

Abstract—The rockfishes of the seabastid genus *Sebastes* are a very important fishery resource off the coasts of California and southern Oregon. However, many of the 54 managed stocks of west coast rockfish have recently reached historically low population levels, leading fishery managers to re-examine current management practices. Management of rockfish stocks as multispecies aggregates, as opposed to independent stocks within the groundfish fishery, can be more desirable when nontargeted bycatch, discard, and management complexity are considered. Rockfish assemblage structure and species co-occurrences were determined by using data from the Alaska Fisheries Science Center triennial continental shelf bottom trawl survey. The weight of rockfish species in trawl catches was expressed as a catch-per-unit-of-effort (CPUE) statistic, from which species spatial distributions, overlaps, diversity, and richness were analyzed. Multidimensional scaling of transformed CPUE data was employed in indirect gradient and multivariate partitioning analyses to quantify assemblage relationships. Results indicated that rockfish distributions closely match the bathymetry of coastal waters. Indirect gradient analysis suggested that depth and latitude are the principal factors in structuring the spatial distributions of rockfish on trawlable habitat. In addition, four assemblages were identified through the joint evaluation of species' distributions and multivariate partitioning analyses: 1) deep-water slope; 2) northern shelf; 3) southern shelf; and 4) nearshore. The slope, shelf, and nearshore groups are found in depth ranges of 200–500 m, 100–250 m, and 50–150 m, respectively. The division of northern and southern shelf assemblages occurs over a broad area between Cape Mendocino and Monterey Canyon. The results of this analysis are likely to have direct application in the management of rockfish stocks off the coasts of southern Oregon and California.

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Distribution and co-occurrence of rockfishes (family: Sebastidae) over trawlable shelf and slope habitats of California and southern Oregon

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Rockfishes (family Sebastidae according to recent work by Eschmeyer (1998) and Kendall (2000), genera *Sebastes* and *Sebastolobus*) are a very important part of the groundfish fishery off the United States west coast, representing a relatively high value in the market. In 1997, rockfish species accounted for 17% of total west coast groundfish landings, but 33% of total exvessel value (Herrick et al.¹). Rockfishes on the U. S. west coast are managed under the groundfish Fishery Management Plan (FMP) by the Pacific Fishery Management Council. Some of the 52 *Sebastes* and 2 *Sebastolobus* species that are included in the FMP are managed as single-species stocks, and other, generally less well-known species, are managed as part of larger multispecies aggregations. Moreover, the 54 “rockfishes” listed in the FMP do not include all of the *Sebastes* spp. found in the region. More than 70 species are known from the northeast Pacific Ocean (Eschmeyer et al., 1983; Chen, 1986).

The current status of the principal west coast rockfish stocks is that many have reached historically low levels and the population sizes of many of the minor species remain virtually unknown. Moreover, seven rockfishes (bocaccio (*S. paucispinis*), cowcod (*S. levis*), canary (*S. pinniger*) darkblotched (*S. crameri*), widow (*S. entomelas*), and yelloweye (*S. ruberrimus*) rockfishes, and Pacific ocean perch (*S. alutus*) have recently been declared overfished by the Na-

tional Marine Fisheries Service. The continuing declines in rockfish populations and other groundfish stocks off the U. S. west coast have prompted changes in harvest policy and other management practices (Ralston, 1998, 2002).

Management of exploited fish stocks on an individual basis often results in discarded bycatch of nontargeted species, which is wasteful. In contrast, management of species as aggregates or complexes can be more practical and desirable (Ralston and Polovina, 1982; Leaman and Nagtegaal, 1986; Fujita et al., 1998). However, the multispecies management approach is only as good as the assemblage or group definitions used, which depend on the availability and accuracy of species-specific distributional information. Most fisheries managers rely on fishery-independent surveys or at-sea observations of fishery catches recorded in vessel logbooks or noted by observers to provide spatial information on fish abundance patterns. Data collection for groundfish population assessments off the coast

¹ Herrick, S. F., J. Hastie, and W. Jacobson. 1998. Economic status of the Washington, Oregon, and California groundfish fisheries. In Pacific Fishery Management Council, Status of the Pacific Coast groundfish fishery through 1998 and recommended biological catches for 1999: stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, Oregon 97201.

of California consists primarily of sampling commercial and recreational landings at ports, and for these landings there is little information on catch location (Pearson and Erwin, 1997; Sampson and Crone, 1997). The National Marine Fisheries Service, Alaska Fisheries Science Center (AFSC) westcoast triennial continental shelf bottom-trawl survey, which enters into California waters, has yielded useful spatial information for determining groundfish distributions and co-occurrences. This survey began in 1977 as a rockfish survey but changed focus in subsequent years, depending on the particular information needs at the time (Dark and Wilkins, 1994; Wilkins et al., 1998). For the eight surveys conducted from 1977 to 1998, the shelf trawl survey covered the area from central Vancouver Island, British Columbia, to Point Conception, California, at depths ranging from 50 to 500 m (Wilkins et al., 1998).

Along the U.S. west coast, 60–65% of the groundfish catch (exclusive of Pacific whiting) is taken off the coasts of Washington and Oregon (PFMC²). This area has been the focus of past studies examining groundfish population distributions and assemblages (e.g. Gabriel and Tyler, 1980; Leaman and Nagtegaal, 1986; Rickey and Lai, 1990; Rogers and Pikitch, 1992; Weinberg, 1994; Jay, 1996; Gunderson, 1997). In these previous studies of rockfish distributions and groupings, rockfish could be broken into shelf and slope assemblages (e.g. Rogers and Pikitch, 1992; Weinberg, 1994). These studies have all indicated that along the Oregon–Washington coast a “slope” or deep-water rockfish assemblage exists, consisting of darkblotched rockfish, Pacific ocean perch, splitnose rockfish (*S. diploproa*), yellowmouth rockfish (*S. reedi*), and shortspine thornyhead (*Sebastolobus alascanus*). In addition, a “shelf” or bottom rockfish assemblage consists of yellowtail rockfish (*S. flavidus*), canary rockfish (*S. pinniger*), sharpchin rockfish (*S. zacentrus*), greenstriped rockfish (*S. elongatus*), rosethorn rockfish (*S. helvomaculatus*), and redstripe rockfish (*S. proriger*). Weinberg (1994) also examined patterns in abundance and number of rockfish species with respect to depth gradients. Both abundance and the number of species increased with depth to a maximum in the range of 151–250 m but both quantities decreased at depths greater than 250 m.

Groundfish assemblages off California have not been studied, primarily because of the absence of detailed at-sea fishery data collection programs and because of smaller landings. Although California landings account for only 35% of the nonwhiting groundfish total (PFMC²), nearly 43% of west coast rockfish landings are taken in California waters (Herrick et al.¹). Thus, an understanding of the distribution and co-occurrence of rockfishes off the California coast would help with efforts to implement effective fishery management actions leading to a sus-

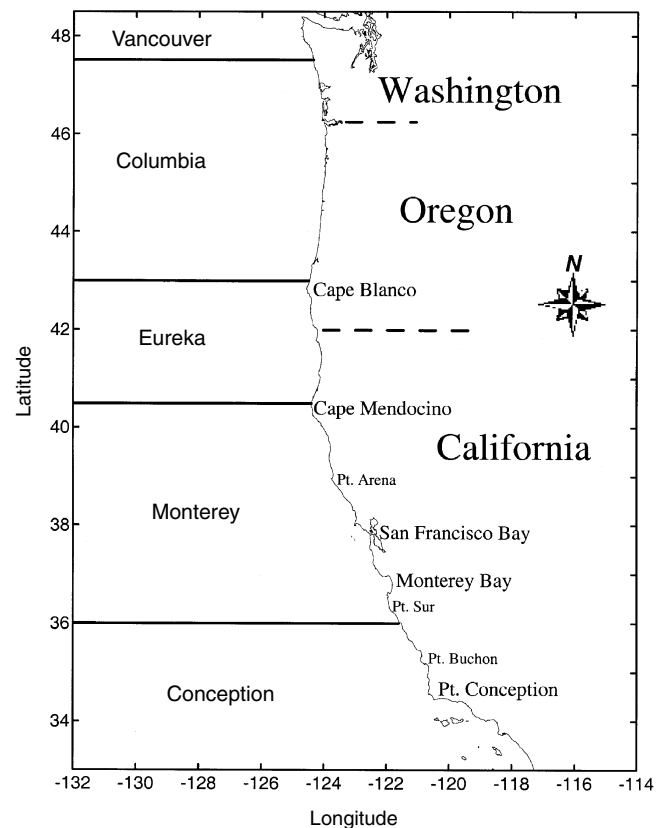


Figure 1

Map of the west coast of the United States, including names of important coastal features and International North Pacific Fisheries Commission management areas.

tainable California rockfish fishery. In particular, an understanding of rockfish distributions and co-occurrences could lead to improved definitions of species complexes. Weinberg (1994) analyzed rockfish assemblages of the “Columbia” and U.S. portion of the “Vancouver” fishery management areas, as specified by the International North Pacific Fisheries Commission (INPFC) (Fig. 1). In part to complement Weinberg’s (1994) analysis, we analyzed the AFSC continental shelf trawl survey data from the more southerly waters of the Eureka, Monterey, and Conception INPFC areas, i.e. all sampling conducted south of lat. 43°N (Fig. 1).

Materials and methods

Rockfish likely form aggregations or complexes as a response to oceanographic and bathymetric features. For this reason the bathymetry of the region encompassed by the limits of the survey area in the Eureka, Monterey, and Conception INPFC areas was characterized. The study area is the area of marine waters located from lat. 34° to 43°N within a depth range of 50–500 m. Bathymetric data for this region were obtained from the National Ocean Service Hydrographic Data Base (NOSHDB). The

² PFMC (Pacific Fishery Management Council). 2000. Status of the Pacific Coast groundfish fishery through 2000 and recommended acceptable biological catches for 2001—stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, Oregon 97201.

