginal" habitats (Marshall and Frank 1995). Patterns in the occupancy of substrate types by flatfish suggest that marginal habitats are associated with areas of mud for Pacific sanddab and areas of sand for rex sole, Pacific halibut, and Dover sole (see Fig. 3.8 in Part 1 "Correlation Between Species Biomass and Incidence, and the Occupation of Substrate Types by Flatfish").

Empirical examination of the conceptual model (Fig. 3.15) was difficult, partly because the model assumes that in scenarios with constant or increasing incidence, geographic sites occupied in time t_1 are occupied in time t_2 ; and similarly, in scenarios with decreasing incidence, no sites become newly occupied in time t_2 . Furthermore, imprecise biomass and incidence estimates for some species made comparisons among

areas and years difficult and could lead to spurious interpretations. Investigating the impact of a species' changing density on species composition is further complicated by the fact that the impact is dependent upon potential changes in the density of co-occurring species. This was exemplified by English sole's unchanging relative abundance within its continuously occupied area from 1980 to 1983, even though it had a two-fold increase in density. Although the model had limited predictive abilities, it was useful in exploring links between the geographic distribution and density of a single species and their impact (or lack of impact) on species composition.

Chapter 4

SUMMARY

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Single-species management practices are inadequate for mixed-species fisheries, primarily because they do not adequately account for the complexity and dynamic nature of biological and environmental systems. Searching for alternative management approaches is challenging; however, it is important that fisheries management move off dead center and invest tangible resources in finding alternative measures of system performance and monitoring programs that can provide useful information for management decisions. Such alternative approaches might result from viewing fishery systems in a more holistic context. A step in this direction, is to examine the composition, distribution, and temporal persistence of co-occurring species or fish assemblages. Herein, data from the National Marine Fisheries Service triennial bottom-trawl surveys (1977-92) were used to examine changes in the distribution of summertime fish assemblages off the west coast of the United States, establish some general features regarding the abundance, density, and spatial distribution of dominant fish species, and compare regional environmental variation to variation in species composition.

Twenty-three fish assemblages were identified from the relative biomass of 33 dominant species, and accounted for about 70% of the total variation in species composition among 2,565 hauls. The persistence of the assemblages, although varying in incidence among surveys, suggests that fishing practices over the last 15 years had no *drastic* impact on the existence of summertime bottom-trawl fish assemblages. This does not imply that changes in fish assemblages have not occurred prior to 1977, or that more subtle and therefore undetectable changes have not been occurring. Also, changes in the relative abundance of rarer species and other attributes of community organization would

not be detected in the present study. It may be useful to monitor the future persistence of bottom-trawl assemblages by classifying future survey hauls into assemblages from the classification functions derived herein (Appendix 2).

Although the assemblages occurred within broad geographic boundaries, some had substantially different spatial distributions among surveys. The perception of boundary stability in bottom-trawl fish assemblages differs among studies and is undoubtedly related to methods of analysis and interpretation, including the accepted level of within-assemblage variation. The ability to differentiate assemblages across five environmental variables (latitude, depth, surface and bottom water temperatures, and surficial substrate) was low; although there was a paucity of measurements in some year/locations and the spatial and qualitative resolution of the surficial substrate may be lacking. Other studies indicate that commercial fishers may be able to sufficiently predict the location of some groups of species based on the knowledge gained from past fishing experiences, suggesting that the concept of assemblage management may be worth considering under some circumstances.

Ubiquitous species such as the flatfish, spiny dogfish, and sablefish, and particularly ubiquitous species that migrate over large geographic regions, notably Pacific hake, overlapped numerous assemblages and may serve as integrators across assemblages. As such, alterations to the performance of these species may trigger widespread changes in energy flow and hence the functioning of fish assemblages within the California Current System. Variation in the distribution and abundance of species

and assemblages, and the imprecision at which these parameters are estimated, highlights the need to take a conservative and cautious approach in determining acceptable levels of harvest.

Five of six flatfish species (Pacific sanddab, rex sole, Pacific halibut, Dover sole, and English sole) exhibited a significant positive linear relationship between incidence and log-transformed biomass which is consistent with density-dependent habitat selection. There was evidence (albeit weak) from patterns in the occupancy of substrate types by these flatfish, that marginal habitats are associated with areas of mud for Pacific sanddab and areas of sand for rex sole, Pacific halibut, and Dover sole.

