

Distribution of bottom-trawl fish assemblages over the continental shelf and upper slope of the U.S. west coast, 1977–1992

Chadwick V. Jay

Abstract: Twenty-three bottom-trawl fish assemblages were identified from the relative biomass of 33 dominant species that occurred in the National Marine Fisheries Service's 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 2565 hauls. Although the assemblages persisted over the 15-year 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.

Résumé : Vingt-trois groupes de poissons capturés par chalutage de fond ont été déterminés à partir de la biomasse relative de 33 espèces dominantes capturées à l'occasion des relevés triennaux au chalut faits par le National Marine Fisheries Service au-dessus du plateau continental et sur le haut de la pente continentale au large de la Californie, de l'Orégon et de l'État de Washington entre 1977 et 1992. L'existence de ces groupes de poissons expliquait environ 70% de la variation totale au niveau de la composition spécifique entre 2565 traits. Bien que les groupes aient persisté pendant les 15 ans couverts par cette étude et qu'ils aient été observés sur un vaste territoire, il demeure que chez certains, la répartition dans l'espace variait beaucoup d'un relevé à l'autre. Il est difficile de différencier les groupes entre eux au regard de cinq variables environnementales (latitude, profondeur, température de l'eau à la surface et en profondeur et substrat à la surface). La prépondérance marquée par les groupes dominés par le merlu partout dans la zone d'étude paraît indiquer que le merlu du Pacifique (*Merluccius productus*) joue un rôle important dans la dynamique des communautés de poissons démersaux au large de la côte ouest des États-Unis.

[Traduit par la Rédaction]

Introduction

Fish associations can be affected directly or indirectly by 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: (i) identifying 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 (ii) identifying 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 with 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 1977–1992 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 1977–1992 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

Received May 4, 1995. Accepted December 13, 1995.
J12906

C.V. Jay,¹ Department of Fisheries and Wildlife, Nash 104,
Oregon State University, Corvallis, OR 97331–3803, U.S.A.

¹ Present address: National Biological Service, Alaska Science
Center, 1011 East Tudor Road, Anchorage, AK 99503,
U.S.A. e-mail: Chad_Jay@nbs.gov

Table 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	<i>Commando</i>	13.40
	<i>David Starr Jordan</i>	13.40
	<i>Pacific Raider</i>	13.40
	<i>Tordenskjold</i>	13.40
1980	<i>Mary Lou</i>	13.40
	<i>Pat San Marie</i>	13.40
1983	<i>Nordfjord</i>	13.40
	<i>Warrior II</i>	13.40
1986	<i>Alaska</i>	13.30 ^a
	<i>Pat San Marie</i>	12.69
1989	<i>Golden Fleece</i>	12.40 ^b
	<i>Pat San Marie</i>	13.40 ^b
1992	<i>Alaska</i>	12.76 ^b
	<i>Green Hope</i>	12.55 ^b

Note: Sources are Gunderson and Sample (1980), Weinberg et al. (1984, 1994), Coleman (1986, 1988), and for the 1992 survey, M. Wilkins, NMFS, Seattle, Wash., personal communication.

^aAverage from polyethylene net of 13.82 m and nylon net of 12.78 m.

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

examine the segregation of assemblages across five environmental variables.

Definitions

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 (for details of the 1977–1989 surveys see Gunderson and Sample 1980; Weinberg et al. 1984, 1994; Coleman 1986, 1988). The surveys were conducted from the 1st or 2nd 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, B.C. Sampling extended from 55 to 366 m deep, except for the 1977 survey, which extended from 91

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. 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 in which "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" (National Marine Fisheries Service 1991, p. 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 km/h tow rate × 0.5-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.

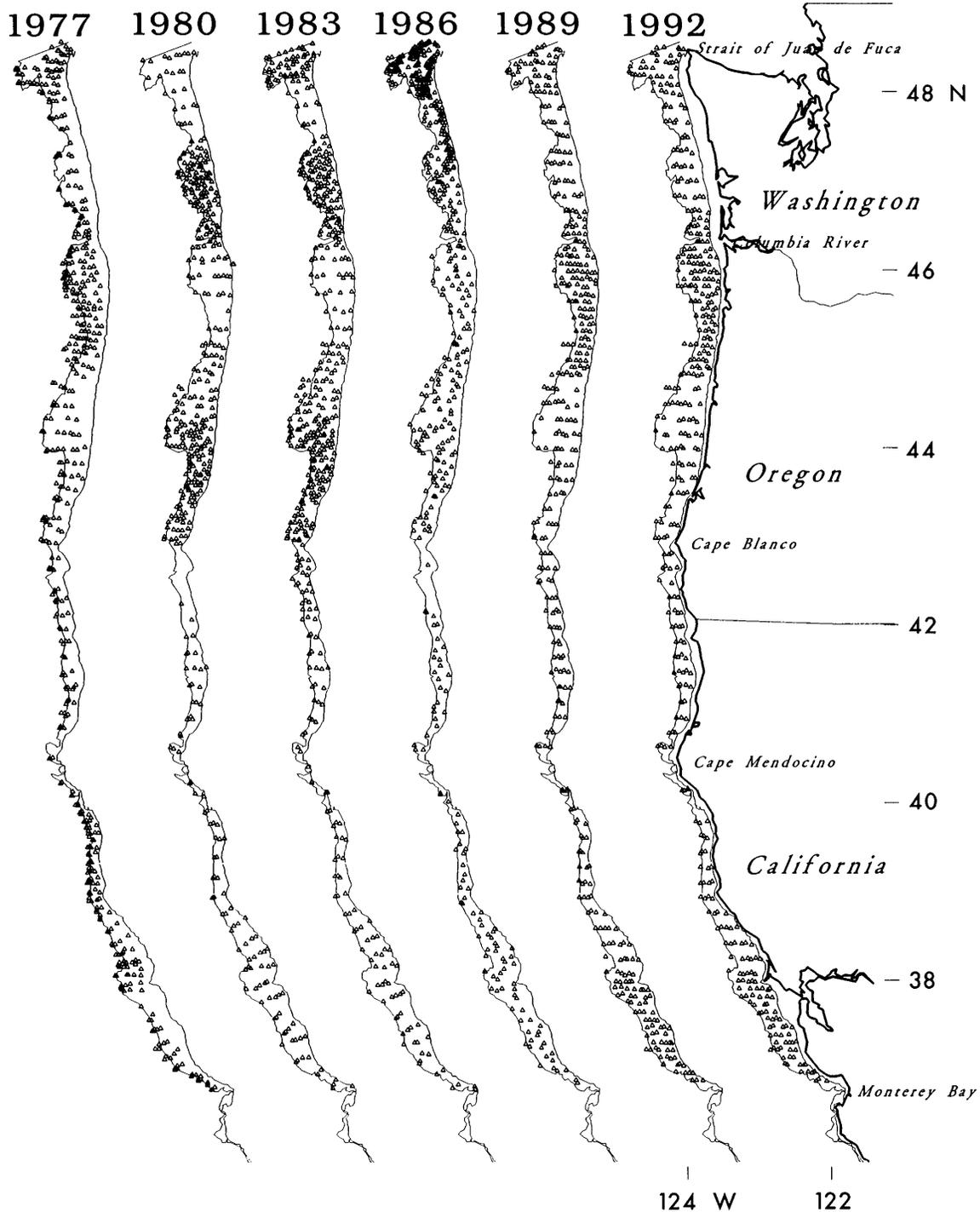
For statistical analyses, I treated the sampling unit as a two-dimensional unit of a constant area of seafloor by adjusting species catch weights (measured to the nearest kilogram) from each tow to a standardized sampling unit of 1 km² of seafloor. The adjustment was achieved by dividing the actual catch 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 1). A sample observation is herein 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, also see Fig. 1). However, apparently for logistical reasons (see Lenarz and Adams 1980), track lines were incorporated into the sampling design. Sampling locations were allocated randomly along track lines, which extended across depth, but track-line 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, track-line 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. Track lines extended seaward and perpendicular to the isobath from which they started. In the 1986 survey, track lines extended seaward and parallel to the seabed slope from starting points separated by 2 min of latitude along the 55-m isobath. In the 1989 and 1992 surveys, track lines 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 track-line 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 track-line starting points and the number of sampling locations allocated to each track-line segment. During sampling, if a designated sampling location was untrawlable, a radius of 1 nautical mile (1 nautical mile = 1.852 km) around the original location was searched for

Fig. 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).



an alternative sampling location. If a suitable location was not found within a reasonable period (about 0.5 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. To identify fish assemblages, I wanted to focus on species that comprised 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°48'–39°30'N, 39°30'–42°30'N, 42°30'–45°30'N, and 45°30'–Washington–Canada border) and two depth intervals (≤ 200 and >200 m). The number of

Table 2. Surface area (km², which represents the number of sampling units) and boundaries of sampling strata.

(A) 1977.				
Latitudinal boundaries (N)	Depth boundaries (m)			
	91–181	182–272	273–364	365–457
36°48'–37°07'	467 (7)	87 (5)	88 (5)	100 (2)
37°07'–37°56'	1157 (13)	183 (3)	160 (5)	185 (5)
37°56'–38°19'	936 (11)	138 (6)	106 (5)	64 (6)
38°19'–38°49'	1042 (10)	221 (4)	95 (4)	50 (3)
38°49'–40°02'	1332 (24)	171 (15)	172 (14)	190 (13)
40°02'–45°00'	7547 (55)	1815 (35)	1506 (28)	1513 (26)
45°00'–46°44'	4028 (60)	1023 (30)	641 (17)	1136 (25)
46°44'–47°51'	2304 (17)	245 (4)	172 (5)	178 (5)
47°51'–border	2150 (26)	727 (15)	319 (12)	124 (5)
(B) 1980.				
Latitudinal boundaries (N)	Depth boundaries (m)			
	55–183	184–220	221–366	184–366
36°48'–42°00'	10 896 (71)	—	—	—
42°00'–42°50'	1 375 (0) ^a	—	—	—
42°50'–44°18'	5 012 (101)	357 (16)	895 (8)	—
44°18'–45°00'	2 647 (26)	—	—	—
45°00'–46°10'	4 092 (34)	—	—	—
46°10'–47°20'	3 915 (128)	219 (9)	272 (7)	—
47°20'–border ^a	3 871 (20)	—	—	—
(C) 1983.				
Latitudinal boundaries (N)	Depth boundaries (m)			
	55–183	184–220	221–366	184–366
36°48'–42°00'	10 896 (87)	—	—	2190 (35)
42°00'–42°50'	1 375 (0) ^a	—	—	382 (0) ^a
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)	—	—	1432 (12)
46°10'–47°20'	3 915 (89)	219 (12)	272 (7)	—
47°20'–47°55'	1 642 (9)	—	—	225 (4)
(D) 1986.				
Latitudinal boundaries (N)	Depth boundaries (m)			
	55–91	92–183	184–219	220–366
36°48'–42°50'	4965 (30)	7200 (53)	718 (5)	1843 (11)
42°50'–45°00'	2512 (17)	5173 (56)	501 (4)	1595 (11)
45°00'–46°10'	1057 (7)	3035 (24)	503 (4)	839 (6)
46°10'–47°00'	1033 (9)	1673 (36)	171 (2)	223 (0) ^a
47°00'–47°50'	1019 (53)	1556 (17)	112 (2)	139 (0) ^a
47°50'–border	349 (11)	2164 (150)	390 (11)	686 (14)
(E) 1989.				
Latitudinal boundaries (N)	Depth boundaries (m)			
	55–183	184–366		
36°48'–38°00'	3818 (61)	513 (5)		
38°00'–40°30'	4724 (40)	1112 (13)		
40°30'–43°00'	4090 (39)	1076 (16)		
43°00'–44°40'	6250 (40)	1508 (14)		
44°40'–46°30'	6014 (97)	2118 (19)		
46°30'–border	6896 (71)	1593 (16)		

Table 2 (concluded).