NOSHDB contains data digitized from hydrographic surveys completed from 1930 to 1965 and from survey data acquired digitally on NOS survey vessels since 1965. The total amount of habitat by depth and latitude, as well as the location of the shelf break, was determined by analysis of the NOSHDB.

Because the NOSHDB contains a vast amount of data, we computed depth profiles only at each 0.5 interval of latitude. Profiles were obtained by contouring a narrow ($0.05^\circ=5.56$ km) swath of depth soundings by using inverse distance to a power for interpolations (Surfer, 1995). After correcting for latitudinal differences in the relationship between longitude and distance, the resulting depth profiles were used to estimate the total amount of habitat [km] in 50-m depth intervals. In addition, the distance offshore and the depth of the continental shelf break were estimated. The location of the shelf break was estimated by using a three-parameter segmented linear model that minimized the sums of squared differences between a contoured depth profile and points along two linear sections of a segmented line. The fitted join point of the two segments was then used to estimate the location of the shelf break. In the estimation procedure, the offshore end of the offshore segment was fixed at the exact 500 m depth value obtained from the computed profiles.

Information on rockfish abundance was obtained from trawl survey data collected by the Resource Assessment and Conservation Engineering division of the AFSC. Trawl samples were generally collected by using a sampling design that was stratified by depth and latitude, and where allocation of sample sizes was based on prior fishery catches (Wilkins et al., 1998). From 1977 to 1998, trawl samples in the Eureka, Monterey, and Conception INPFC areas (Fig. 1) were typically taken between 50 and 500 m from June to August with a standardized Nor'western high-opening rockfish bottom trawl rigged with roller gear. Measurements recorded for each trawl sample were the following: trawl net width and height; time of the tow; distance traveled; and the number and weight of species in the catch (Wilkins et al., 1998).

The fundamental objective of the AFSC triennial continental shelf trawl survey is to estimate the distribution and abundance of fishes vulnerable to capture by bottom trawl along the U. S. west coast. This basic goal has not changed since the first year of the survey in 1977, although specific objectives have changed over time, which has resulted in alterations in the distribution of sampling effort. For example, sampling effort in 1977 was stratified by depth and latitude according to rockfish fishery information. Sampling efforts in 1980, 1983, and 1986 were shifted to improve biomass estimates of canary and yellowtail rockfish. However, the lack of any significant improvement in the precision of the rockfish biomass estimates prompted a shift in the 1989 and 1992 surveys to include all demersal groundfish and to improve estimates of Pacific hake (*Merluccius productus*) and juvenile sablefish (*Anoplopoma fimbria*) abundance. More recently in 1995 and 1998 the survey was expanded to include slope rockfish found in deeper waters (to 500 m) with an emphasis on obtaining a uniform sampling density. These changes in the goals and

objectives of the AFSC shelf survey significantly altered the data on the spatial distribution of samples over time, which, in turn, confounded interannual comparisons of the spatial distributions of rockfish species.

Due to changes in survey design detailed above, all years of the survey were simply pooled into a single composite data set, from which the starting position of each haul, depth of haul [m], net width (m), distance towed (km), numbers of species collected, and species weights (kg) were extracted for analysis. The distribution of all hauls was analyzed by depth and latitude to reveal any patterns that might affect inferences about rockfish distributions or co-occurrences. Because management is primarily concerned with biomass estimates of abundance, only species weights were used in our analysis. All trawl-specific species weight measurements were converted to a catch-per-unit-of-effort (CPUE) statistic by dividing species catch weight by the product of the distance towed and net width, i.e. the area swept (ha). An analysis of the frequency of occurrence of each species in trawls was conducted to obtain a subset of the most ubiquitous rockfishes for use in all subsequent analyses. These species were selected based on their occurrence in at least six of the eight survey years, with the exception of halfbanded rockfish (*S. semicinctus*), which was included because it yielded moderately frequent catches in five of eight years (Table 1).

The data representing the selected subset of species were plotted by depth and latitude to display distributional patterns of CPUE. Next, interspecific distributional overlaps were computed by calculating the percentage of joint occurrences with other species based on presence or absence (Krebs, 1989). Joint occurrences were determined both on a trawl-specific basis and after catches had been aggregated into 50-m depth and 0.5° -latitude intervals. In addition, *Sebastes* diversity and species richness were computed for each haul to summarize the overall distribution of rockfishes captured in the survey. For our analysis, diversity was computed by using the Shannon-Wiener index, and the number of species was used to scale richness (Krebs, 1989). Diversity and richness measures were then spatially contoured over depth and latitude dimensions to display spatial structure (Surfer, 1995).

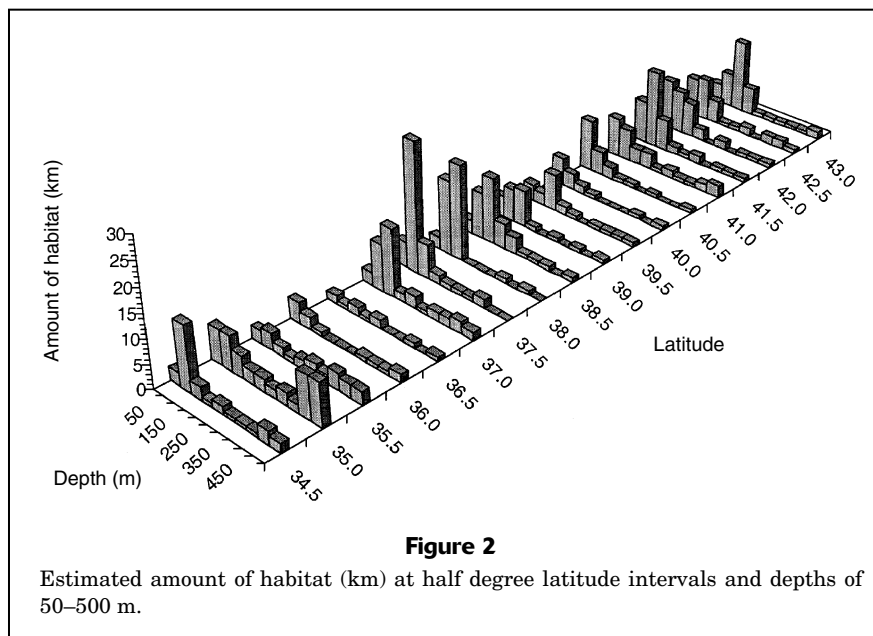
Distributional patterns and groupings of rockfish based on the CPUE data were analyzed by indirect gradient analysis by using multivariate ordination and partitioning methods. Multivariate analyses are often strongly influenced by the choice of distance or (dis)similarity measure. Members of the set of Minkowski distance measures (e.g. Manhattan, Euclidean, maximum, etc.) tend to be strongly affected by extreme values. Moreover, species composition data from trawl surveys have a high proportion of zero catches and a distance measure that is little affected by this property is desirable. The Bray-Curtis index, also known as Czekanowski's quantitative index, is a commonly used statistic in other similar applications and is robust to the presence of zero values (see Bloom, 1981; Field et al., 1982; Krebs, 1989; Rogers and Pickett, 1992; Weinberg, 1994; Meuter, 1999). A fourth-root transformation of the data was conducted before calculation of the Bray-Curtis index, as suggested by Field et al. (1982) and as implemented by

Meuter (1999). A different measure of similarity, based on converting the data to presence-absence binary form and computing the proportion of nonzero values held in common, has also been used (Krebs, 1989). However, preliminary analyses indicated very little difference between the Bray-Curtis and binary similarity measures ($r=0.973$). Therefore, the Bray-Curtis similarity measure was used in all subsequent multivariate analyses.

Ordination techniques used in indirect gradient analysis were principal components, detrended correspondence analysis, and multidimensional scaling (Rogers and Pikitch, 1992; Mahon et al., 1998; Meuter, 1999). Multidimensional scaling (MDS) has the advantage of not requiring an assumption about the underlying response model and has been shown to be robust to different relationships of species abundances and environmental gradients (Minchin, 1987; Meuter, 1999). In our study we used MDS in conjunction with the Bray-Curtis similarity measure, similar to previous analyses (Field et al., 1982; Meuter, 1999). The first three dimensions from the MDS were extracted, plotted, and correlated with suspected gradients, which were then used to numerically define assemblage groupings in the data.

Species groupings or assemblages were also determined by partitioning cluster analysis, rather than using other commonly employed hierarchical cluster analyses (e.g. Rogers and Pikitch, 1992; Weinberg, 1994; Mahon et al., 1998). Hierarchical cluster techniques result in dendrogram trees whose shape and structure depend largely on the division and linking methods used, frequently resulting in little similarity among the many methods (Johnson and Wichern, 1992; Ripley, 1996). Results from this type of analysis are often reported for a single method, indicating results consistent with the analyst's expectations, while neglecting to report the range of variability produced by the other alternative hierarchical methods. A more objective method of determining groupings is to use a partitioning technique such as the classical k -means algorithm (Hartigan and Wong, 1979), where the number of groups (k) is specified *a priori* and a single solution to the grouping structure is determined.