The greatest amount of intersurvey variation in species composition occurred in the shallow shelf region off California, and the shallow and deep regions between Cape Mendocino and Cape Blanco which correspond to areas with the greatest amount of annual variation in upwelling. There was an unanticipated negative correlation between variation in bottom temperature and variation in species composition. It would be interesting to know whether areas of high variability in species composition correspond to areas of high commercial by-catch.

Future analyses might benefit from incorporating age and size composition information and a separate treatment of migratory (e.g. Pacific hake, jack and chub mackerel) and less migratory species (e.g. flatfish species). Information on the functioning of assemblages within the California Current System might be obtained using

trophic categories as the diet of dominant species become better known. However, it should be kept in mind that generalizations made from the trawl surveys contain inherent bias from gear selectivity. For example, while the use of roller gear on the survey trawl enables fishing over rough ground, it decreases the catchability of flatfish.

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APPENDICES

Appendix 1. Species identified within the study area (36°48' N to the Washington/Canada border) from each of the National Marine Fisheries Service triennial surveys from 1977-1992 (X = encountered, - = not encountered).

Family and species	Common name	Year					
		1977	1980	1983	1986	1989	1992
<hr/>							
Myxinidae							
Myxinidae sp.	hagfish unidentified	X	-	X	X	-	-
<i>Eptatretus deani</i>	black hagfish	-	X	X	-	-	-
<i>Eptatretus stouti</i>	Pacific hagfish	-	X	X	X	X	X
Petromyzontidae							
Petromyzontidae sp.	lamprey unidentified	-	-	-	-	X	X
<i>Lampetra tridentata</i>	Pacific lamprey	-	X	X	-	-	X
Hexanchidae							
<i>Hexanchus griseus</i>	sixgill shark	-	-	X	X	X	X
Alopiidae							
<i>Alopias vulpinus</i>	thresher shark	-	-	X	-	-	-
Scyliorhinidae							
Scyliorhinidae sp.	cat shark unidentified	X	-	-	-	-	-
<i>Apristurus brunneus</i>	brown cat shark	X	X	X	X	X	X
<i>Apristurus kampae</i>	longnose cat shark	X	-	-	-	X	-
<i>Parmaturus xaniurus</i>	filetail cat shark	X	-	-	-	-	-
Carcharhinidae							
<i>Galeorhinus zyopterus</i>	soupfin shark	X	X	X	X	-	X
<i>Mustelus henlei</i>	brown smoothhound	-	-	-	-	-	X
<i>Prionace glauca</i>	blue shark	X	-	X	-	-	-
Squalidae							
<i>Squalus acanthias</i>	spiny dogfish	X	X	X	X	X	X
Torpedinidae							
<i>Torpedo californica</i>	Pacific electric ray	X	X	X	X	X	X
Rajidae							
Rajidae sp.	skate unidentified	-	-	X	X	X	X
<i>Bathyraja spinosissima</i>	white skate	-	-	-	-	X	-
<i>Raja badia</i> ^b	roughshoulder skate	-	-	X	-	-	-
<i>Raja binoculata</i>	big skate	X	X	X	X	X	X
<i>Raja inornata</i>	California skate	-	X	X	X	X	X
<i>Raja interrupta</i>	Bering skate	X	X	X	X	X	X
<i>Raja parmifera</i>	Alaska skate		-	-	-	X	-

(Appendix 1 — continued)