(F) 1992.

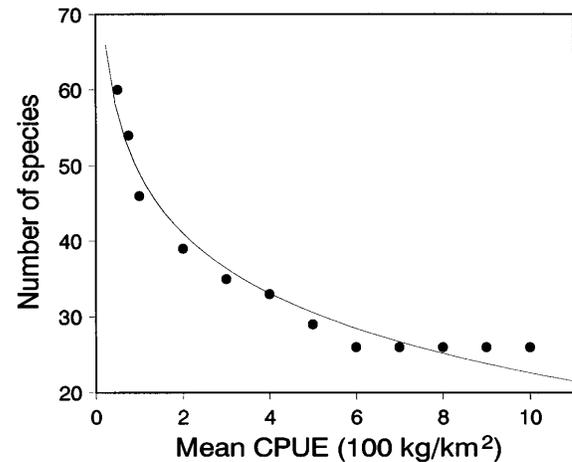
Latitudinal boundaries (N)	Depth boundaries (m)	
	55–183	184–366
36°48'–38°00'	3818 (60)	513 (4)
38°00'–40°30'	4724 (39)	1112 (12)
40°30'–43°00'	4090 (37)	1076 (16)
43°00'–44°40'	6250 (41)	1508 (16)
44°40'–46°30'	6014 (97)	2118 (18)
46°30'–border	6896 (66)	1593 (14)

Note: The number of hauls in each stratum is indicated in parentheses. Border indicates the Washington–Canada border. Sources are Gunderson and Sample (1980), Weinberg et al. (1984, 1994), Coleman (1986, 1988), and for the 1992 survey, M. Wilkins, NMFS, Seattle, Wash., personal communication.

^aStratum contained one or no hauls, so for estimations it was combined with its adjacent southern stratum.

^bI 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.

Fig. 2. Number of species that reached or exceeded given levels of mean abundance (CPUE) within any of eight regions in any year. The curve was derived by fitting a simple linear regression of number of species on log₁₀(mean CPUE) ($R^2 = 0.76$).



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) and leveled off at about 26 species at a CPUE of 600 kg/km². 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/km² within any region in any year, resulting in a list of 33 species (Table 3). Subsequent estimates of fish biomass indicated that the 33 species comprised 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.

Identification of fish assemblages

Hauls from all six surveys combined were classified into groups with similar species compositions primarily by using hierarchical agglom-

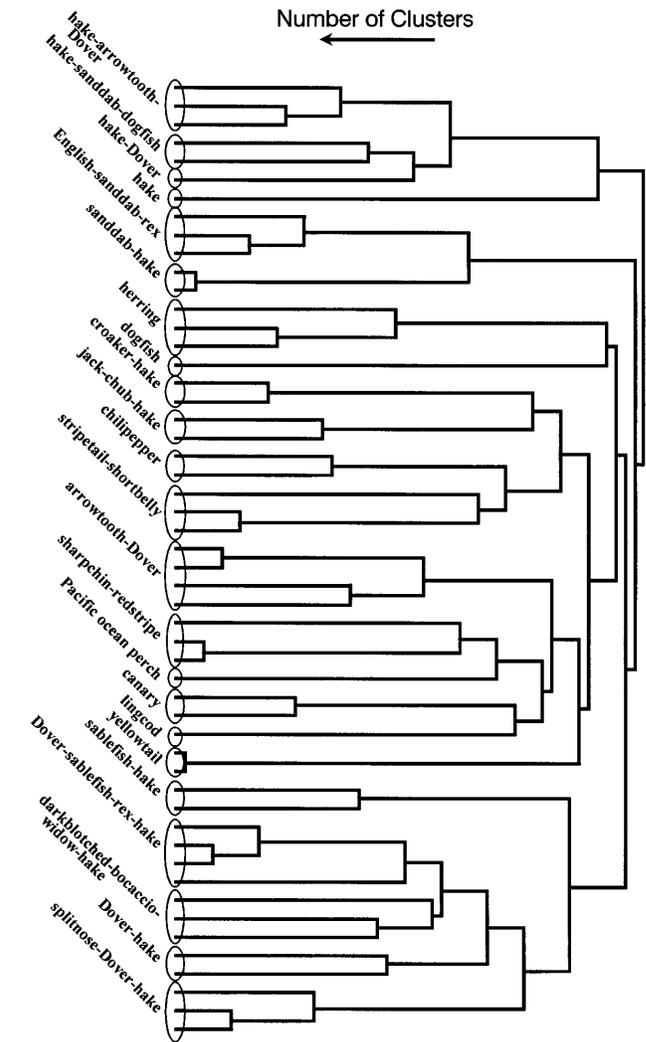
Table 3. Dominant species that were used to identify bottom-trawl fish assemblages from the NMFS 1977–1992 triennial surveys.

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 alascamus</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>

erative 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 0 and a standard deviation of 1 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 comprise 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.

Fig. 3. 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.



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 was used as an aid in determining a starting point for identifying the number of clusters that may be present in the data. The R^2 values leveled off at about 0.80, 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. 3) if the cluster (i) did not appear to be distinct in species composition (a qualitative interpretation) or (ii) 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; Orłóci 1978). In the reclassification procedure, the clusters were the known groups and the relative 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 for 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; SAS Institute Inc. 1988; subsequently referred to 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 1980–1992 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 conductivity–temperature–depth probe, 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 stripetail–shortbelly and splitnose–Dover–hake assemblages, contained fewer than 15 observations in the northern region ($> 42^\circ\text{N}$). 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 19 assemblages comprising 1525 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 transformation 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. 3, Table 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 4). Of the remaining 19 assemblages, 8 were dominated by rockfish species and 5 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 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 ($SD_m = 0.016$) than the other assemblages, which have standard deviations ranging from 0.032 for the hake–Dover assemblage to 0.066 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 above; see Fig. 3) but did not occur over a sufficiently large area (criterion 2 was not met), and therefore they have relatively high standard deviations (0.062 and 0.061).

The mean relative abundance of the single most dominant species in each assemblage (Table 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 ($\bar{x} = 0.87$). Other assemblages with moderately high species dominance (\bar{x} greater than about 0.60) were the herring, sanddab–hake, yellowtail, dogfish, croaker–hake, and chilipepper assemblages. Assemblages with low species dominance (\bar{x} less than about 0.35) were the Dover–sablefish–rex–hake, English–sanddab–rex, hake–arrowtooth–Dover, sharpchin–redstripe, stripetail–shortbelly, and darkblotched–bocaccio–widow–hake assemblages.

Generally, deviations about the mean relative abundance for a given species within an assemblage (Table 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 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. 4), 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 ($>42^\circ\text{N}$; Fig. 4a) and over the continental shelf (approximated by areas ≤ 200 m deep, Fig. 4b), probably partly because these regions form a disproportionately greater portion of the study area. The northern and continental shelf regions comprise about 67 and 81% of the study area, respectively (estimates were derived similarly to the derivation of assemblage incidence estimates).

The stripetail–shortbelly, croaker–hake, and chilipepper assemblages occurred primarily to the south ($<42^\circ\text{N}$; 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 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 across depth for comparable distances, indicating the potential existence of sharper environmental gradients across depth than latitude.

Most assemblages were encountered over the entire study period (Table 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 1980–1992 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 in other years (Fig. 5). These differences are not apparent from incidence estimates for the entire study area (Table 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 was indicated. The assemblage occurred over the continental shelf more than over the upper slope from 1977 to 1986 (Fig. 6), although there is no evidence that this occurred in 1989 and 1992 (also see Fig. 7).

The arrowtooth–Dover assemblage occurred in the northern region only (Figs. 5 and 7). 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 5, Fig. 7). 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 three times that of similar estimates for previous years (Table 5). This increase was apparently due primarily to increases in its occurrence within the southern region (Fig. 5) over the continental shelf (Figs. 6 and 7).

The sanddab–hake assemblage was encountered rarely in 1977 (possibly because the 1977 survey covered a slightly deeper area than subsequent surveys) and occurred infre-

Table 4. Bottom-trawl fish assemblages identified from the NMFS 1977–1992 triennial surveys.

Assemblage	SD _m	Species	n	\bar{x}	CV _{SD}	IQR
Hake	0.016	Pacific hake	409	0.87	0.10	0.80–0.95
Hake–Dover	0.032	Pacific hake	227	0.55	0.20	0.47–0.64
		Dover sole		0.10	0.77	0.04–0.15
		Sablefish		0.06	1.12	0.01–0.09
		Rex sole		0.05	1.07	0.01–0.06
Hake–sanddab–dogfish	0.038	Pacific hake	148	0.45	0.29	0.3–0.57
		Pacific sanddab		0.12	0.78	0.04–0.19
		Spiny dogfish		0.10	1.20	0.00–0.19
		English sole		0.09	0.89	0.02–0.15
		Rex sole		0.07	1.00	0.02–0.10
Dover–sablefish–rex–hake	0.045	Dover sole	175	0.21	0.45	0.14–0.27
		Sablefish		0.15	0.74	0.05–0.23
		Rex sole		0.11	0.97	0.03–0.16
		Pacific hake		0.10	0.87	0.03–0.14
		Arrowtooth flounder		0.07	0.95	0.01–0.12
		Shortspine thornyhead		0.06	1.19	0.01–0.10
		Darkblotched rockfish		0.05	1.34	0.00–0.08
English–sanddab–rex	0.043	English sole	133	0.32	0.46	0.22–0.38
		Pacific sanddab		0.26	0.52	0.15–0.34
		Rex sole		0.13	0.80	0.06–0.18
		Spiny dogfish		0.06	1.58	0.00–0.06
		Pacific hake		0.06	1.40	0.00–0.09
Dover–hake	0.036	Dover sole	170	0.46	0.27	0.36–0.52
		Pacific hake		0.17	0.78	0.04–0.29
		Rex sole		0.09	0.86	0.03–0.13
		Sablefish		0.07	0.94	0.02–0.11
Sablefish–hake	0.038	Sablefish	105	0.55	0.33	0.41–0.64
		Pacific hake		0.12	1.07	0.02–0.20
		Dover sole		0.08	0.93	0.02–0.10
		Arrowtooth flounder		0.05	1.58	0.00–0.06
Arrowtooth–Dover	0.046	Arrowtooth flounder	151	0.39	0.47	0.27–0.50
		Dover sole		0.10	0.87	0.03–0.15
		Spiny dogfish		0.09	1.35	0.00–0.14
		Sablefish		0.07	1.02	0.01–0.11
		Pacific hake		0.06	1.38	0.00–0.09
		Rex sole		0.05	1.22	0.01–0.06
Herring	0.046	Pacific herring	84	0.60	0.40	0.38–0.82
		Spiny dogfish		0.07	1.87	0.00–0.08
		Pacific sanddab		0.06	1.52	0.00–0.08
		Pacific hake		0.06	1.66	0.00–0.10
		English sole		0.05	1.70	0.00–0.05
		Pacific sanddab		0.06	1.52	0.00–0.08
Sanddab–hake	0.034	Pacific sanddab	82	0.62	0.24	0.49–0.71
		Pacific hake		0.10	1.28	0.00–0.16
		English sole		0.08	0.76	0.03–0.13
		Rex sole		0.06	0.94	0.02–0.08
Hake–arrowtooth–Dover	0.050	Pacific hake	102	0.26	0.61	0.12–0.34
		Arrowtooth flounder		0.10	0.88	0.02–0.16
		Dover sole		0.10	0.97	0.02–0.16
		Yellowtail rockfish		0.08	1.26	0.00–0.16
		Spiny dogfish		0.08	1.21	0.02–0.12
		Walleye pollock		0.08	1.67	0.00–0.12
		Sablefish		0.05	1.26	0.00–0.08
Sharpchin–redstripe	0.062	Sharpchin rockfish	67	0.28	0.97	0.04–0.43
		Redstripe rockfish		0.27	1.03	0.01–0.47
		Canary rockfish		0.05	1.71	0.00–0.05
Yellowtail	0.042	Yellowtail rockfish	74	0.59	0.32	0.44–0.75
		Pacific hake		0.09	1.48	0.00–0.12
Stripetail–shortbelly	0.061	Stripetail rockfish	82	0.36	0.61	0.22–0.52