For our partitioning analysis we used a more robust variant of the k -means method, which is termed k -medians (Kaufman and Rousseeuw, 1990). The k -means and k -medians methods rely on the minimization of the (dis)similarity between cluster centers and their members. Specifically, the k -means algorithm minimizes the squared (dis)similarities, and k -medians minimizes the untransformed (dis)similarities, resulting in a measure that is less sensitive to extreme values (Kaufman and Rousseeuw, 1990; Ripley, 1996). In our study a range of k 's

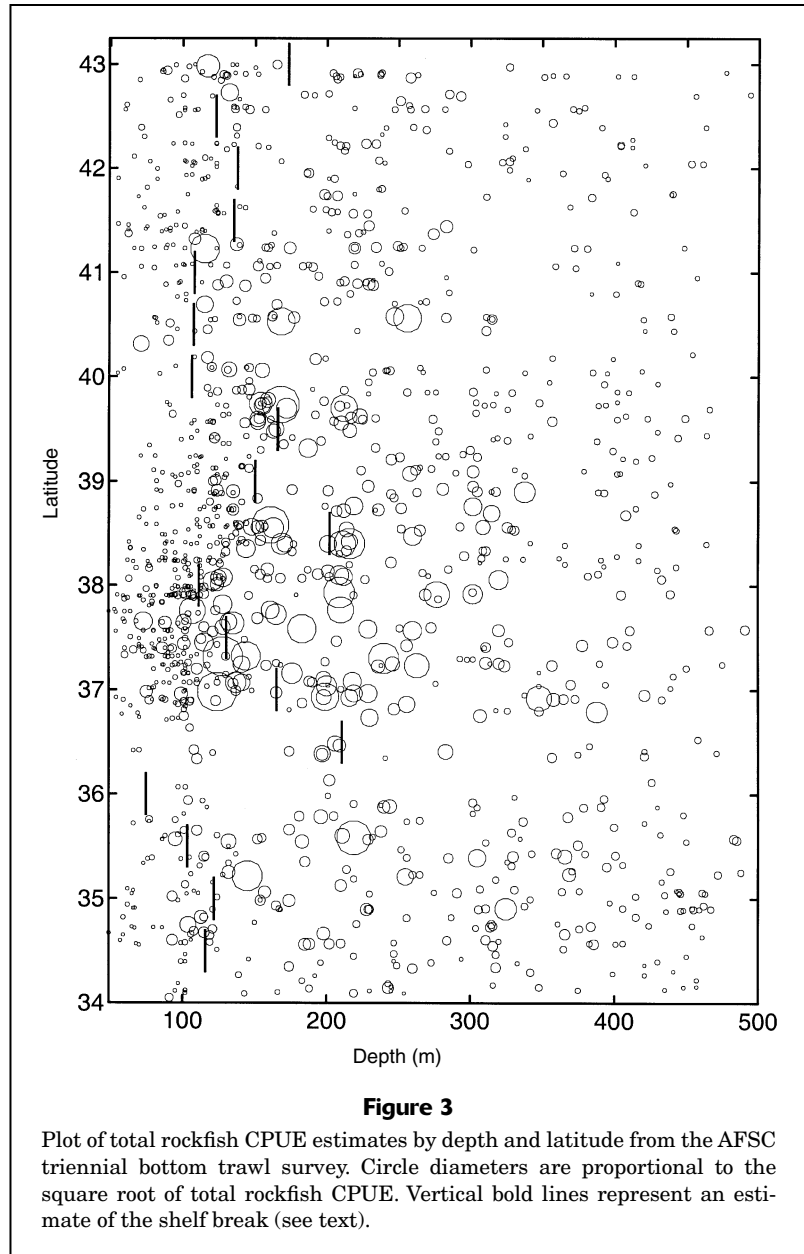


or cluster numbers was evaluated and the best grouping structure for the data was determined according to the highest average silhouette measure (Rousseeuw, 1987). To detect misclassifications, the final rockfish assemblage structure was compared to the several dimensions obtained from the MDS ordination analysis and to our mapped CPUE distributions.

Results

There are a number of large-scale bathymetric features in the Eureka, Monterey, and Conception INPFC areas that may influence the distribution and abundance of shelf and slope rockfish species. For example, the Mendocino Escarpment is a large fracture zone that forms a huge submarine ridge near Cape Mendocino that extends nearly 2500 km westward into the Pacific Ocean and that measures 100 km across at its widest point. Well to the south of the escarpment are a number of large submarine canyons in the region of Monterey Bay and Point Sur. These submarine features, including Monterey and Sur Canyons, result in a coastal bathymetry characterized by limited shelf area and rapidly increasing depth. Farther south, in the vicinity of Point Buchon, is a large offshore area that rises to 430 m depth, i.e. the Santa Lucia Bank. Lastly, Point Conception divides zoogeographic provinces and forms the southern boundary of the area of this study.

Our restricted analysis of the bathymetry at 0.5°-latitude intervals indicates that variability in depth profiles reflects some of the important features described above. The amount of habitat in each 50-m depth interval seems to peak in the 100 to 150-m depth range for latitudes greater than 37.0°N (Fig. 2). The observed decrease in the total amount of habitat at 40.0°N, especially in waters shallower than 200 m, is due primarily to the Mendocino



Escarpment. Likewise, the abrupt decrease in the amount of shallow depth habitat from 35.5° to 36.5°N is directly attributable to the occurrence of submarine canyons, and the increase in habitat from 450 to 500 m at 35.0°N is due to the Santa Lucia Bank (Fig. 2). The depth at which the shelf break occurs seems to be fairly constant, generally ranging from 100 to 175 m (Fig. 3). The relatively deep (210 m) estimated shelf break at 36.5°N is due to the presence of Monterey Canyon (Fig. 3).

For the combined Eureka, Monterey, and Conception IN-PFC areas, the shelf trawl survey database pooled over the 1977–98 period totaled 1296 hauls that together captured 49 rockfish species, including an unidentified category (Table 1). Based on the frequency of positive trawl samples for each of the rockfish species, 26 were selected for detailed

analysis (Table 1). In Table 1, the effect of changing survey sampling objectives is evident in the interannual variation in frequency of occurrence for some of the species. Perhaps most noticeable is the abrupt decline in samples of aurora (*S. aurora*) and blackgill (*S. melanostomus*) rockfish in the years 1980–92 (Table 1). Both are deep-water species and, clearly, the relatively high frequencies of occurrence in 1977, 1995, and 1998 were due to increased sampling at deeper depths that resulted from the altered objectives of the sampling design discussed earlier.

The distribution of trawl sampling locations and CPUE by depth and latitude indicated that the sampling pattern followed some of the bathymetric features mentioned above (Fig. 3). One notable feature was the paucity of samples in the 36.5°N latitude region, which was partly

Table 2

Percentage overlap of rockfish species captured in the AFSC triennial shelf bottom trawl survey by smoothed depth (50–500 m) and taken in trawls containing the species listed in the columns. POP = Pacific ocean perch.

	stripetail	chili-pepper	split-nose	short-spine	green-striped	bocaccio	short-belly	dark-blotched	aurora	widow	canary
stripetail	100	52	37	4	3	30	39	9	2	7	4
chilipepper	57	100	25	3	3	29	33	7	0	7	5
splitnose	19	12	100	7	1	8	14	12	4	1	1
shortspine	17	11	61	100	3	11	7	35	47	6	3
greenstriped	94	85	39	24	100	79	68	52	2	57	60
bocaccio	78	69	41	6	6	100	41	13	1	16	8
shortbelly	50	39	36	2	3	20	100	7	0	5	4
darkblotched	36	25	89	30	6	20	21	100	7	11	6
aurora	9	2	42	53	0	1	1	10	100	1	0
widow	84	88	36	15	23	80	49	35	1	100	36
canary	51	60	18	9	25	42	43	21	1	38	100
redbanded	52	36	99	89	14	42	32	92	30	23	15
sharpchin	88	80	52	17	18	76	57	48	1	41	25
bank	31	30	76	21	3	27	26	56	8	8	5
yellowtail	20	21	5	4	17	21	10	8	0	17	41
POP	44	11	91	64	13	28	6	98	8	17	8
blackgill	18	8	75	63	1	7	5	20	83	3	2
halfbanded	50	99	31	1	11	51	97	1	0	4	7
greenspotted	98	97	65	30	75	96	84	55	3	72	64
cowcod	100	96	97	30	20	95	93	56	7	37	21
rosethorn	81	80	95	60	40	93	61	94	12	60	36
brown	14	57	18	3	20	91	12	2	0	35	54
copper	24	19	16	5	13	33	15	2	0	15	72
vermillion	71	83	47	23	21	79	65	21	7	28	36
redstripe	21	17	18	15	21	17	21	16	1	19	24
yelloweye	97	96	80	37	52	89	72	76	2	91	57

due to the precipitous Big Sur coastline, with its marked reduction in the amount of trawlable habitat in the 50–500 m depth range. Moreover, the 1980, 1983, and 1986 surveys did not sample south of Monterey Bay. Similarly, the increase in the number of samples in the 37.0–39.0°N area (Fig. 3) was attributable to an increase in the total amount of shelf habitat in that region (Fig. 2). Starting at the shallowest depths, there was a tendency for the size of the total rockfish catch to increase to a maximum in deeper waters just beyond the shelf break (~200 m), followed by a slight decrease in catch in the deepest waters (Fig. 3). Not apparent to the eye in Figure 3 is a slight, but significant trend in the distribution of sample locations towards deeper waters at more southerly sites (linear slope = -0.26, P -value = 0.0041). This was probably due to the decreasing amount of shelf habitat and the increasing quantity of slope habitat as one moves south along the California coast (Fig. 2).

The amount of interspecific overlap in spatial distributions among the subset of 26 species differed, depending

on whether co-occurrence was assessed from a categorization of the catches into depth-latitude intervals or by specific trawl locations (Tables 2 and 3). As expected, depth-latitude overlaps were greater than the site-specific trawl catch overlaps, due to the effect of spatial smoothing. Inspection of the depth-latitude species overlaps (Table 2) indicated that stripetail (*S. saxicola*), splitnose, chilipepper (*S. goodei*), bocaccio, and shortbelly (*S. jordani*) rockfish were most widespread with respect to co-occurrence with other rockfishes. Similarly, overlaps measured from actual trawl catches indicated that bocaccio, chilipepper, stripetail, canary, and widow rockfish have relatively high likelihoods of co-occurring with other rockfish species (Table 3).