<i>Raja rhina</i>	longnose skate	X	X	X	X	X	X
<i>Raja stellulata</i>	starry skate	-	X	-	-	-	X
<i>Raja trachura</i>	rougtail skate	X	-	-	-	X	-
Chimaeridae							
<i>Hydrolagus coliei</i>	spotted ratfish	X	X	X	X	X	X
Acipenseridae							
<i>Acipenser medirostris</i>	green sturgeon	-	-	-	-	X	X
Clupeidae							
<i>Alosa sapidissima</i>	American shad	X	X	X	X	X	X
<i>Clupea harengus pallasii</i>	Pacific herring	X	X	X	X	X	X
<i>Sardinops sagax</i>	Pacific sardine	-	-	-	-	-	X
Engraulidae							
<i>Engraulis mordax</i>	northern anchovy	X	X	X	X	X	X
Salmonidae							
Salmonidae sp.	trout unidentified	X	-	-	-	-	-
<i>Oncorhynchus keta</i>	chum salmon	-	X	-	-	-	-
<i>Oncorhynchus kisutch</i>	coho salmon	X	X	X	X	X	X
<i>Oncorhynchus tshawytscha</i>	chinook salmon	X	X	X	X	X	X
Sternoptychidae							
Sternoptychidae sp.	hatchetfish unidentified	X	X	X	-	X	-
Osmeridae							
Osmeridae sp.	smelt unidentified	X	X	X	-	X	-
<i>Allosmerus elongatus</i>	whitebait smelt	X	X	X	X	X	X
<i>Hypomesus pretiosus</i>	surf smelt	X	-	X	-	X	-
<i>Spirinchus starksi</i>	night smelt	-	X	X	-	-	-
<i>Thaleichthys pacificus</i>	eulachon	X	X	X	X	X	X
Argentinidae							
Argentinidae sp.	argentine unidentified	-	-	X	X	-	X
<i>Argentina sialis</i>	Pacific argentine	-	-	X	-	X	X
Bathylagidae							
<i>Bathylagus pacificus</i>	Pacific blacksmelt	-	-	X	-	-	-
Melanostomiidae							
<i>Bathophilus flemingi</i>	highfin dragonfish	X	-	-	-	-	-
<i>Tactostoma macropus</i>	longfin dragonfish	X	X	X	-	-	-
Chauliodontidae							
Chauliodontidae sp.	viperfish unidentified	X	X	X	-	X	-
<i>Chauliodus macouni</i>	Pacific viperfish	X	-	X	-	-	-
Synodontidae							
<i>Synodus lucioceps</i>	California lizardfish	-	-	-	-	-	X

(Appendix 1 — continued)

Idiacanthidae							
<i>Idiacanthus antrostomus</i>	Pacific blackdragon	-	-	X	-	-	-
Myctophidae							
Myctophidae sp.	lanternfish unidentified	X	X	X	X	X	X
<i>Diaphus theta</i>	California headlightfish	-	X	-	X	-	-
<i>Stenobranchius leucopsarus</i>	northern lampfish	-	X	X	X	-	-
<i>Tarletonbeania crenularis</i>	blue lanternfish	-	-	-	-	X	-
Batrachoididae							
<i>Porichthys notatus</i>	plainfin midshipman	X	X	X	X	X	X
Lophiidae							
Lophiidae sp.	goosefish unidentified	-	-	X	-	-	-
Gadidae							
<i>Gadus macrocephalus</i>	Pacific cod	X	X	X	X	X	X
<i>Merluccius productus</i>	Pacific hake	X	X	X	X	X	X
<i>Microgadus proximus</i>	Pacific tomcod	X	X	X	X	X	X
<i>Theragra chalcogramma</i>	walleye pollock	X	X	X	X	X	X
Macrouridae							
Macrouridae sp.	grenadier unidentified	X	-	-	-	-	X
Ophidiidae							
Ophidiidae sp.	cuskeel unidentified	-	-	-	-	-	X
<i>Chilara taylori</i>	spotted cuskeel	X	X	X	X	X	X
<i>Ophidion scrippsae</i>	basketweave cuskeel	X	-	-	-	-	-
Zoarcidae							
Zoarcidae sp.	eelpout unidentified	X	X	X	X	X	X
<i>Aprodon corteziensis</i>	bigfin eelpout	X	X	X	X	X	X
<i>Lycodapus fierasfer</i>	blackmouth eelpout	X	X	-	-	-	-
<i>Lycodapus mandibularis</i>	pallid eelpout	X	-	-	-	-	-
<i>Lycodes brevipes</i>	shortfin eelpout	-	-	-	X	X	-
<i>Lycodes diapterus</i>	black eelpout	X	X	X	X	X	X
<i>Lycodes palearis</i>	wattled eelpout	-	-	-	X	-	-
<i>Lycodopsis pacifica</i>	blackbelly eelpout	-	X	X	X	X	X
Scomberesocidae							
<i>Cololabis saira</i>	Pacific saury	-	X	-	-	X	X
Trachipteridae							
<i>Trachipterus altivelis</i>	king-of-the-salmon	X	-	X	-	X	-
Carangidae							
<i>Trachurus symmetricus</i>	jack mackerel	X	X	X	X	X	X
Bramidae							
<i>Brama japonica</i>	Pacific pomfret	-	-	-	-	-	X