Table 4 (concluded).

Assemblage	SD _m	Species	<i>n</i>	\bar{x}	CV _{SD}	IQR
Dogfish	0.035	Shortbelly rockfish	86	0.18	1.71	0.00–0.21
		Pacific hake		0.09	1.30	0.00–0.15
		Chilipepper		0.09	1.24	0.00–0.15
		Dover sole		0.07	1.20	0.01–0.09
		Spiny dogfish		0.66	0.24	0.54–0.77
Splitnose–Dover–hake	0.049	Pacific hake	75	0.05	1.78	0.00–0.06
		Splitnose rockfish		0.43	0.46	0.28–0.56
		Dover sole		0.15	0.89	0.03–0.23
		Pacific hake		0.11	1.28	0.01–0.16
		Sablefish		0.06	1.42	0.00–0.10
Darkblotched–bocaccio–widow–hake	0.066	Darkblotched rockfish	62	0.06	1.29	0.00–0.09
		Bank rockfish		0.05	2.77	0.00–0.00
		Darkblotched rockfish		0.22	1.13	0.00–0.38
		Bocaccio		0.13	1.52	0.00–0.25
		Widow rockfish		0.12	1.96	0.00–0.03
		Pacific hake		0.10	1.23	0.01–0.15
		Dover sole		0.07	1.11	0.01–0.10
Canary	0.045	Sablefish	64	0.06	1.35	0.00–0.08
		Canary rockfish		0.53	0.41	0.34–0.73
		Pacific hake		0.07	1.55	0.00–0.10
Lingcod	0.048	Lingcod	63	0.06	1.35	0.00–0.08
		Lingcod		0.41	0.40	0.29–0.47
		Spiny dogfish		0.07	1.47	0.00–0.10
		Arrowtooth flounder		0.07	1.60	0.00–0.11
		English sole		0.06	1.40	0.00–0.12
		Dover sole		0.06	1.35	0.00–0.08
		Pacific sanddab		0.06	1.67	0.00–0.09
		Pacific hake		0.05	1.75	0.00–0.05
Croaker–hake	0.040	Rex sole	40	0.05	1.16	0.00–0.07
		White croaker		0.59	0.35	0.41–0.76
		Pacific hake		0.13	1.09	0.03–0.20
		Pacific sanddab		0.07	1.38	0.01–0.08
Jack–chub–hake	0.050	English sole	49	0.06	1.10	0.01–0.08
		Jack mackerel		0.54	0.44	0.38–0.72
		Chub mackerel		0.15	1.29	0.00–0.27
		Pacific hake		0.12	1.20	0.00–0.18
Chilipepper	0.041	Pacific sanddab	49	0.05	1.43	0.00–0.08
		Chilipepper		0.59	0.36	0.39–0.76
		Pacific hake		0.09	1.48	0.01–0.13
Pacific ocean perch	0.041	Stripetail rockfish	68	0.06	1.44	0.00–0.12
		Dover sole		0.05	1.20	0.01–0.07
		Pacific ocean perch		0.46	0.36	0.33–0.59
		Dover sole		0.09	0.96	0.02–0.12
		Sablefish		0.07	1.28	0.01–0.10
		Pacific hake		0.07	1.45	0.00–0.10
		Arrowtooth flounder		0.06	0.97	0.01–0.08
		Sharpchin rockfish		0.05	1.58	0.00–0.08

Note: 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}, coefficient of variation (SD/mean); IQR, interquartile range.

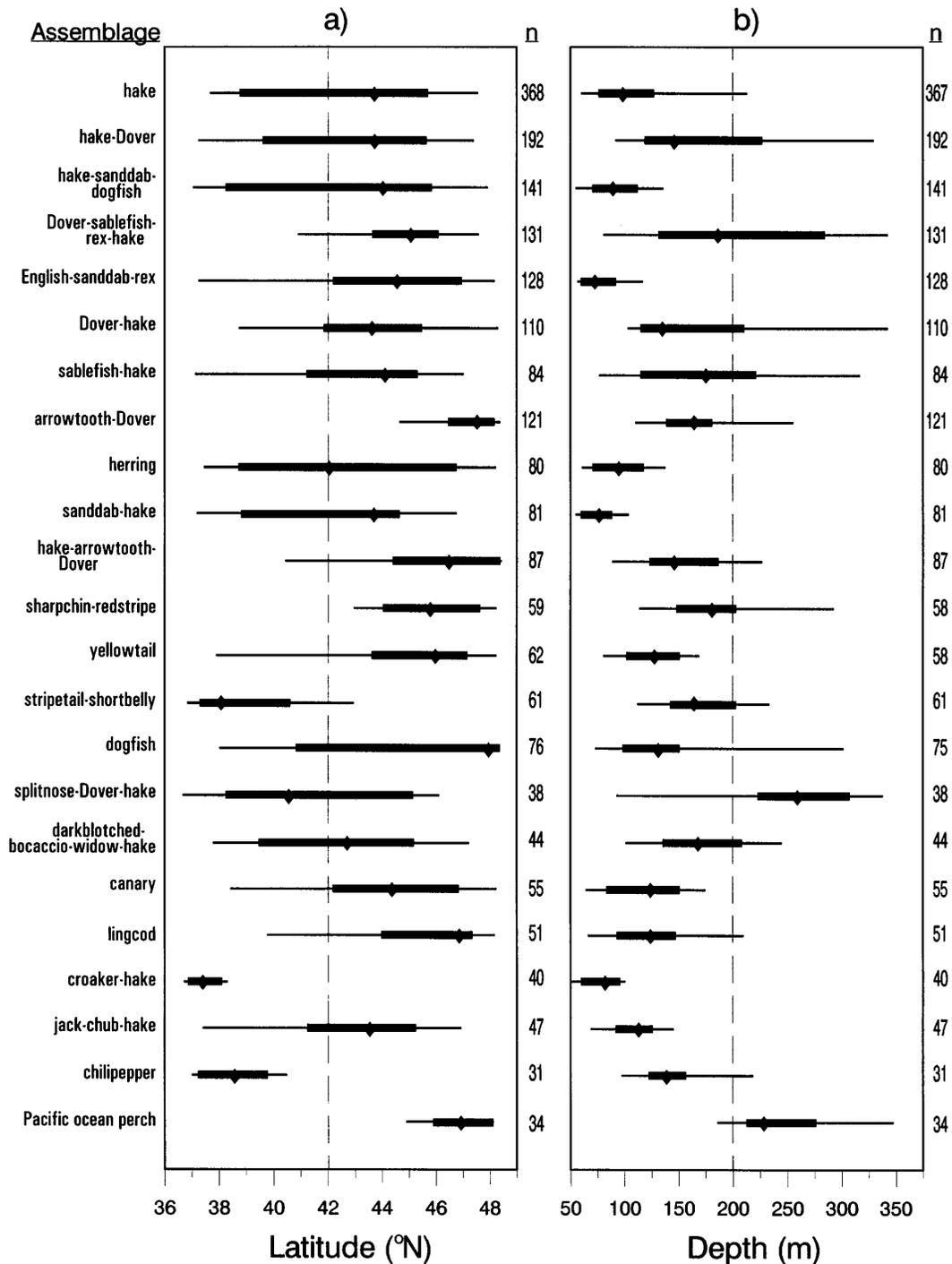
quently in 1980 but occurred over about 7% of the study area in 1989 (Table 5). Its increased occurrence in 1989 can be ascribed to increases in its incidence within the southern region over the continental shelf (Figs. 5–7).

The croaker–hake assemblage had an incidence of 1% or less in all but the 1992 survey, when its incidence was about 6% (Table 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. 5 and 6) in shallow waters near San Francisco Bay (Fig. 7).

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 5) and occurred entirely within the continental shelf region (Fig. 6). Increases

Fig. 4. 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.



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. 5 and 7).

Maps of the distribution of assemblages reveal that they generally occurred within broad geographic boundaries, but their distributions were largely discontinuous (Fig. 7). 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 correlations between any two variables were only

Table 5. Estimated incidence (\hat{I}) of bottom-trawl fish assemblages identified from the NMFS 1977–1992 triennial surveys.