The spatial distribution of rockfish over the continental shelf and slope generally indicated a ridge of increased diversity at approximately 250 m depth, at least for samples taken at northern latitudes (38.0–43.0°N) (Fig. 4). In contrast, for southern latitudes (34.0–38.0°N), the ridge of high diversity veered well offshore to a depth of 450

Table 2

latitude (34.0–43.0°N) locations. Individual table elements represent the percentage of occurrence of a species (reading across the row)

red-banded	sharp-chin	yellow-bank	yellow-tail	POP	black-gill	half-banded	green-spotted	cow-cod	rose-thorn	brown	copper	vermilion	red-stripe	yellow-eye
1	7	5	2	2	1	1	1	2	1	0	0	0	0	0
1	7	5	2	0	1	2	1	2	1	0	0	0	0	0
1	2	6	0	2	3	0	0	1	0	0	0	0	0	0
12	6	16	2	11	23	0	1	2	2	0	0	1	1	1
13	47	14	45	15	3	6	12	11	9	0	2	3	7	8
3	16	11	4	3	1	2	1	4	2	0	0	1	0	1
1	6	5	1	0	1	2	1	2	1	0	0	0	0	0
10	15	35	2	14	6	0	1	4	3	0	0	0	1	1
4	0	7	0	2	33	0	0	1	0	0	0	0	0	0
8	42	17	17	8	2	1	5	8	5	0	1	2	2	6
5	27	10	44	4	2	1	4	5	3	0	4	2	3	4
100	23	47	5	28	33	1	5	8	12	0	0	4	3	3
8	100	26	8	13	1	0	3	8	7	0	0	1	4	5
8	13	100	0	4	10	0	1	6	3	0	0	1	0	2
2	8	1	100	3	0	1	2	1	1	1	2	1	6	2
21	28	16	6	100	2	0	1	0	4	0	0	0	3	4
12	2	21	0	1	100	0	1	2	2	0	0	1	0	0
2	2	2	6	0	0	100	4	4	0	0	3	14	0	0
26	54	43	33	6	11	13	100	44	21	0	4	16	3	18
14	38	57	3	1	11	4	14	100	20	0	1	4	0	2
49	80	61	15	19	17	1	16	48	100	0	0	3	9	12
5	3	1	76	0	0	7	1	6	0	100	64	34	0	0
1	2	3	36	0	0	13	5	2	1	10	100	22	0	0
22	12	26	24	3	20	44	17	15	4	5	18	100	1	1
7	29	7	46	12	1	0	2	1	6	0	0	0	100	13
19	91	68	27	30	3	1	20	8	17	0	0	1	29	100

m, and there was some indication of a secondary increase in diversity at 150 m for the most southerly latitudes 34.0–36.0°N (Fig. 4). The distribution of species richness indicated that the existence of a distinct ridge at depths of 200–250 m—the highest portion of the ridge occurring between 36.0 and 39.0°N latitude (Fig. 5). In that region, in excess of eight distinct species co-occurred in individual trawl samples. A solitary peak in richness occurred at a depth of 500 m near 37.5°N latitude (Fig. 5). Inspection of the raw data revealed that this peak was heavily influenced by a single trawl sample, but there was no indication of a data recording error in this sample.

The spatial distribution of CPUE for each of the rockfish species is shown in Figures 6–10. The particular sequence of species in these figures corresponded to clustering results that are presented below. Careful examination of these 26 distributions revealed that the depth distributions of almost all species were not related to latitude. The sole exception to this generalization was the depth distribution for shortspine thornyhead, which showed a

significant interaction between depth of capture and latitude, based on results from a two-way factorial ANOVA. For that species, depth distribution shifts into deep water at more southerly latitudes (Fig. 6).

Latitudinal boundaries of rockfish distributions appeared to be influenced by two of the main bathymetric features on the U.S. west coast. In particular, the Mendocino Escarpment (ME), located at approximately 40.4°N latitude, and Monterey Canyon (MC), located near 36.8°N latitude, appear to form distributional impediments for some of the species, and other species appeared to be distributed more uniformly across the entire latitudinal range of the study (Figs. 1, 6–10). Examples of species whose distributional boundaries appeared to be influenced by the ME were blackgill rockfish (*S. melanostomus*), Pacific ocean perch, chilipepper (*S. goodei*), shortbelly rockfish (*S. jordani*), bocaccio, and greenspotted rockfish. Species whose distributions appeared to border on MC were dark-blotched, greenstriped, canary, yellowtail, widow, sharp-chin, and rosethorn rockfish (Figs. 6–10).

Table 3

Percentage overlap of rockfish species captured in the AFSC triennial shelf bottom trawl survey. Individual table elements represent Pacific ocean perch.

	stripetail	chili-pepper	split-nose	short-spine	green-striped	bocaccio	short-belly	dark-blotched	aurora	widow	canary
stripetail	100	35	11	1	3	9	12	5	0	3	1
chilipepper	29	100	4	1	3	10	8	2	0	6	2
splitnose	10	4	100	4	0	3	3	9	1	1	0
shortspine	12	8	50	100	3	7	3	30	27	3	2
greenstriped	48	57	7	4	100	26	27	9	0	18	15
bocaccio	23	31	8	2	4	100	8	7	0	8	6
shortbelly	9	7	3	0	1	2	100	1	0	1	1
darkblotched	27	15	57	14	3	15	6	100	1	3	2
aurora	3	0	24	38	0	0	0	4	100	0	0
widow	14	29	3	1	5	14	6	3	0	100	6
canary	9	22	2	1	7	19	7	3	0	11	100
redbanded	37	21	61	53	5	33	13	51	8	7	3
sharpchin	38	47	14	4	9	46	24	10	0	20	7
bank	11	11	48	7	1	9	3	39	1	3	1
yellowtail	4	16	0	0	6	12	1	1	0	20	18
POP	25	2	44	28	6	25	4	72	1	9	2
blackgill	3	2	41	32	1	2	2	9	45	0	0
halfbanded	2	34	0	0	3	5	18	0	0	1	3
greenspot	41	72	20	6	55	52	35	5	0	32	44
cowcod	64	39	73	8	10	93	21	10	2	10	8
rosethorn	26	41	37	32	37	56	29	36	2	32	20
brown	0	2	0	0	0	47	1	0	0	56	36
copper	1	4	0	0	3	23	2	0	0	11	73
vermilion	6	14	3	1	1	31	6	2	1	11	19
redstripe	4	8	0	0	4	8	15	0	0	8	4
yelloweye	16	72	10	2	34	63	18	12	0	63	75

A general comparison of interspecific relationships, based on depth-latitude distributions, can be gathered by inspection of a plot of CPUE-weighted depth-latitude centroids (Fig. 11). From results presented in Figure 11, some species (e.g. copper [*S. caurinus*] and brown [*S. auriculatus*] rockfish) appear to have very similar depth-latitude distributions. Aurora and blackgill rockfish are clearly deep-water southern species, whereas halfbanded (*S. semicinctus*) and vermilion (*S. miniatus*) rockfish are southern species found principally in shallow water. Although this plot is useful for identifying related species by their average distribution in space, it does not fully represent actual joint co-occurrences and assemblage relationships, as does a complete multivariate community analysis.

The results of the multidimensional scaling of the fourth-root transformed CPUE data, with the Bray-Curtis similarity measure, revealed highly significant correlations of the first three dimensions with mean depth ($r=0.90$, $P<0.0001$), total CPUE^{0.25} ($r=-0.82$, $P<0.0001$), and mean latitude ($r=-0.74$, $P<0.0001$), respectively. How-

ever, these first three dimensions accounted for only 39% of the total variance in the data.

The k -medians partitioning analysis was used to examine a range of k 's or cluster numbers, effectively predefining the number of distinct assemblages. The best fits were determined by the highest average silhouette measures of 0.143 and 0.140 for $k = 8$ and $k = 4$, respectively (Table 4). According to Kaufman and Rouseeuw (1990) an average silhouette measure less than 0.25 does not indicate any substantial structure in the data. Despite the low average silhouette measurements, the suggested groupings of four and eight clusters were used as an initial guideline in determining distinct species assemblages. The species groups defined in Table 4 by a division into four clusters (A, B, C, and D), and further delineated in Figure 11, show that these assemblages generally follow depth and the latitude distributions of their member species.

The first three dimensions from the multidimensional scaling analysis, along with the $k = 8$ cluster divisions, are shown in Figure 12. The eight clusters comprising the 26

Table 3

the percentage of occurrence of a species (reading across the row) taken in trawls containing the species listed in the columns. POP =

red-banded	sharp-chin	bank	yellow-tail	POP	black-gill	half-banded	green-spotted	cow-cod	rose-thorn	brown	copper	vermilion	red-stripe	yellow-eye
1	3	1	1	1	0	0	0	1	0	0	0	0	0	0
0	4	1	2	0	0	1	1	0	0	0	0	0	0	0
1	1	4	0	1	1	0	0	1	0	0	0	0	0	0
11	4	7	1	9	10	0	1	1	2	0	0	0	0	0
1	13	1	15	3	0	1	9	2	4	0	0	0	3	2
1	10	2	5	2	0	0	1	2	1	1	0	1	1	1
0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
5	5	19	1	11	1	0	0	1	1	0	0	0	0	0
2	0	2	0	1	21	0	0	0	0	0	0	0	0	0
1	8	1	14	1	0	0	2	0	1	2	0	1	1	1
0	5	1	21	0	0	0	4	1	1	2	4	2	1	3
100	12	15	0	17	5	0	3	2	6	0	0	1	0	0
2	100	9	1	3	0	0	2	1	3	0	0	0	9	3
3	10	100	0	2	2	0	1	2	1	0	0	0	0	0
0	0	0	100	0	0	0	2	0	0	3	1	1	0	0
10	9	8	3	100	1	0	0	0	1	0	0	0	1	0
3	0	6	0	1	100	0	0	0	1	0	0	0	0	0
0	0	0	1	0	0	100	4	1	0	0	1	3	0	0
5	21	11	29	1	1	7	100	7	4	0	1	2	2	10
3	10	22	0	0	1	1	8	100	11	0	0	1	0	2
17	47	14	9	6	3	0	8	18	100	1	1	1	23	15
0	0	0	71	0	0	0	0	0	1	100	13	12	0	0
0	0	0	24	0	0	2	1	0	1	11	100	25	0	0
1	1	2	13	0	0	6	2	1	1	8	19	100	0	0
0	20	0	0	0	0	0	1	0	3	0	0	0	100	5
0	68	0	13	2	0	0	24	5	20	0	0	1	42	100

species and listed in Table 4 closely follow the ordination plots. In particular, dimensions one and three in combination showed clear segregation of the eight distinct clusters (lower panel in Fig. 12). Clearly, the A-1 group in Table 4 stands out as a distinct assemblage in the MDS ordinations (Fig. 12). Because dimensions one and three were highly correlated with depth and latitude, respectively, we concluded that the species groups are defined by depth and latitude. However, the low amount of variance explained by the dimensions, the small sample sizes for some species, and the relatively low average silhouette measures in the partitioning analysis, would indicate that some caution should be exercised when using these results. In fact, there appeared to be some discrepancies in depth-latitude distributions and partitioning groups for the rockfish species (Table 4, Fig. 11).