(Appendix 1 — continued)

Sciaenidae							
<i>Genyonemus lineatus</i>	white croaker	X	X	X	X	X	X
Embiotocidae							
Embiotocidae sp.	surfperch unidentified	X	-	-	-	-	-
<i>Cymatogaster aggregata</i>	shiner perch	-	-	X	-	X	X
<i>Hyperprosopon anale</i>	spotfin surfperch	-	-	-	-	-	X
<i>Rhacochilus vacca</i>	pile perch	-	-	X	-	-	-
<i>Zalembius rosaceus</i>	pink perch	X	X	X	X	X	X
Bathymasteridae							
<i>Bathymaster signatus</i>	searcher	-	-	-	-	X	-
<i>Ronquilus jordani</i>	northern ronquil	-	-	-	-	-	X
Stichaeidae							
<i>Plectobranchnus evides</i>	bluebarred prickleback	-	-	X	-	-	-
<i>Poroclinus rothrocki</i>	whitebarred prickleback	-	-	X	X	-	X
Anarhichadidae							
<i>Anarrhichthys ocellatus</i>	wolf-eel	-	-	X	X	X	-
Cryptacanthodidae							
<i>Delolepis gigantea</i>	giant wrymouth	X	X	X	-	X	X
Zaproridae							
<i>Zaprora silemus</i>	prowfish	-	X	-	-	-	X
Scombridae							
Scombridae sp.	mackerel unidentified	-	X	X	-	-	-
<i>Scomber japonicus</i>	chub mackerel	-	-	X	X	X	X
Stromateidae							
<i>Icichthys lockingtoni</i>	medusafish	-	-	X	-	-	X
<i>Peprilus simillimus</i>	Pacific pompano	-	-	X	-	X	X
Icosteidae							
<i>Icosteus aenigmaticus</i>	ragfish	-	X	-	-	X	X
Scorpaenidae							
Scorpaenidae sp.	rockfish unidentified	X	X	X	X	X	X
<i>Sebastes aleutianus</i>	roughey rockfish	X	X	X	X	X	X
<i>Sebastes alutus</i>	Pacific ocean perch	X	X	X	X	X	X
<i>Sebastes auriculatus</i>	brown rockfish	-	X	X	X	X	X
<i>Sebastes aurora</i>	aurora rockfish	X	-	X	X	-	X
<i>Sebastes babcocki</i>	redbanded rockfish	X	X	X	X	X	X
<i>Sebastes borealis</i>	shortraker rockfish	X	X	X	X	-	X
<i>Sebastes brevispinis</i>	silvergray rockfish	X	X	X	X	X	X
<i>Sebastes caurinus</i>	copper rockfish	X	X	X	X	X	X
<i>Sebastes chlorostictus</i>	greenspotted rockfish	X	X	X	X	X	X
<i>Sebastes ciliatus</i>	dusky rockfish	X	-	-	-	-	-
<i>Sebastes constellatus</i>	starry rockfish	-	-	-	-	X	-
<i>Sebastes crameri</i>	darkblotched rockfish	X	X	X	X	X	X

(Appendix 1 — continued)