Assemblage		Year						1980–1992 \bar{x}
		1977 ^a	1980	1983	1986	1989	1992	
Hake	\hat{I}	0.15 ^b	0.25	0.15 ^b	0.22	0.18	0.18	0.20
	2SE	0.04	0.06	0.04	0.04	0.04	0.04	
Hake–Dover	\hat{I}	0.09	0.03 ^b	0.10	0.08	0.12	0.10	0.09
	2SE	0.03	0.02	0.03	0.03	0.03	0.03	
Hake–sanddab–dogfish	\hat{I}	0.02 ^b	0.02 ^b	0.08	0.06	0.08	0.10	0.07
	2SE	0.02	0.02	0.03	0.03	0.03	0.03	
Dover–sablefish–rex–hake	\hat{I}	0.09	0.06	0.09	0.10	0.06	0.03 ^b	0.07
	2SE	0.03	0.03	0.03	0.03	0.02	0.02	
English–sanddab–rex	\hat{I}	0.02 ^b	0.05	0.05	0.05	0.07	0.08	0.06
	2SE	0.02	0.03	0.03	0.02	0.03	0.03	
Dover–hake	\hat{I}	0.10 ^b	0.06	0.05	0.09 ^b	0.03	0.02 ^b	0.05
	2SE	0.03	0.02	0.02	0.03	0.02	0.02	
Sablefish–hake	\hat{I}	0.05	0.08	0.04	0.05	0.03	0.04	0.05
	2SE	0.02	0.04	0.02	0.02	0.02	0.02	
Arrowtooth–Dover	\hat{I}	0.07 ^b	0.03	0.02 ^b	0.06	0.06	0.01 ^b	0.04
	2SE	0.02	0.02	0.01	0.02	0.02	0.01	
Herring	\hat{I}	0.01 ^b	0.03	0.02 ^b	0.00 ^b	0.04	0.12 ^b	0.04
	2SE	0.01	0.02	0.01	0.01	0.02	0.03	
Sanddab–hake	\hat{I}	0.00 ^b	0.01 ^b	0.03	0.03	0.07 ^b	0.05	0.04
	2SE	0.00	0.01	0.02	0.02	0.02	0.02	
Hake–arrowtooth–Dover	\hat{I}	0.04	0.02	0.05	0.03	0.03	0.02	0.03
	2SE	0.02	0.02	0.02	0.01	0.02	0.02	
Sharpchin–redstripe	\hat{I}	0.02	0.03	0.03	0.02	0.02	0.03	0.03
	2SE	0.02	0.02	0.01	0.01	0.01	0.02	
Yellowtail	\hat{I}	0.04	0.07 ^b	0.03	0.03	0.02	0.01 ^b	0.03
	2SE	0.03	0.03	0.02	0.02	0.01	0.01	
Stripetail–shortbelly	\hat{I}	0.03	0.05	0.03	0.03	0.02	0.04	0.03
	2SE	0.02	0.03	0.02	0.02	0.01	0.02	
Dogfish	\hat{I}	0.03	0.03	0.06 ^b	0.01 ^b	0.03	0.03	0.03
	2SE	0.02	0.02	0.02	0.01	0.02	0.02	
Splitnose–Dover–hake	\hat{I}	0.04 ^b	0.04	0.01	0.03	0.01	0.01	0.02
	2SE	0.01	0.02	0.01	0.02	0.01	0.01	
Darkblotched–bocaccio–widow–hake	\hat{I}	0.04	0.04	0.03	0.02	0.01	0.01	0.02
	2SE	0.02	0.03	0.01	0.02	0.01	0.01	
Canary	\hat{I}	0.03	0.02	0.05 ^b	0.02	0.01	0.00 ^b	0.02
	2SE	0.02	0.02	0.02	0.01	0.01	0.01	
Lingcod	\hat{I}	0.05	0.03	0.02	0.02	0.01	0.01	0.02
	2SE	0.03	0.02	0.01	0.01	0.01	0.01	
Croaker–hake	\hat{I}	— ^c	0.01	0.01	0.01	0.01	0.06 ^b	0.02
	2SE	— ^c	0.01	0.01	0.01	0.01	0.02	
Jack–chub–hake	\hat{I}	0.01	— ^c	0.01	0.01	0.06 ^b	0.04	0.02
	2SE	0.01	— ^c	0.01	0.01	0.02	0.02	
Chilipepper	\hat{I}	0.03	0.02	0.02	0.01	0.03	0.01	0.02
	2SE	0.02	0.02	0.02	0.01	0.02	0.01	
Pacific ocean perch	\hat{I}	0.05 ^b	0.02	0.02	0.01	0.01	0.01	0.01
	2SE	0.02	0.02	0.01	0.01	0.01	0.01	

Note: Total sample sizes for each year are 444, 322, 470, 501, 418, and 410. 2SE, two standard errors.

^aA slightly deeper depth range was covered in 1977 than in subsequent surveys.

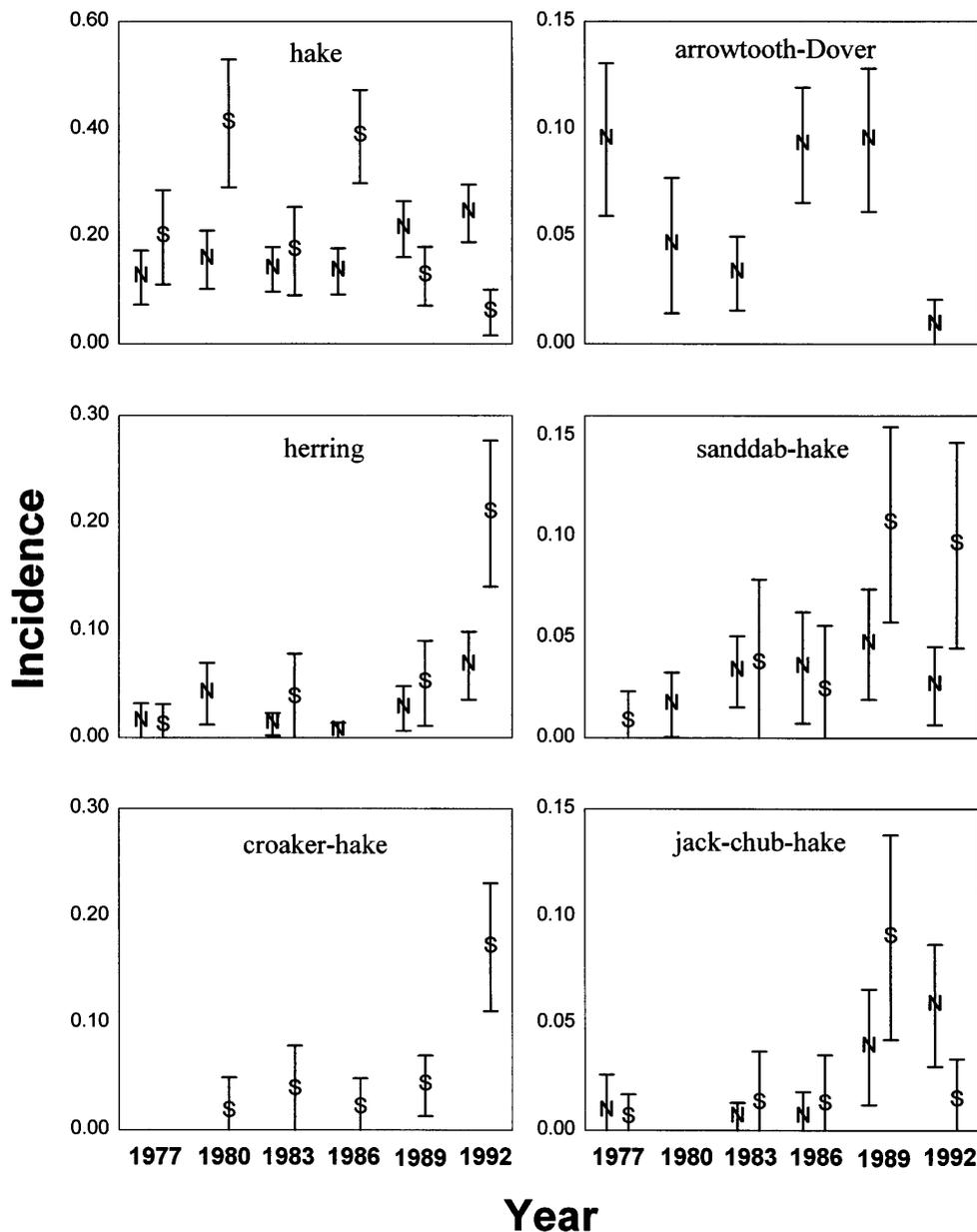
^bIncidence estimates whose ± 2 SE range did not include the 1980–1992 mean.

^cAssemblage was not encountered.

moderate negative correlations between bottom temperature and latitude and between bottom temperature and depth (total sample correlation coefficients; Table 6). The first and second canonical functions captured 64 and 28% of the total variation among all observations (cumulative eigenvalue = 92%).

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

Fig. 5. Estimates of regional incidence from 1977 to 1992 for assemblages that showed significant differences in incidence between the regions north (N) and south (S) of 42°N.

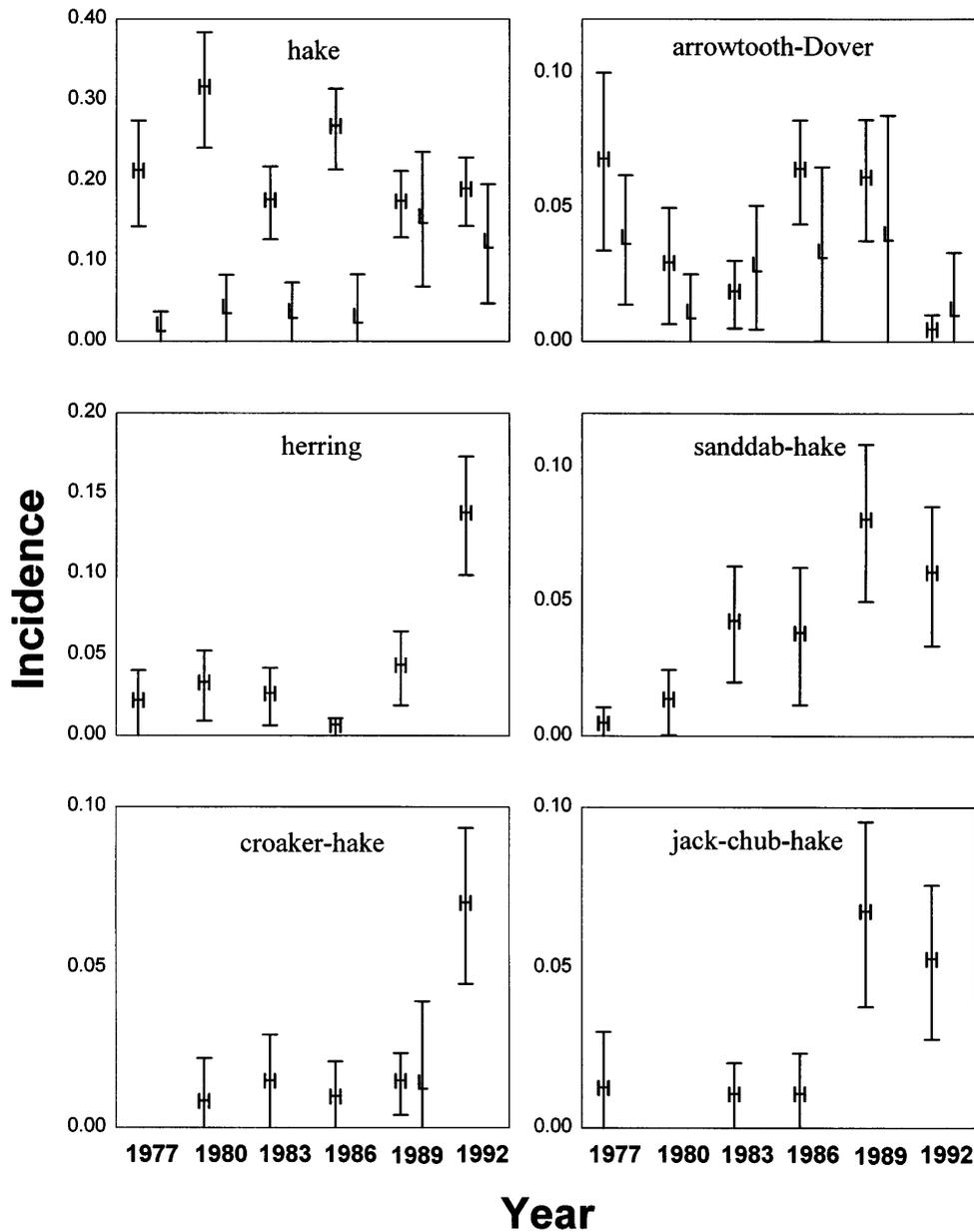


assemblages. Accordingly, the assemblages explained only 40 and 22% of the variation of the first and second canonical variates, respectively (squared canonical correlation). Total canonical structure coefficients are correlations between each discriminating variable and the discriminant functions (Klecka 1980). The first and second functions were highly correlated with depth and latitude, respectively (total canonical structure). In short, relatively little discrimination between groups was achieved by the five environmental variables, and the discrimination that was achieved was obtained primarily from depth and secondarily 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%.