Group A-1 in Table 4 represents the deep-water slope species of rockfish, and the species in groups B-2 and B-3 represent the nearshore species of rockfish. The separation of halfbanded rockfish from the nearshore group suggested by the $k = 8$ clustering was likely the result of a

more southerly distribution for this species than that for the other members of the group (Fig. 7). The remaining C and D groups in Table 4 represent shelf species, group C being a southern shelf group and D representing a northern shelf group. A likely misclassification in the clustering results was the inclusion of green-spotted rockfish in the northern shelf assemblage, which was not warranted by the distribution of catches shown in Figure 9. Within the C group, the separation of cowcod as an isolate in the $k = 8$ analysis was due to this species' relatively deep distribution (Fig. 8). The separation of canary and yellowtail rockfish as a distinct cluster was the result of their relatively northern distribution and their inclusion in the southern shelf species group by the partitioning analysis was probably the result of a boundary effect (Fig. 9). Lastly, the division of the northern shelf group into D-7 and D-8 subgroups, suggested by the $k = 8$ partitioning, was likely the result of differences in the survey's total catch of rockfish (MDS dimension 2), which is not evident in distributional patterns (Table 4).

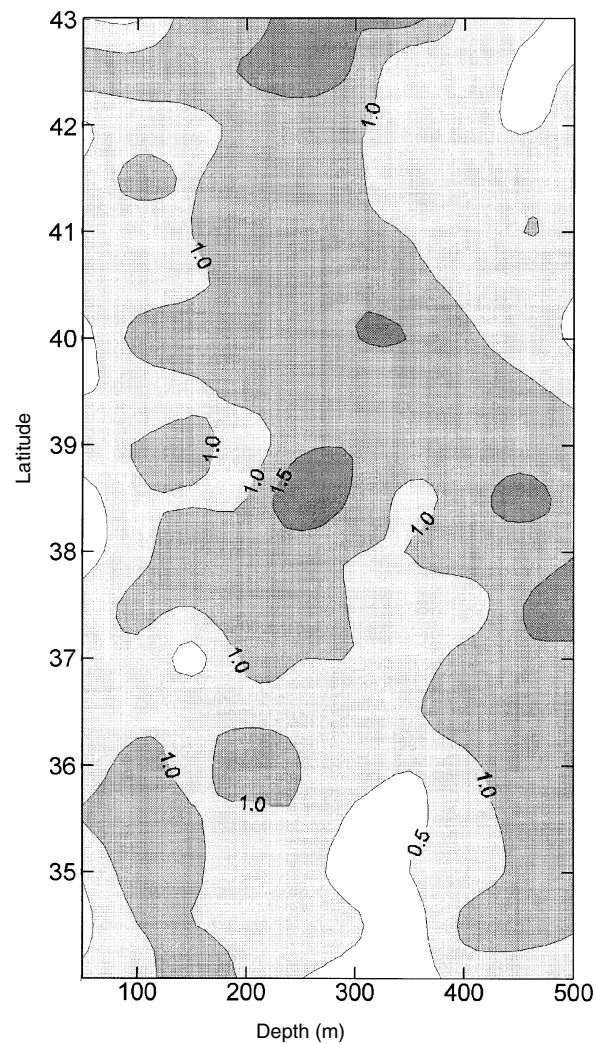


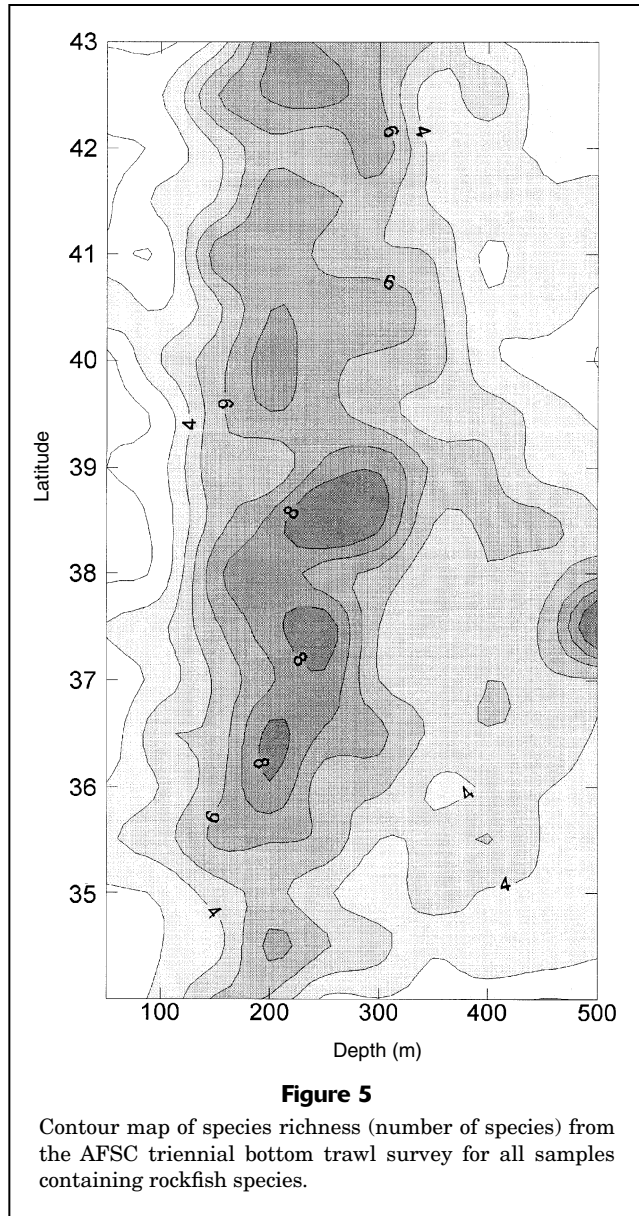
Figure 4

Contour map of Shannon-Weiner diversity indices from the AFSC triennial bottom trawl survey for all samples containing rockfish species (abundance is measured by biomass).

Table 4

Separation of rockfish species into four and eight groups, labeled by letters and numbers, respectively, based on *k*-medians analysis of AFSC triennial bottom trawl surveys from 1977 to 1998.

Group	Species	Group	Species
A-1	blackgill rockfish, aurora rockfish, shortspine thornyhead, bank rockfish, darkblotched rockfish, Pacific ocean perch, redbanded rockfish, splitnose rockfish	C-4	chilipepper, shortbelly rockfish, bocaccio, stripetail rockfish, greenstriped rockfish
B-2	copper rockfish, vermilion rockfish, brown rockfish	C-5	cowcod
B-3	halfbanded rockfish	C-6	canary rockfish, yellowtail rockfish
		D-7	greenspotted rockfish, widow rockfish, sharpchin rockfish, rosethorn rockfish
		D-8	yelloweye rockfish, redstripe rockfish