<i>Sebastes diploproa</i>	splitnose rockfish	X	X	X	X	X	X
<i>Sebastes elongatus</i>	greenstriped rockfish	X	X	X	X	X	X
<i>Sebastes entomelas</i>	widow rockfish	X	X	X	X	X	X
<i>Sebastes eos</i>	pink rockfish	X	-	-	-	-	-
<i>Sebastes flavidus</i>	yellowtail rockfish	X	X	X	X	X	X
<i>Sebastes goodei</i>	chilipepper	X	X	X	X	X	X
<i>Sebastes helvomaculatus</i>	rosethorn rockfish	X	X	X	X	X	X
<i>Sebastes jordani</i>	shortbelly rockfish	X	X	X	X	X	X
<i>Sebastes levis</i>	cowcod	X	X	X	-	X	X
<i>Sebastes maliger</i>	quillback rockfish	X	-	X	X	X	X
<i>Sebastes melanops</i>	black rockfish	-	X	X	X	X	X
<i>Sebastes melanostomus</i>	blackgill rockfish	X	X	X	-	-	X
<i>Sebastes miniatus</i>	vermillion rockfish	X	-	X	-	X	X
<i>Sebastes mystinus</i>	blue rockfish	-	-	-	-	X	X
<i>Sebastes nigrocinctus</i>	tiger rockfish	-	X	X	X	-	-
<i>Sebastes ovalis</i>	speckled rockfish	-	X	-	X	X	-
<i>Sebastes paucispinis</i>	bocaccio	X	X	X	X	X	X
<i>Sebastes phillipsi</i>	chameleon rockfish	X	-	-	-	-	-
<i>Sebastes pinniger</i>	canary rockfish	X	X	X	X	X	X
<i>Sebastes proriger</i>	redstripe rockfish	X	X	X	X	X	X
<i>Sebastes reedi</i>	yellowmouth rockfish	X	X	X	X	X	X
<i>Sebastes rosenblatti</i>	greenblotched rockfish	-	-	X	-	X	X
<i>Sebastes ruberrimus</i>	yelloweye rockfish	X	X	X	X	X	X
<i>Sebastes rubrivinctus</i>	flag rockfish	X	-	-	X	X	-
<i>Sebastes rufus</i>	bank rockfish	X	X	X	X	X	X
<i>Sebastes saxicola</i>	stripetail rockfish	X	X	X	X	X	X
<i>Sebastes semicinctus</i>	halfbanded rockfish	-	-	-	-	X	X
<i>Sebastes variegatus</i>	harlequin rockfish	X	-	-	-	-	-
<i>Sebastes wilsoni</i>	pygmy rockfish	X	X	X	X	X	X
<i>Sebastes zacentrus</i>	sharpchin rockfish	X	X	X	X	X	X
<i>Sebastolobus alascanus</i>	shortspine thornyhead	X	X	X	X	X	X
<i>Sebastolobus altivelis</i>	longspine thornyhead	X	-	-	-	-	-
Anoplopomatidae							
<i>Anoplopoma fimbria</i>	sablefish	X	X	X	X	X	X
Hexagrammidae							
<i>Hexagrammos</i> sp.	greenling unidentified	-	X	X	-	-	-
<i>Hexagrammos decagrammus</i>	kelp greenling	-	X	X	X	X	X
<i>Hexagrammos stelleri</i>	whitespotted greenling	-	-	X	-	-	-
<i>Ophiodon elongatus</i>	lingcod	X	X	X	X	X	X
<i>Oxylebius pictus</i>	painted greenling	-	-	-	-	-	X
<i>Zaniolepis frenata</i>	shortspine combfish	-	-	-	X	-	X
<i>Zaniolepis latipinnis</i>	longspine combfish	-	X	X	X	X	X
Cottidae							
Cottidae sp.	sculpin unidentified	X	-	X	X	X	X
<i>Hemilepidotus hemilepidotus</i>	red Irish lord	-	-	X	X	-	-
<i>Hemilepidotus spinosus</i>	brown Irish lord	-	-	X	-	X	X
<i>Icelinus filamentosus</i>	threadfin sculpin	X	X	X	X	X	X
<i>Icelinus oculatus</i>	frogmouth sculpin	-	-	-	-	-	X
<i>Icelinus tenuis</i>	spotfin sculpin	X	-	X	-	-	X

(Appendix 1 — continued)