Fig. 6. Estimates of regional incidence from 1977 to 1992 for assemblages that showed significant differences in incidence between the continental shelf (H) and upper slope (L).



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 meth-

ods 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 solely on the basis of 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

Fig. 7. Location of assemblages within the study area from 1977 to 1992 (50- and 250-m isobaths are shown).

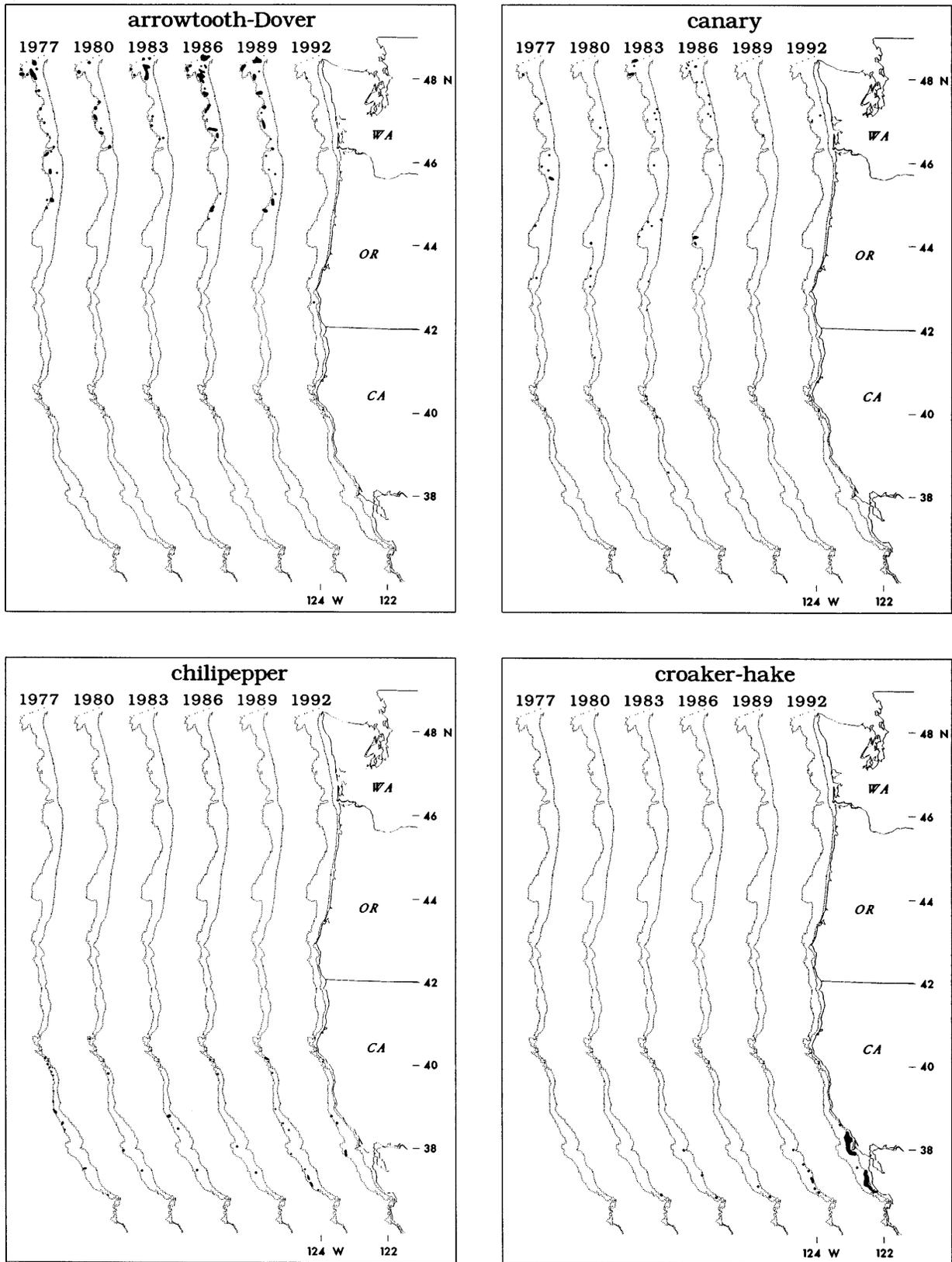


Fig. 7 (continued).

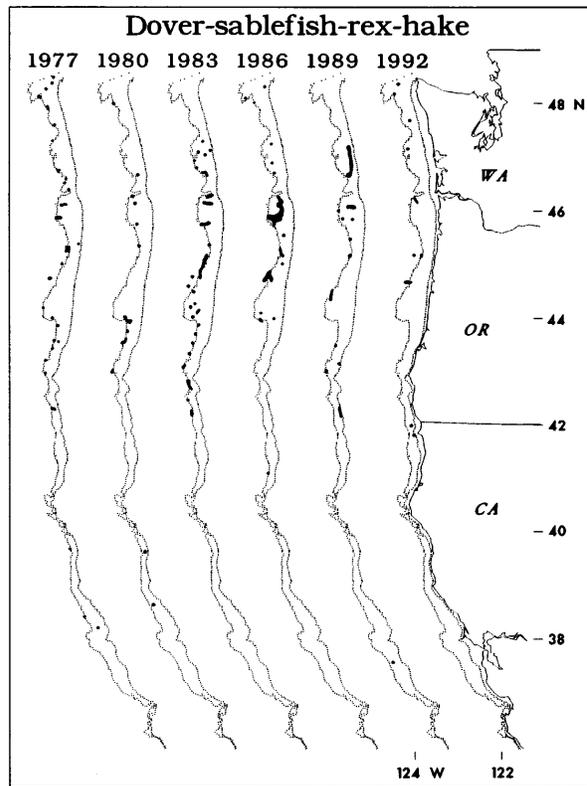
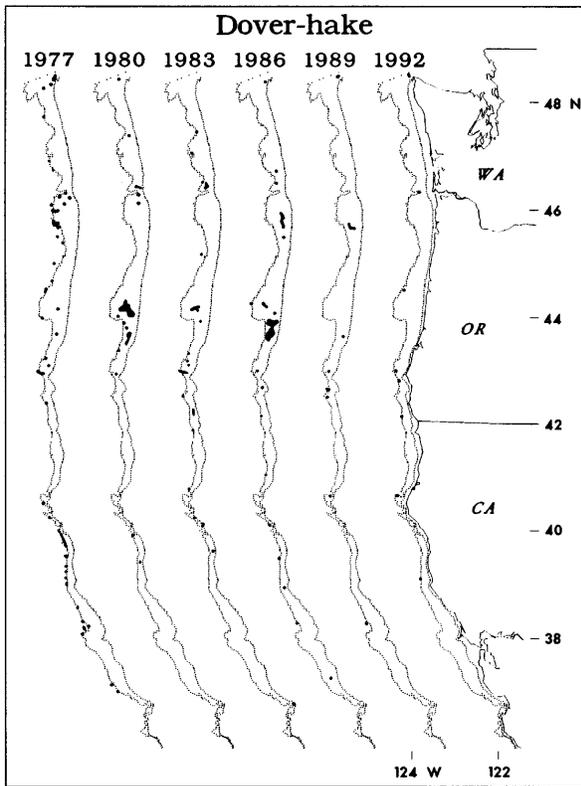
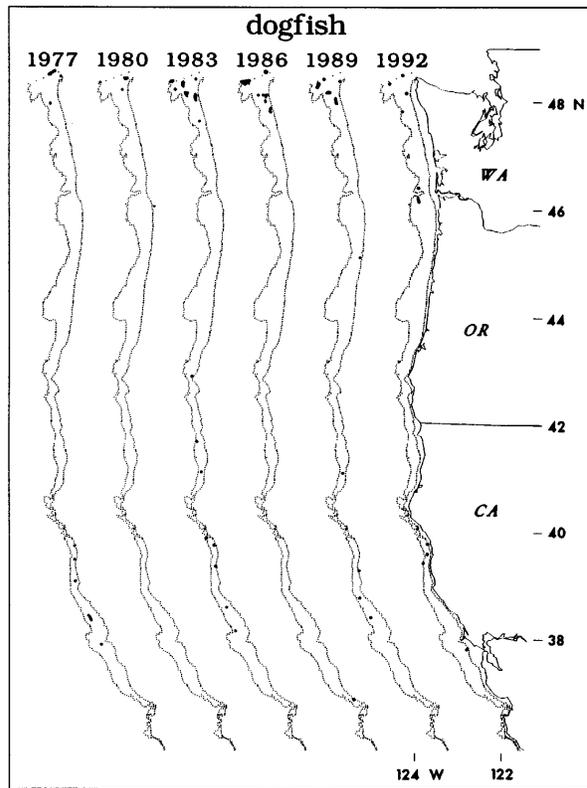
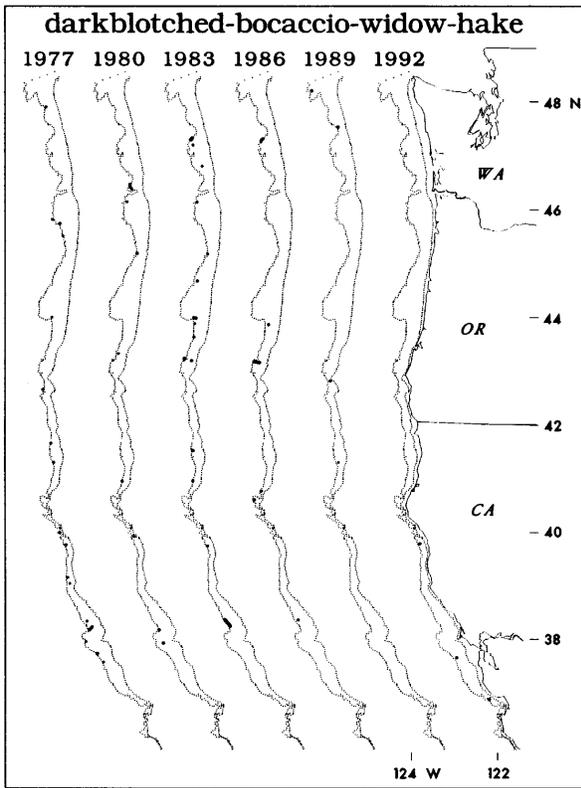


Fig. 7 (continued).