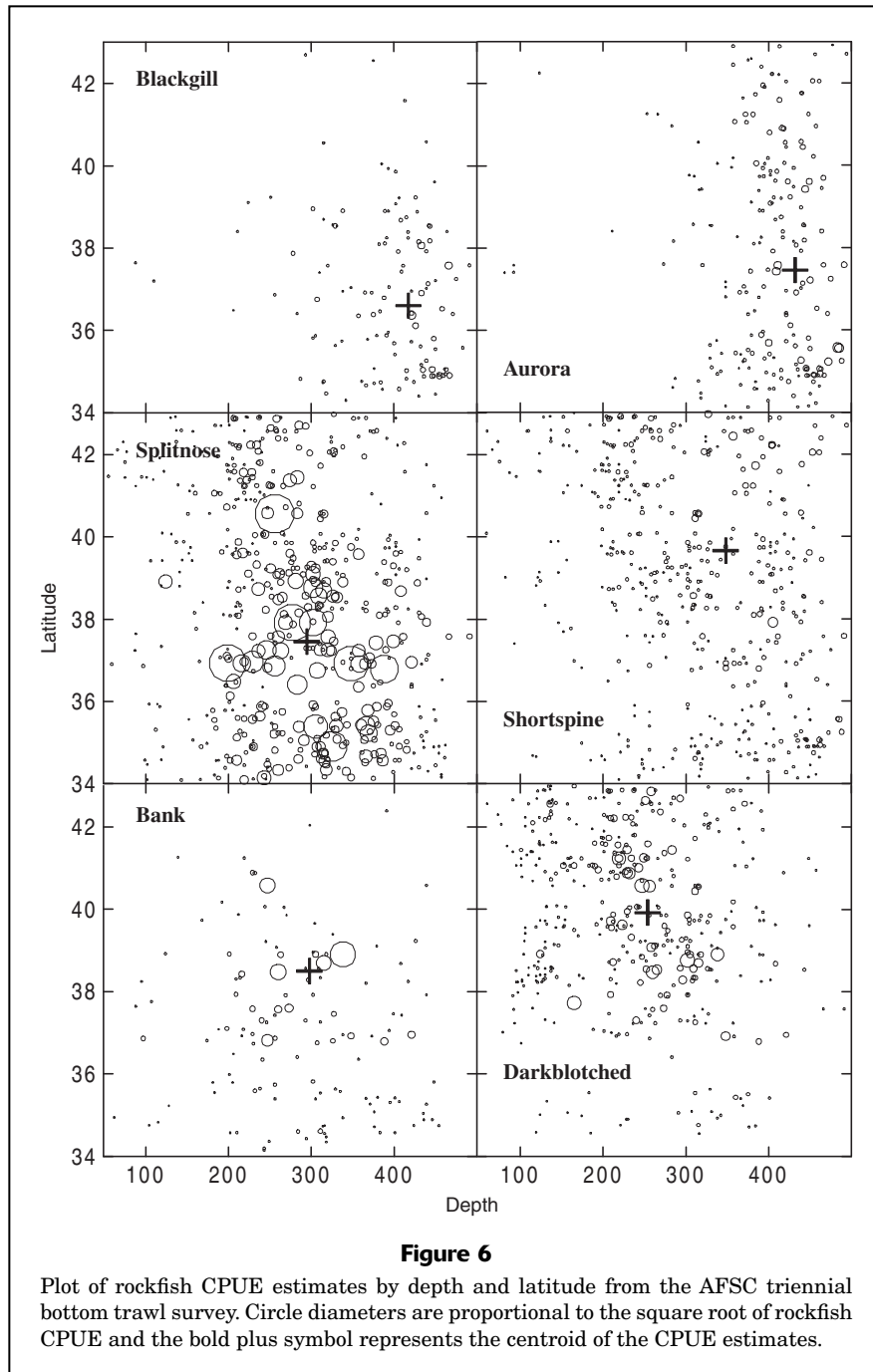


Discussion

Our data were the result of pooling samples collected during AFSC triennial continental shelf trawl surveys conducted from 1977 to 1998. Because this interval represents a period of substantial fishery removals (Ralston, 1998), one might expect that rockfish assemblage structure changed over time as commercially important species were serially removed (e.g. bocaccio and canary rockfish). Although we did not perform year-specific analyses that would allow us to address this possibility, results from Weinberg (1994) showed that, over a comparable period of time (1977–92), the trawlable assemblages of rockfishes off Oregon and Washington were reasonably stable in composition. In particular, his year-specific recurrent group analyses revealed good agreement among surveys,

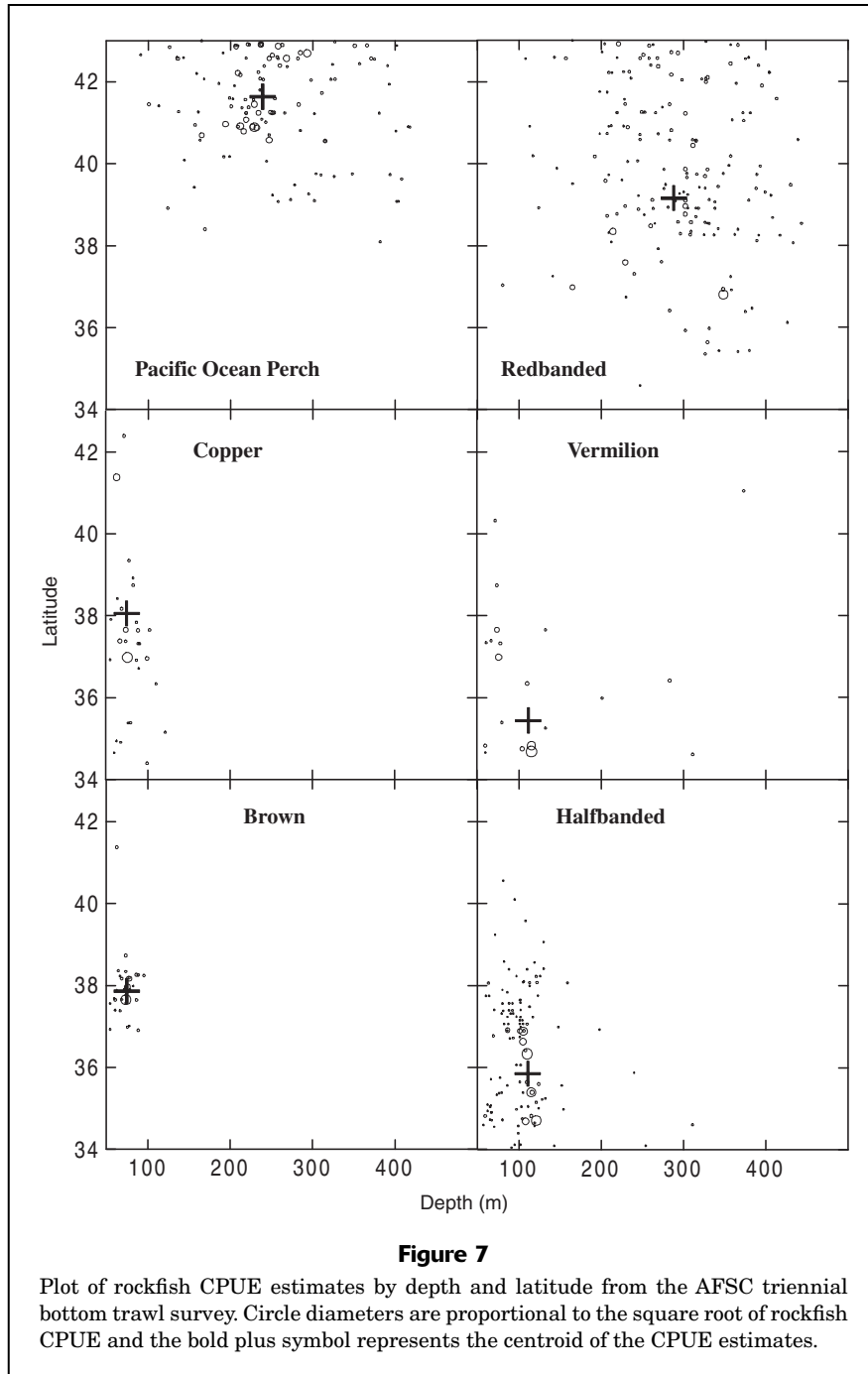
from which he inferred the existence of three groups representing a deep-water assemblage (shortspine thornyhead, Pacific ocean perch, darkblotched, and redbanded (*S. babcocki*) rockfish), a mid-shelf assemblage (canary, yellowtail, and greenstriped rockfish), and a shelf-break assemblage (sharpchin, rosethorn, and redstriped rockfish). Notably, there was substantial overlap between the latter two groups, which is consistent with our findings.

It is no surprise that rockfish distributions are related to bathymetric features, particularly when viewed through bottom trawl survey samples, as we did in our study. It is noteworthy that physical barriers, particularly the Mendocino Escarpment and Monterey Canyon, seem to affect the latitudinal distribution of certain rockfishes. The former may act as a barrier to dispersal because converging currents at Cape Mendocino create conditions



that result in offshore transport (Magnell et al., 1990). Likewise, Monterey Canyon may act as a distributional barrier because continental shelf habitats constrict severely, creating a potential bottleneck to dispersion. Some support for this hypothesis is evident in the rockfish distributional maps (Figs. 6–10), which show that shallow water species are more likely to have Monterey Canyon as a distributional boundary when compared to the deeper dwelling species, for which there apparently exists ample habitat.

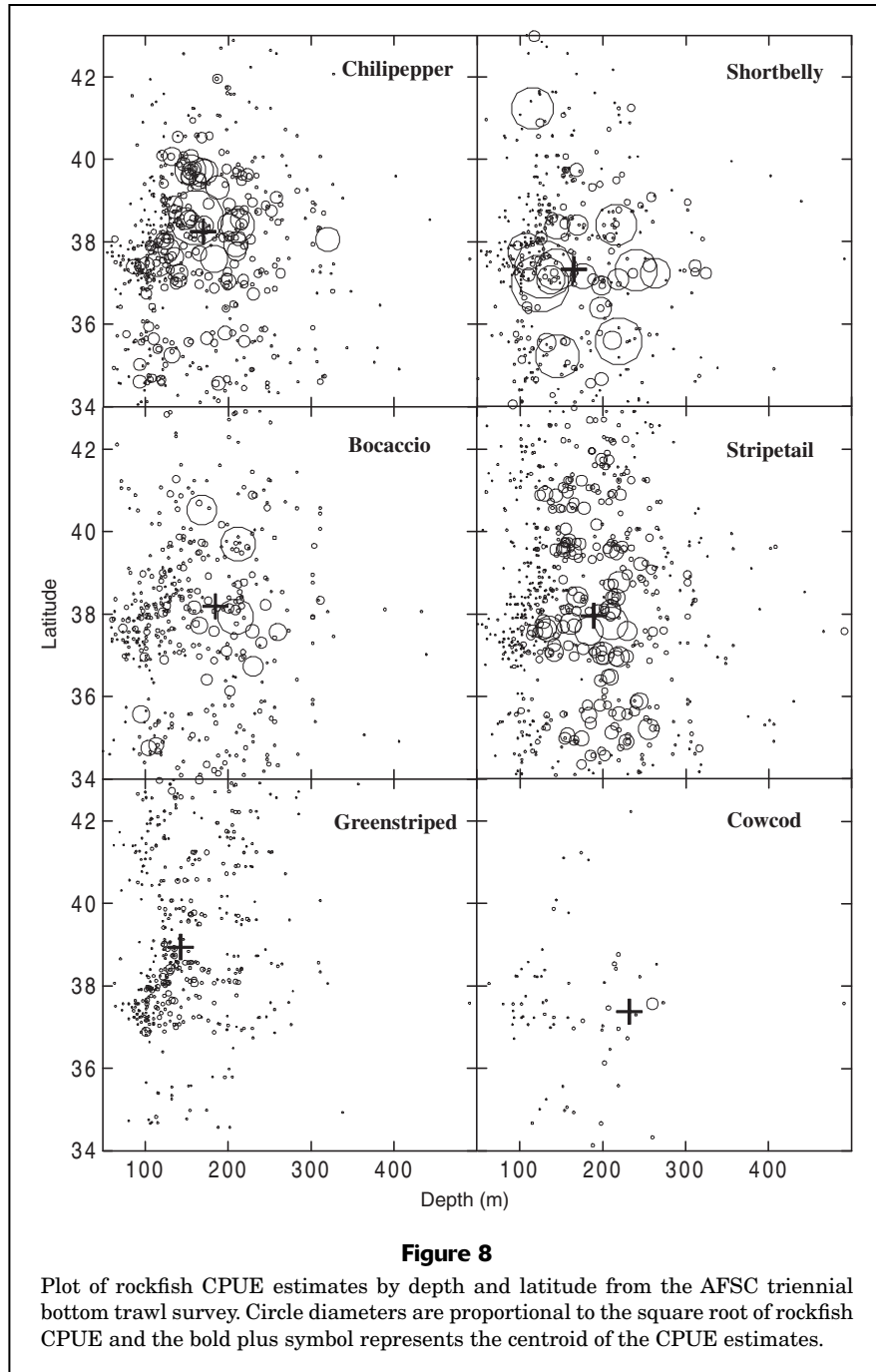
Overall, depth appears to be the single most important determinant of rockfish distributions. Most of the abundance patterns we observed followed the distribution of habitats by depth. Species diversity in the study area also seemed to follow the pattern of depth habitat distribution. However, species richness did not follow this pattern, but instead followed the region of overlap between shelf and slope rockfish assemblages. In fact, the contoured ridge of highest richness may be useful in spatially delineating the shelf and slope assemblages. This ridge appeared to