<i>Icelus spiniger</i>	thorny sculpin	-	-	X	-	-	-
<i>Jordania zonope</i>	longfin sculpin	X	-	-	-	-	-
<i>Leptocottus armatus</i>	Pacific staghorn sculpin	X	X	X	X	X	X
<i>Malacocottus kincaidi</i>	blackfin sculpin	-	-	-	-	-	X
<i>Paricelinus hopliticus</i>	thornback sculpin	-	-	-	-	-	X
<i>Radulinus asprellus</i>	slim sculpin	-	-	-	-	-	X
<i>Scorpaenichthys marmoratus</i>	cabezon	-	-	-	-	X	X
<i>Triglops macellus</i>	roughspine sculpin	-	-	X	-	-	-
Agonidae							
Agonidae sp.	poacher unidentified	X	X	X	-	X	X
<i>Agonopsis vulsa</i>	northern spearnose poacher	-	-	X	-	X	X
<i>Agonus acipenserinus</i>	sturgeon poacher	-	-	-	X	X	X
<i>Bathyagonus alascanus</i>	gray starsnout	-	-	-	X	-	-
<i>Bathyagonus nigripinnis</i>	blackfin poacher	-	-	-	-	X	-
<i>Bathyagonus pentacanthus</i>	bigeye poacher	-	-	X	-	X	X
<i>Ocella verrucosa</i>	warty poacher	X	-	-	-	-	X
<i>Odontopyxis trispinosa</i>	pygmy poacher	X	-	-	-	X	-
<i>Sarritor frenatus</i>	sawback poacher	-	-	-	X	-	-
<i>Xeneretmus latifrons</i>	blacktip poacher	-	-	X	X	X	X
<i>Xeneretmus leiops</i>	smootheye poacher	-	-	-	-	-	X
Cyclopteridae							
Cyclopteridae sp.	snailfish unidentified	X	-	X	-	X	X
<i>Careproctus abbreviatus</i>	?	X	-	-	-	-	-
<i>Careproctus gilberti</i>	smalldisk snailfish	-	-	X	-	-	-
<i>Careproctus rastrinus</i>	salmon snailfish	X	-	-	-	-	-
<i>Careproctus melanurus</i>	blacktail snailfish	X	X	X	X	X	X
<i>Laparis</i> sp.	snailfish unidentified	-	-	-	-	-	X
Bothidae							
Bothidae sp.	lefteye flounder unidentified	-	-	-	X	-	-
<i>Citharichthys</i> sp.	sanddab unidentified	X	-	-	-	-	-
<i>Citharichthys sordidus</i>	Pacific sanddab	X	X	X	X	X	X
Pleuronectidae							
<i>Atheresthes stomias</i>	arrowtooth flounder	X	X	X	X	X	X
<i>Embassichthys bathybius</i>	deepsea sole	X	-	-	-	-	-
<i>Eopsetta jordani</i>	petrale sole	X	X	X	X	X	X
<i>Glyptocephalus zachirus</i>	rex sole	X	X	X	X	X	X
<i>Hippoglossoides elassodon</i>	flathead sole	X	X	X	X	X	X
<i>Hippoglossus stenolepis</i>	Pacific halibut	X	X	X	X	X	X
<i>Isopsetta isolepis</i>	butter sole	X	X	X	X	X	X
<i>Lepidopsetta bilineata</i>	rock sole	X	X	X	X	X	X
<i>Lyopsetta exilis</i>	slender sole	X	X	X	X	X	X
<i>Microstomus pacificus</i>	Dover sole	X	X	X	X	X	X
<i>Parophrys vetulus</i>	English sole	X	X	X	X	X	X
<i>Platichthys stellatus</i>	starry flounder	-	X	X	X	X	X
<i>Pleuronichthys decurrens</i>	curlfin sole	X	X	X	X	X	X
<i>Pleuronichthys verticalis</i>	hornyhead turbot	X	-	-	-	-	-
<i>Psettichthys melanostictus</i>	sand sole	-	X	X	X	X	X

(Appendix I — continued)

Cynoglossidae							
<i>Symphurus atricauda</i>	California tonguefish	-	-	-	-	X	-
Molidae							
<i>Mola mola</i>	ocean sunfish	-	X	X	-	-	X

Appendix 2. Linear classification functions used to assign hauls to assemblages using the estimated minimum total probability of misclassification rule for equal covariance normal populations (Johnson and Wichern 1991). Assemblage membership is based on the proportional abundance of the 33 dominant species in the haul. The measurement for each variable (species) is the species log-transformed proportional biomass ($\ln(1 + x)$). The haul's classification score is calculated for each assemblage using the coefficients given, and the haul is assigned to the assemblage yielding the highest score.