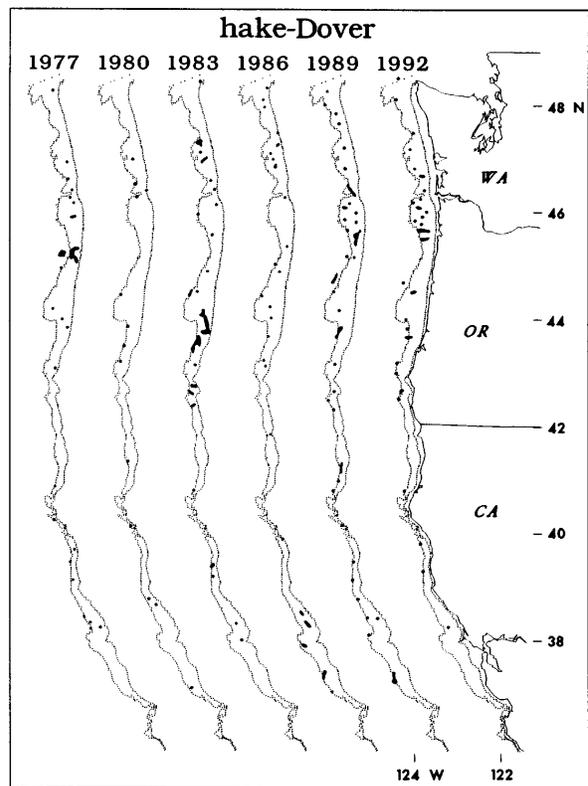
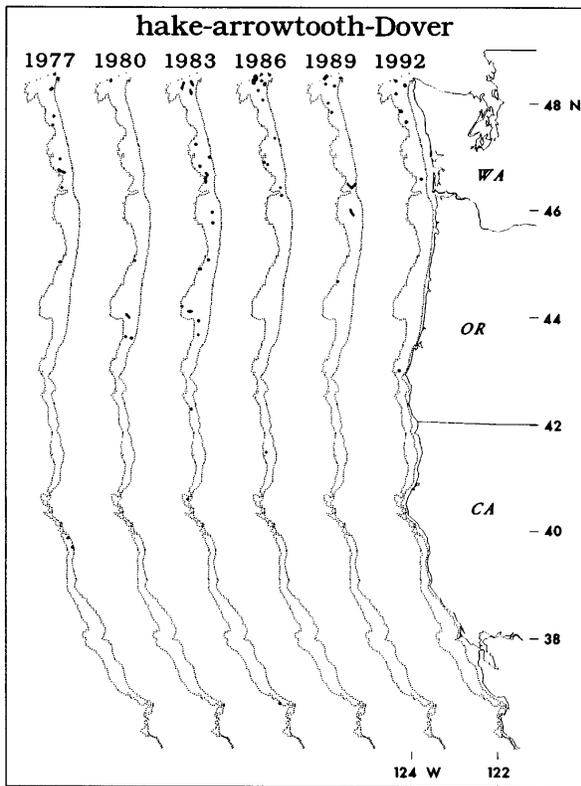
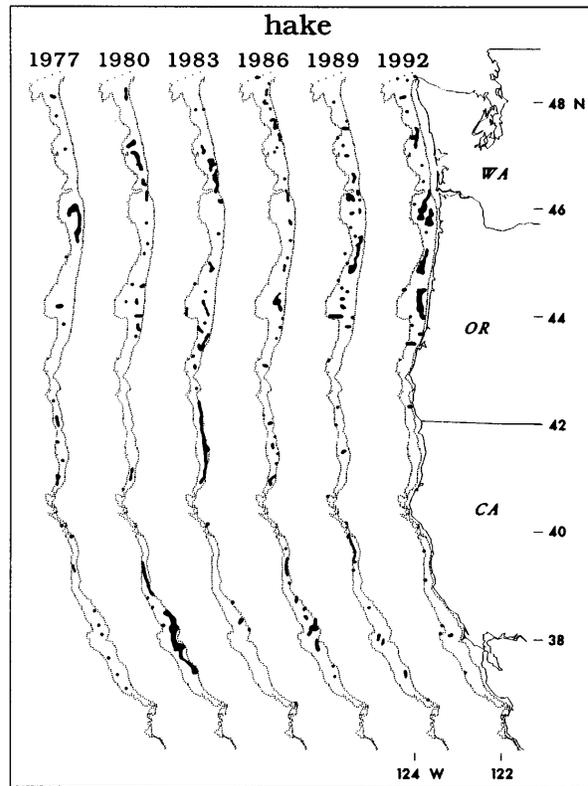
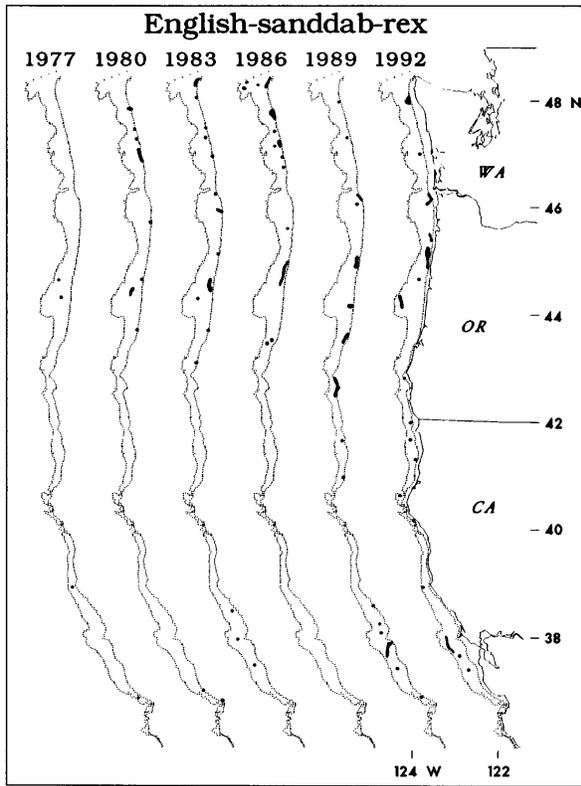


Fig. 7 (continued).

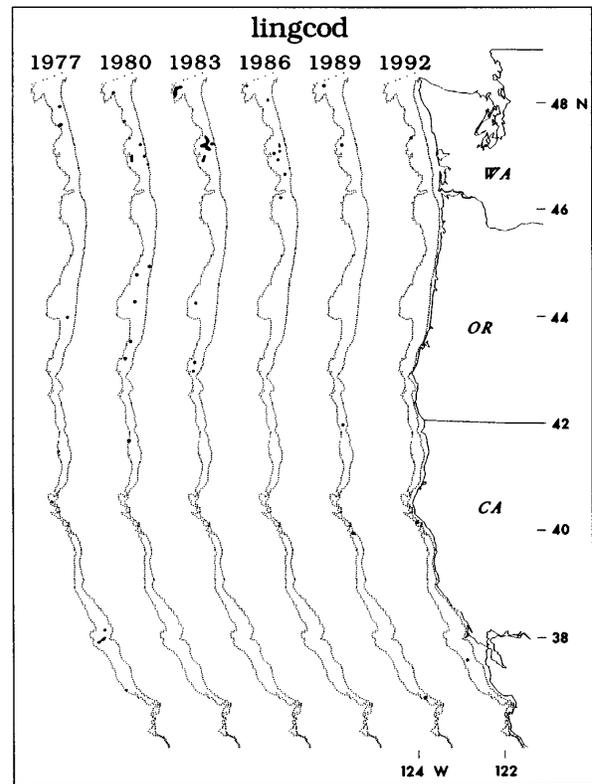
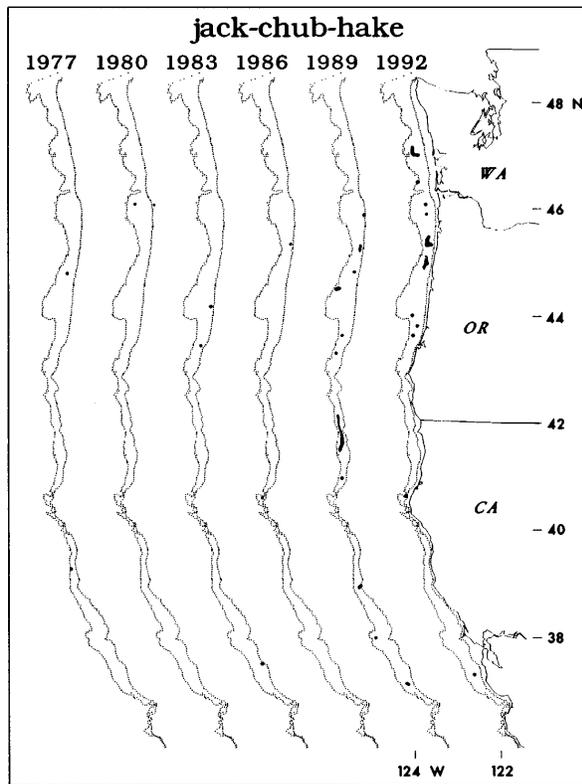
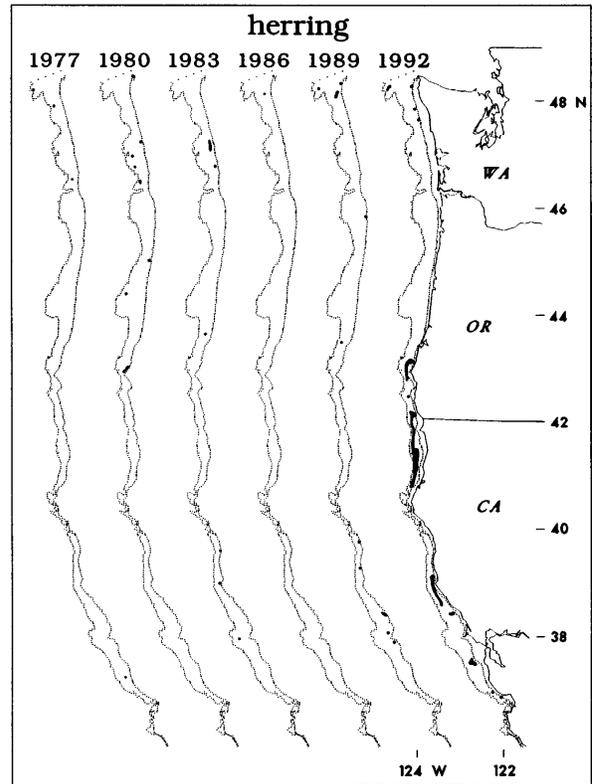
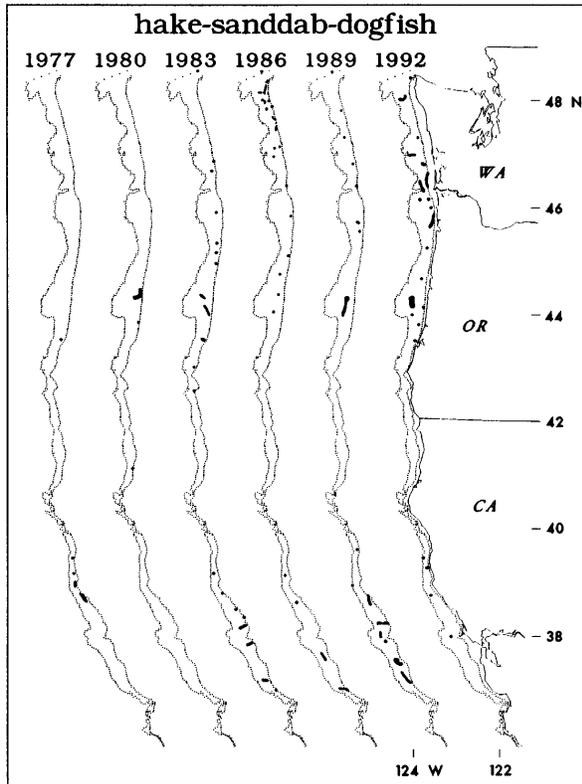


Fig. 7 (continued).