be fairly constant at ~200–250 m across all latitudes included in our study.

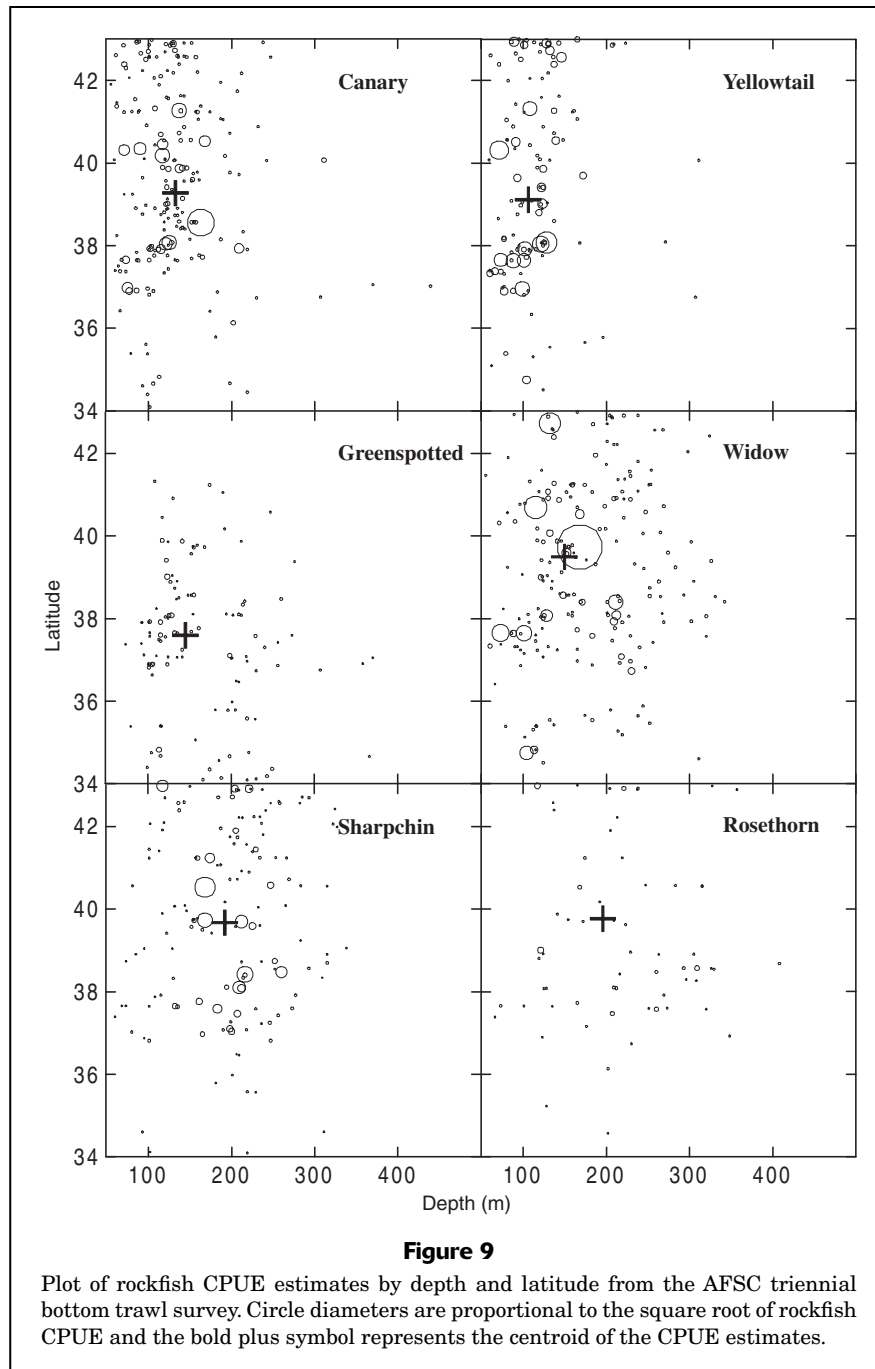
The ridge of increased species richness indicated that there is substantial overlap in rockfish distributions. The analysis of rockfish overlap in our study was computed in two ways, i.e. by smoothed depth-latitude abundance and by raw trawl catches. The smoothed species-specific abundance estimates for all depth-latitude combinations could not be presented here because of space limitations. However, such data could be useful for detailed spatial analyses of rockfish

co-occurrences in future analyses. The trawl-catch overlap data represent the best estimate of bottom trawl co-occurrence probabilities for the study area. A potential limitation of the overlap estimates presented in our study is that they came from only one survey, which employed a single sampling gear. However, the bottom trawl gear used in the AFSC triennial survey is generally similar to the fishing gear used by commercial fishermen, and previous studies have shown that catch rates from the continental shelf bottom trawl survey closely match commercial catch rates (Fox and Starr,



1996). Another potential criticism of bottom trawl gear is its selectivity for capturing demersal fishes. Of the rockfishes included in our analysis, shortbelly and widow rockfish are two species that are known to be distributed in the water column (Lenarz, 1980; Wilkins, 1986; Chess et al., 1988). Despite their occurrence off the bottom, however, both species were captured with regularity in the bottom trawl survey (Table 1). We conclude that, at least for the trawl sector of the groundfish fishery, the results of our study should prove useful in defining assemblages for rockfish management.

As previously discussed, the assemblage descriptions given in Table 4 contain some inconsistencies with respect to the spatial distributions of the species. These apparent misclassifications may be the result of temporal variability in total rockfish abundance, as was captured by the second dimension of the MDS analysis. Because the estimated abundance of a species in our analysis was influenced by population levels of the stock at the time of each survey, which can change over time, our pooled analysis may not provide the best indication of historical assemblage asso-



ciations (see Weinberg, 1994). Furthermore, overfishing of rockfish stocks may alter spatial distributions. A good example is cowcod, which has shown a dramatic decline in abundance in recent years within the southern California Bight; most of the remaining population resides in relatively deep water (Butler et al.³).

Because the total abundance of each species of rockfish may have affected the results of the assemblage analysis, the species distributions were carefully re-examined and a final assemblage structure determined (Table 5).

The changes from Table 4 for the $k=4$ groups include the placement of greenspotted rockfish into the southern shelf assemblage and canary and yellowtail rockfish into the

³ Butler, J. L., L. D. Jacobson, J. T. Barnes, H. G. Moser, and R. Collins. 1999. Stock assessment of cowcod. *In* Pacific Fishery Management Council, Status of the Pacific Coast groundfish fishery through 1999 and recommended biological catches for 2000: stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, Oregon 97201.

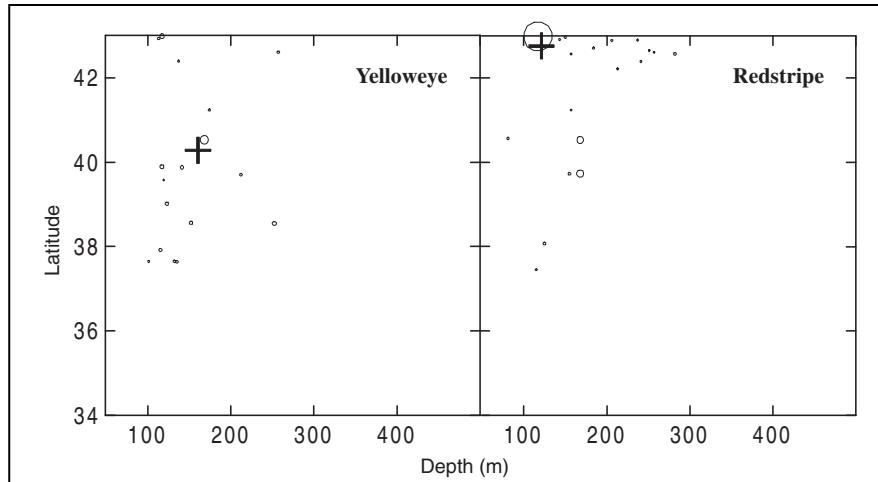


Figure 10

Plot of rockfish CPUE estimates by depth and latitude from the AFSC triennial bottom trawl survey. Circle diameters are proportional to the square root of rockfish CPUE and the bold plus symbol represents the centroid of the CPUE estimates.