Variable	Assemblage			
	hake	sablefish-hake	sanddab-hake	dogfish
CONSTANT	-215	-263	-270	-246
Pacific hake	589	583	568	550
splitnose rockfish	564	619	596	588
chilipepper	569	623	594	590
bank rockfish	531	586	555	548
Pacific sanddab	504	549	724	551
English sole	489	543	540	525
Dover sole	476	517	513	506
rex sole	446	515	470	481
lingcod	498	552	523	520
sablefish	503	678	540	536
shortspine thornyhead	427	469	477	472
darkblotched rockfish	460	521	499	487
widow rockfish	506	575	541	527
bocaccio	441	507	474	462
stripetail rockfish	520	582	551	544
yellowtail rockfish	554	619	597	598
canary rockfish	562	618	606	600
shortbelly rockfish	595	660	625	622
spiny dogfish	491	544	546	636
jack mackerel	544	582	593	560
American shad	490	556	527	531
arrowtooth flounder	521	576	564	556
white croaker	599	634	657	610
sharpchin rockfish	547	604	584	581
Pacific herring	606	664	670	656
Pacific ocean perch	518	586	549	543
redstripe rockfish	541	604	577	567
Pacific cod	467	509	517	492
Pacific halibut	468	527	499	489
silvergray rockfish	470	500	502	502
walleye pollock	546	595	572	545
yellowmouth rockfish	454	491	475	469
chub mackerel	484	515	518	494

(Appendix 2 — continued)

Variable	chilipepper	hake-Dover	yellowtail	arrowtooth-Dover
CONSTANT	-368	-258	-341	-277
Pacific hake	615	633	604	603
splitnose rockfish	646	644	649	646
chilipepper	1124	645	663	645
bank rockfish	500	600	596	603
Pacific sanddab	570	564	577	579
English sole	563	548	561	559
Dover sole	564	551	552	562
rex sole	519	515	515	525
lingcod	580	564	557	575
sablefish	588	578	585	588
shortspine thornyhead	499	491	527	488
darkblotched rockfish	564	529	546	529
widow rockfish	601	578	564	584
bocaccio	484	510	532	515
stripetail rockfish	603	588	596	592
yellowtail rockfish	656	631	1001	655
canary rockfish	641	638	656	653
shortbelly rockfish	729	673	682	678
spiny dogfish	566	555	575	581
jack mackerel	614	607	606	605
American shad	597	567	620	581
arrowtooth flounder	598	592	619	708
white croaker	662	661	655	661
sharpchin rockfish	647	621	638	647
Pacific herring	692	682	695	697
Pacific ocean perch	588	587	606	619
redstripe rockfish	642	616	617	647
Pacific cod	530	524	538	566
Pacific halibut	543	538	548	539
silvergray rockfish	533	528	539	607
walleye pollock	628	615	758	593
yellowmouth rockfish	512	511	522	503
chub mackerel	543	550	540	537

(Appendix 2 — continued)

Variable	hake-sanddab- dogfish	Dover-hake	hake-arrowtooth- Dover	jack-chub- hake
CONSTANT	-266	-254	-290	-388
Pacific hake	634	589	641	590
splitnose rockfish	640	624	665	613
chilipepper	643	627	672	617
bank rockfish	600	592	621	569
Pacific sanddab	610	552	596	572
English sole	591	536	577	553
Dover sole	546	610	582	524
rex sole	527	506	541	486
lingcod	562	552	592	542
sablefish	581	558	607	554
shortspine thornyhead	499	488	521	479
darkblotched rockfish	528	515	561	507
widow rockfish	577	564	599	550
bocaccio	507	499	542	489
stripetail rockfish	590	565	615	555
yellowtail rockfish	635	620	742	605
canary rockfish	643	624	683	622
shortbelly rockfish	674	655	703	632
spiny dogfish	583	548	595	545
jack mackerel	627	585	633	1168
American shad	562	561	663	556
arrowtooth flounder	596	580	643	571
white croaker	702	639	686	701
sharpchin rockfish	624	617	658	591
Pacific herring	706	669	719	663
Pacific ocean perch	590	574	624	561
redstripe rockfish	617	617	647	578
Pacific cod	537	513	580	510
Pacific halibut	536	530	559	507
silvergray rockfish	536	522	558	505
walleye pollock	613	603	805	594
yellowmouth rockfish	513	515	534	489
chub mackerel	552	523	562	972

(Appendix 2 — continued)