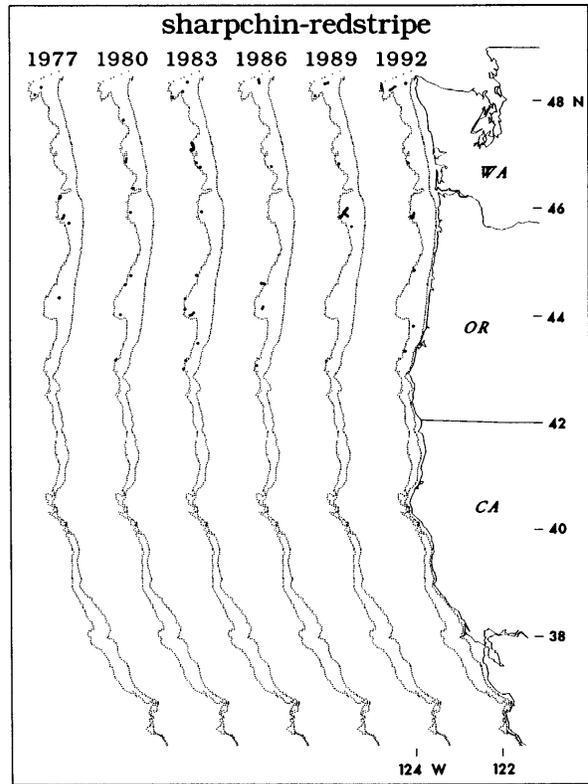
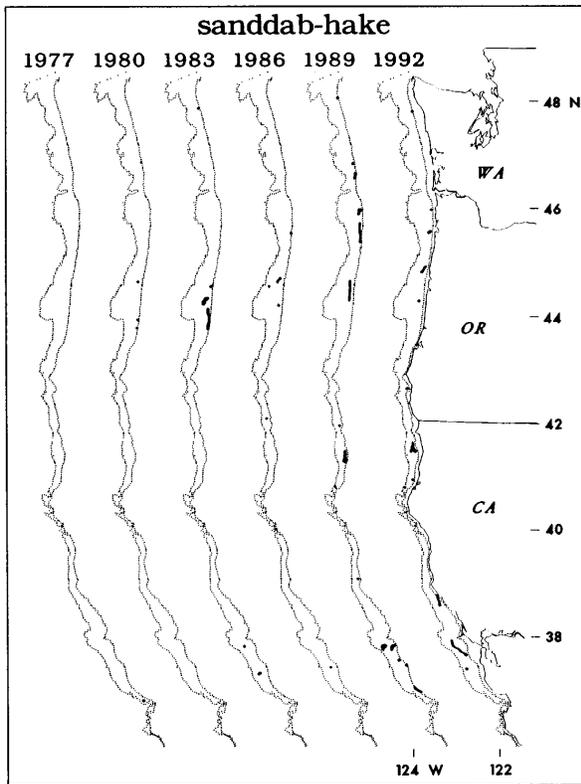
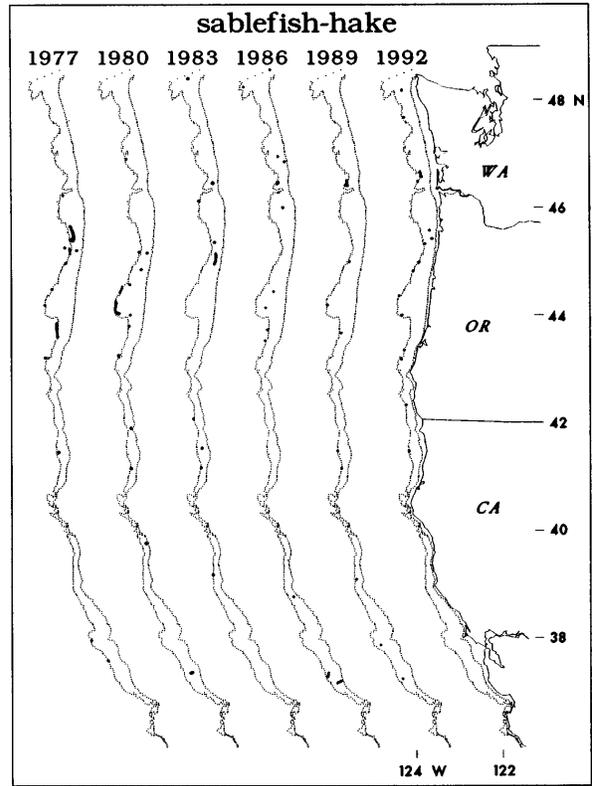
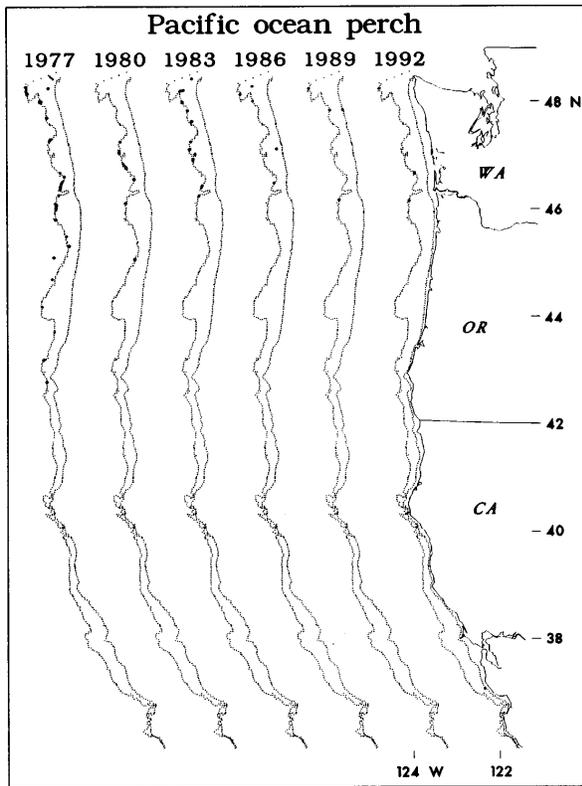


Fig. 7 (concluded).

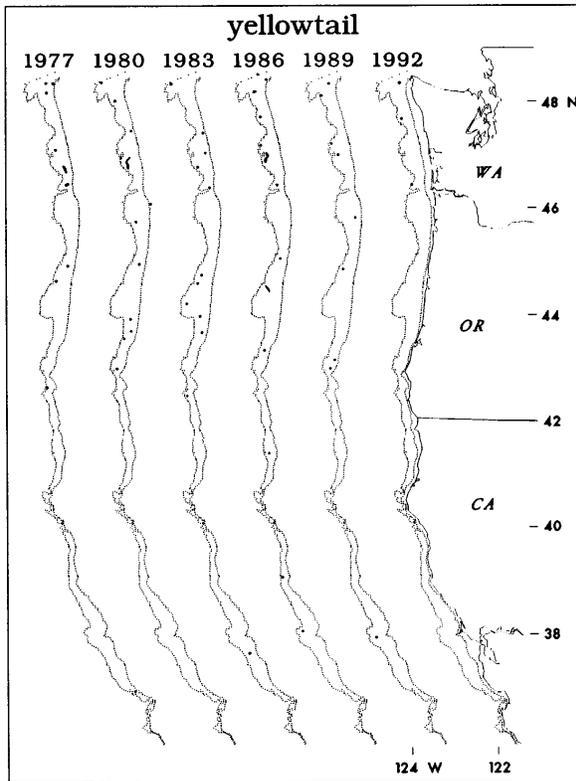
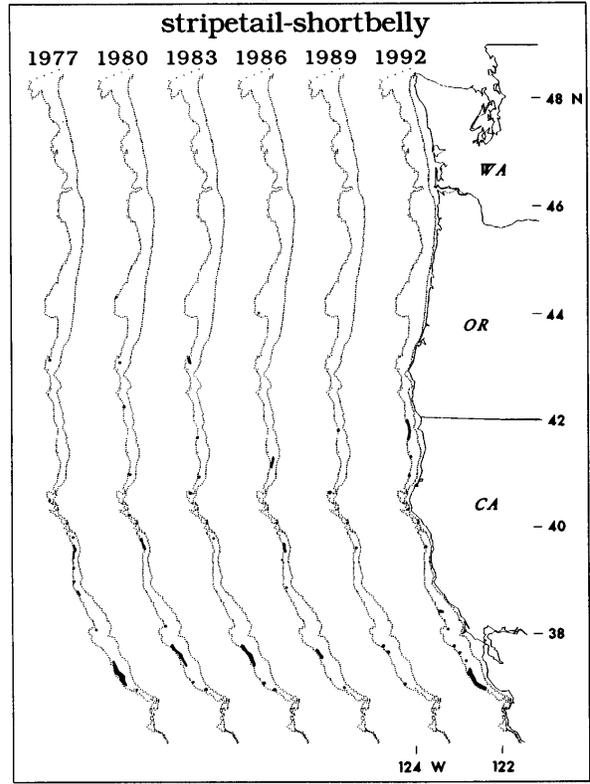
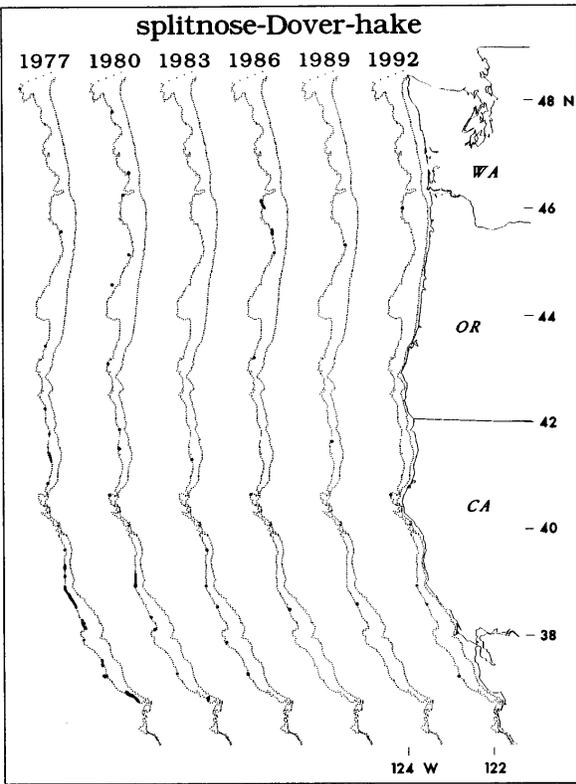


Table 6. Results of discriminant analysis of 19 assemblages using five environmental discriminating variables in the northern region (>42°N) of the study area (no. of observations = 1525).