Variable	Pacific ocean perch	herring	Dover-sablefish- rex-hake	stripetail- shortbelly
CONSTANT	-318	-351	-273	-334
Pacific hake	606	624	611	614
splitnose rockfish	638	656	669	633
chilipepper	641	659	657	705
bank rockfish	605	612	621	598
Pacific sanddab	569	614	576	575
English sole	556	603	569	563
Dover sole	553	567	581	553
rex sole	532	547	557	522
lingcod	576	592	589	577
sablefish	599	600	614	595
shortspine thornyhead	463	522	579	508
darkblotched rockfish	520	550	563	554
widow rockfish	599	597	606	617
bocaccio	537	522	539	513
stripetail rockfish	600	614	599	958
yellowtail rockfish	658	657	658	650
canary rockfish	648	673	655	641
shortbelly rockfish	685	700	689	938
spiny dogfish	567	604	575	569
jack mackerel	603	636	613	608
American shad	586	593	596	586
arrowtooth flounder	624	621	615	600
white croaker	657	687	669	662
sharpchin rockfish	677	644	645	630
Pacific herring	688	1046	705	696
Pacific ocean perch	914	607	610	609
redstripe rockfish	688	636	545	631
Pacific cod	537	560	542	532
Pacific halibut	546	559	568	543
silvergray rockfish	551	544	547	529
walleye pollock	597	629	629	626
yellowmouth rockfish	362	528	527	515
chub mackerel	535	551	545	531

(Appendix 2 — continued)

Variable	croaker-hake	English-sanddab- rex	lingcod	splitnose- Dover-hake
CONSTANT	-494	-271	-287	-326
Pacific hake	636	589	596	616
splitnose rockfish	651	625	636	975
chilipepper	655	624	644	655
bank rockfish	608	582	588	871
Pacific sanddab	638	635	577	573
English sole	608	663	556	559
Dover sole	557	532	551	578
rex sole	538	531	520	533
lingcod	570	548	767	577
sablefish	590	572	581	590
shortspine thornyhead	511	508	504	466
darkblotched rockfish	541	522	534	533
widow rockfish	577	566	581	593
bocaccio	517	496	499	506
stripetail rockfish	601	577	583	587
yellowtail rockfish	648	624	628	649
canary rockfish	656	637	652	648
shortbelly rockfish	686	658	670	691
spiny dogfish	585	570	567	570
jack mackerel	678	608	603	610
American shad	576	551	583	585
arrowtooth flounder	610	585	601	608
white croaker	1652	680	653	664
sharpchin rockfish	637	614	624	638
Pacific herring	724	702	699	694
Pacific ocean perch	600	577	591	577
redstripe rockfish	629	606	625	643
Pacific cod	553	542	533	534
Pacific halibut	549	538	527	557
silvergray rockfish	546	525	512	539
walleye pollock	626	597	617	630
yellowmouth rockfish	522	498	520	616
chub mackerel	589	534	534	547

(Appendix 2 — continued)

Variable	sharpchin-redstripe	canary	darkblotched- bocaccio-widow-hake
CONSTANT	-354	-330	-285
Pacific hake	612	613	589
splitnose rockfish	661	652	612
chilipepper	671	646	651
bank rockfish	598	606	550
Pacific sanddab	579	590	556
English sole	566	582	543
Dover sole	574	562	535
rex sole	532	523	505
lingcod	600	594	558
sablefish	594	590	580
shortspine thornyhead	528	515	488
darkblotched rockfish	538	537	709
widow rockfish	586	584	798
bocaccio	504	512	741
stripetail rockfish	604	595	594
yellowtail rockfish	654	655	627
canary rockfish	680	966	625
shortbelly rockfish	692	681	679
spiny dogfish	576	579	545
jack mackerel	611	630	588
American shad	598	594	569
arrowtooth flounder	630	619	582
white croaker	667	670	639
sharpchin rockfish	1027	664	613
Pacific herring	700	713	670
Pacific ocean perch	642	605	583
redstripe rockfish	1009	626	613
Pacific cod	546	530	519
Pacific halibut	555	548	536
silvergray rockfish	557	544	514
walleye pollock	632	658	611
yellowmouth rockfish	666	512	498
chub mackerel	536	545	520