(A) Total sample correlation coefficients.					
Variable	Latitude	Depth	Substrate	Surface temperature	Bottom temperature
Latitude	1.00				
Depth	-0.07	1.00			
Substrate	0.04	-0.20	1.00		
Surface temperature	0.20	0.16	-0.12	1.00	
Bottom temperature	-0.31	-0.34	0.08	0.10	1.00

(B) Eigenvalues and canonical correlations of the canonical functions.		
Canonical function	Cumulative eigenvalue	Squared canonical correlation
1	0.64	0.40
2	0.92	0.22
3	0.96	0.04
4	0.98	0.02
5	1.00	0.02

(C) Total canonical structure.					
Variable	Canonical function				
	1	2	3	4	5
Latitude	-0.068	0.975	0.204	-0.046	-0.015
Depth	0.980	0.034	-0.182	0.005	0.071
Substrate	-0.260	0.140	-0.390	0.806	-0.333
Surface temperature	0.305	0.074	0.842	0.409	0.157
Bottom temperature	-0.398	-0.315	-0.026	0.340	0.792

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 on the basis of two practical criteria. The 23 clusters I derived accounted for about 70% of the total variation among 2565 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: (i) estimates of variance associated with the estimated mean relative abun-

dance of each species within each assemblage (Table 4), (ii) a multivariate measure of within-assemblage deviation (SD_m ; Table 4), and (iii) 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 4). Many of the assemblages that Gabriel identified are not directly comparable with 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 ($>42^{\circ}\text{N}$) 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, dark-blotched-bocaccio-widow-hake, canary, and Pacific ocean perch assemblages (Figs. 4 and 7), albeit they occurred infrequently in some years (Table 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 disjoint assemblage boundaries across depth and latitude (Fig. 7). 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 5 years (Gabriel and Tyler 1980; Fargo and Tyler 1991) and off the Northwest Atlantic coast over about a 15-year period during the 1960s and 1970s (Colvocoresses and Musick 1984; Overholtz and Tyler 1985). A more recent study shows that substantial shifts in assemblage boundaries in the Northwest Atlantic 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 United States, indicates changes in assemblage boundaries over the 1977-1992 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 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 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-year 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 suggest 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. 4) indicates greater segregation of assemblages across depth than across latitude for comparable distances, 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 bot-

tom 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.

Acknowledgments

This work was partially supported by grant No. NA89AA-D-SG108 (project Nos. R/ES-16 and R/OPF-39) from the National Oceanic and Atmospheric Administration (NOAA) to the Oregon State University Sea Grant College Program and by appropriations made by the Oregon State Legislature. The views expressed herein are those of the author and do not necessarily reflect the views of NOAA or any of its subagencies. I thank all those involved in the collection of the National Marine Fisheries Service west coast triennial survey data and Mark Wilkins for making these data available to me. Dr. David Sampson was particularly supportive of this work and provided useful comments to the manuscript. David Fox provided assistance in obtaining surficial substrate data. Additional support was provided by the National Biological Service, Alaska Science Center, Anchorage, Alaska.

References

- Coleman, B.A. 1986. The 1980 Pacific West Coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, length and age composition. NOAA Tech. Memo. NMFS F/NWC-100. National Oceanic and Atmospheric Administration, Washington, D.C.
- Coleman, B.A. 1988. The 1986 Pacific West Coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, length, and age composition. NOAA Tech. Memo. NMFS F/NWC-152. National Oceanic and Atmospheric Administration, Washington, D.C.
- Colvocoresses, J.A., and Musick, J.A. 1984. Species associations and community composition of Middle Atlantic Bight continental shelf demersal fishes. *Fish. Bull.* **82**: 295-313.
- Dark, T.A., and Wilkins, M.E. 1994. Distribution, abundance, and biological characteristics of groundfish off the coast of Washington, Oregon, and California, 1977-1986. NOAA Tech. Rep. NMFS 117.
- Dickie, L.M., and Kerr, S.R. 1982. Alternative approaches to fisheries management. *In* Multispecies approaches to fisheries management advice. *Edited by* M.C. Mercer. *Can. Spec. Publ. Fish. Aquat. Sci.* No. 59. pp. 18-23.
- Everitt, B. 1980. Cluster analysis. Halsted Press, New York.
- Fargo, J., and Tyler, A.V. 1991. Sustainability of flatfish-dominated fish assemblages in Hecate Strait, British Columbia, Canada. *Neth. J. Sea Res.* **27**: 237-253.
- Gabriel, W.L. 1982. Structure and dynamics of northeastern Pacific demersal fish assemblages. Ph.D. thesis, Oregon State University, Corvallis, Oreg.
- Gabriel, W.L., and Tyler, A.V. 1980. Preliminary analysis of Pacific coast demersal fish assemblages. *Mar. Fish. Rev.* **42**: 83-88.
- Gleason, H.A. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club.* **53**: 7-26.
- Gomes, M.C., Haedrich, R.L., and Villagarcia, M.G. 1995. Spatial and temporal changes in the groundfish assemblages on the northeast Newfoundland/Labrador Shelf, north-west Atlantic, 1978-1991. *Fish. Oceanogr.* **4**: 85-101.
- Gunderson, D.R., and Sample, T.M. 1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. *Mar. Fish. Rev.* **42**: 2-16.
- Hixon, M.A., Tissot, B.N., and Pearcy, W.G. 1991. Fish assemblages of rocky banks of the Pacific Northwest. MMS 91-0052. U.S. Department of the Interior, Washington, D.C.
- Klecka, W.R. 1980. Discriminant analysis. Sage Publications, Newbury Park, Calif.
- Leaman, B.M., and Nagtegaal, D.A. 1987. Identification of species assemblages and results of management applications for shelf and slope rockfishes off British Columbia. *In* Proceedings of the International Rockfish Symposium, Anchorage, Alaska, October 1986. *Edited by* B. Melteff. Alaska Sea Grant College Program, University of Alaska, Fairbanks, Alaska. pp. 309-328.
- Lenarz, W.H., and Adams, P.B. 1980. Some statistical considerations of the design of trawl surveys for rockfish (Scorpaenidae). *Fish. Bull.* **78**: 659-674.
- Magurran, A.E. 1988. Ecological diversity and its measurements. Princeton University Press, Princeton, N.J.
- Moore, G.W., and Luken, M.D. 1979. Offshore sand and gravel resources of the Pacific Northwest. U.S. Geological Survey, Menlo Park, Calif.
- Murawski, S.A., and Finn, J.T. 1988. Biological bases for mixed-species fisheries: species co-distribution in relation to environmental and biotic variables. *Can. J. Fish. Aquat. Sci.* **45**: 1720-1735.
- Mysak, L.A. 1986. El Niño, interannual variability and fisheries in the northeast Pacific Ocean. *Can. J. Fish. Aquat. Sci.* **43**: 464-497.
- National Marine Fisheries Services. 1991. ADP code book. U.S. Department of Commerce, Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering Division, Seattle, Wash.
- Norton, J., McLain, D., Brainard, R., and Husby, D. 1985. The 1982-83 El Niño event off Baja and Alta California and its ocean climate context. *In* El Niño north: Niño effects in the eastern subarctic Pacific Ocean. *Edited by* W.S. Wooster and D.L. Fluharty. Washington Sea Grant Program, University of Washington, Seattle, Wash. pp. 44-72.
- Orlói, L. 1978. Multivariate analysis in vegetation research. Dr. W. Junk Publishers, The Hague, The Netherlands.
- Overholtz, W.J., and Tyler, A.V. 1985. Long-term responses of the demersal fish assemblages of Georges Bank. *Fish. Bull.* **83**: 507-520.
- Pearcy, W.G., and Schoener, A. 1987. Changes in the marine biota coincident with the 1982-1983 El Niño in the northeastern subarctic Pacific ocean. *J. Geophys. Res.* **92**: 14 417 - 14 428.
- Pennington, M. 1983. Efficient estimators of abundance, for fish and plankton surveys. *Biometrics*, **39**: 281-286.
- Pielou, E.C. 1977. Mathematical ecology. John Wiley & Sons, New York.
- Rogers, J.B., and Pikitch, E.K. 1992. Numerical definition of groundfish assemblages caught off the coasts of Oregon and Washington

- using commercial fishing strategies. *Can. J. Fish. Aquat. Sci.* **49**: 2648–2656.
- SAS Institute Inc. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute Inc., Cary, N.C.
- Scheaffer, R.L., Mendenhall, W., and Ott, L. 1990. Elementary survey sampling. PWS-Kent Publishing, Boston.
- Smith, S.J. 1988. Evaluating the efficiency of the Δ -distribution mean estimator. *Biometrics*, **44**: 485–493.
- Smith, S.J. 1990. Use of statistical models for the estimation of abundance from groundfish trawl survey data. *Can. J. Fish. Aquat. Sci.* **47**: 894–903.
- Sneath, P.H.A., and Sokal, R.R. 1973. Numerical taxonomy: the principles and practice of numerical classification. W.H. Freeman, San Francisco, Calif.
- Tyler, A.V., Gabriel, W.L., and Overholtz, W.J. 1982. Adaptive management based on structure of fish assemblages of northern continental shelves. *In* Multispecies approaches to fisheries management advice. *Edited by* M.C. Mercer. *Can. Spec. Publ. Fish. Aquat. Sci.* No. 59. pp. 149–156.
- Weinberg, K.L. 1994. Rockfish assemblages of the middle shelf and upper slope off Oregon and Washington. *Fish. Bull.* **92**: 620–632.
- Weinberg, K.L., Wilkins, M.E., and Dark, T.A. 1984. The 1983 Pacific West Coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, age and length composition. NOAA Tech. Memo. NMFS-F/NWC-70. National Oceanic and Atmospheric Administration, Washington, D.C.
- Weinberg, K.L., Wilkins, M.E., Lauth, R.R., and Raymore, P.A. Jr. 1994. The 1989 Pacific West Coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, and length and age composition. NOAA Tech. Memo. NMFS-AFSC-33. National Oceanic and Atmospheric Administration, Washington, D.C.
- Williams, B.K., and Titus, K. 1988. Assessment of sampling stability in ecological applications of discriminant analysis. *Ecology*, **69**: 1275–1285.
- Wright, D.H. 1991. Correlations between incidence and abundance are expected by chance. *J. Biogeogr.* **18**: 463–466.