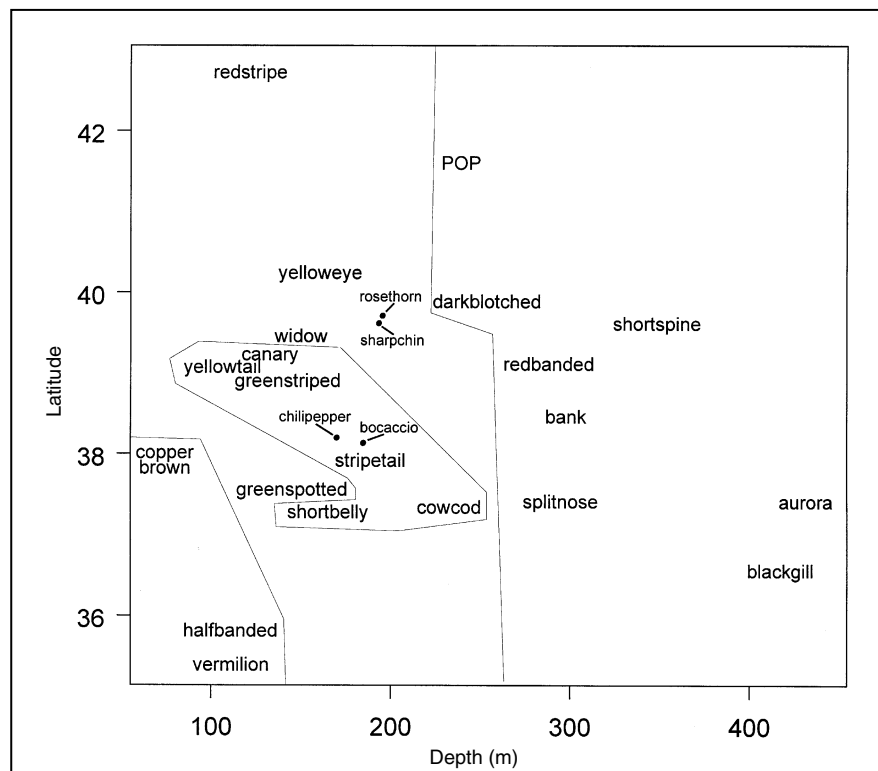


Figure 11

Plot of CPUE weighted mean depth and latitude for 26 rockfish species (center of names correspond to point estimates except for labeled points) from the AFSC triennial bottom trawl survey. Lines indicate divisions of species into clusters based on a *k*-medians (with *k*=4) partitioning analysis (see text).

northern shelf assemblage. Greenspotted rockfish has a distribution that clearly warrants its inclusion in the southern shelf assemblage. Canary and yellowtail rockfish

were placed into the northern shelf assemblage because of their known abundance in northern waters outside the area of our study (see Weinberg, 1994).

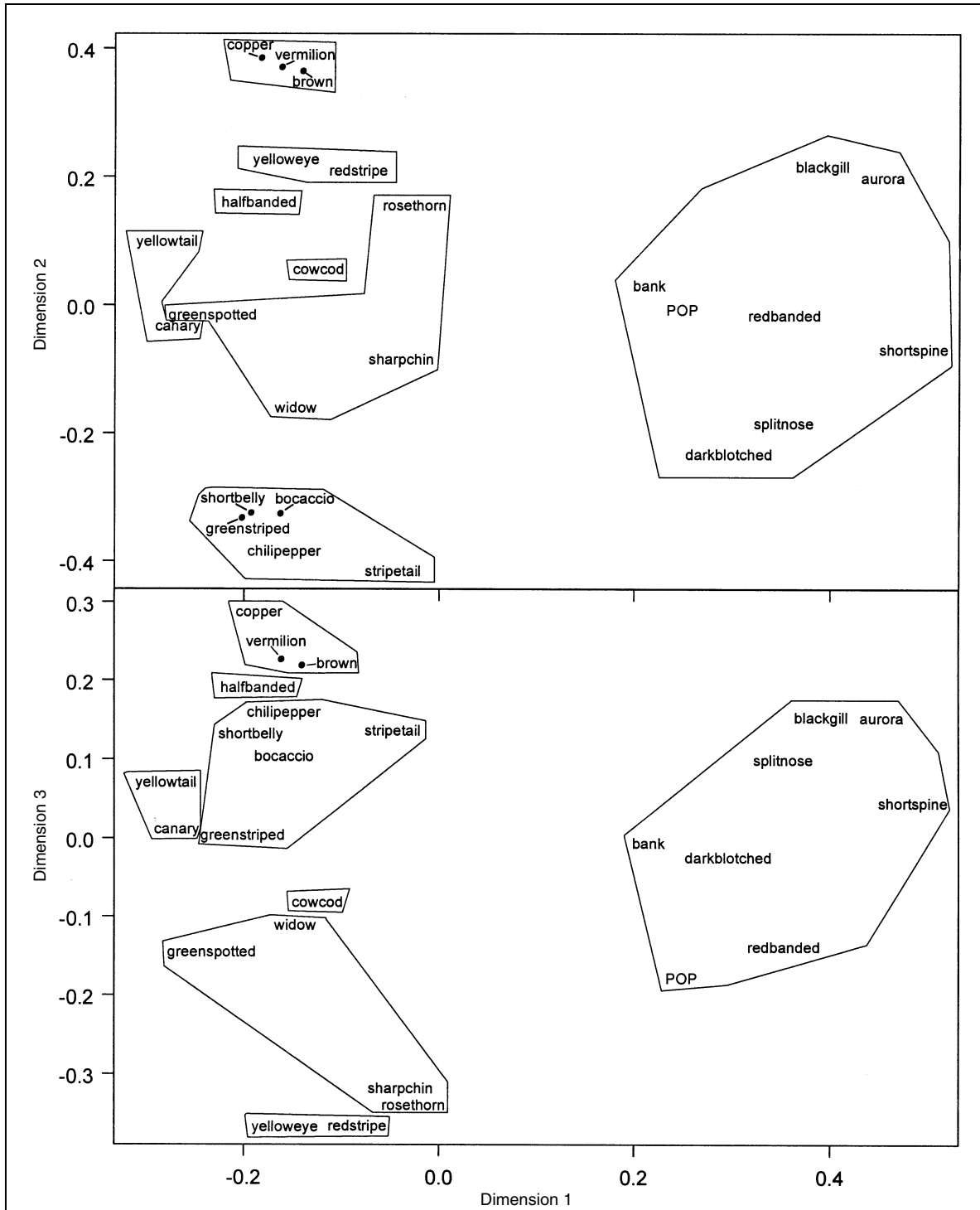


Figure 12

First three dimensions from a multidimensional scaling analysis of 26 rockfishes (center of names correspond to point estimates except for labeled points) from the AFSC triennial bottom trawl survey. Clusters suggested by a *k*-medians (with *k*=8) partitioning analysis are indicated by the enclosing lines (see text).

The dividing line between the assemblages based on depth and latitude was determined by visual examination of the distributions in Figures 6–10. The separation

between shelf and slope species is roughly at 200–250 m; very few slope species were captured at depths less than 200 m. Most of the shelf species did not occur below 250 m,

Table 5

Suggested species assemblages based on distribution, ordination, and partitioning analyses completed in this study.

Habitat	Species
Deepwater slope	blackgill rockfish, aurora rockfish, shortspine thornyhead, bank rockfish, darkblotched rockfish, Pacific ocean perch, redbanded rockfish, splitnose rockfish
Nearshore	copper rockfish, vermilion rockfish, brown rockfish, halfbanded rockfish
Southern shelf	chilipepper, shortbelly rockfish, bocaccio, stripetail rockfish, greenstriped rockfish, greenspotted rockfish, cowcod
Northern shelf	canary rockfish, yellowtail rockfish, widow rockfish, sharpchin rockfish, rosethorn rockfish, yelloweye rockfish, redstripe rockfish

leaving the 200–250 m zone as an area of overlap for the two assemblages, which is exactly where the peak in richness occurred. The species in the nearshore assemblage seem to reside in waters less than 150 m depth. Perhaps the 100–150 m zone represents an area of overlap between the shelf and nearshore species.

Latitudinal divisions between species in the northern and southern shelf assemblages are not as well defined as those based on depth. It appears that most of the southern shelf group are uncommon above the Mendocino Escarpment (40.8°N latitude), with the exception of stripetail and greenspotted rockfish. The northern shelf species tend to range as far south as Monterey Canyon, leaving the area between Monterey Canyon and the Mendocino Escarpment as an area of overlap for these assemblages. This overlap is confirmed in the species richness contour plot which indicates the areas where the highest number of species were found in that latitude zone (Fig. 5). The only questionable assemblage assignment was the placement of greenstriped rockfish, which does not range south of the Monterey Canyon region but whose center of its distribution was observed in the 38.0°N latitude area.

Overall, the results of our study indicate that rockfish can be classified into fairly distinct assemblages based on their depth and latitude distributions. This study also provides estimates of the co-occurrence in the form of overlap measures for the important rockfish species off the coast of California. Both the assemblage and co-occurrence information should prove useful to fishery managers for modeling fishery dynamics, solving bycatch issues, establishing area closures, and determining effective marine reserves. Although our study highlights some uses of spatial information, the limited amount of data that is now available prevents a more thorough analysis of interannual variability in the distribution of species. We would therefore

like to stress the importance of collecting more information describing the spatial distribution and co-occurrence of catches and the usefulness of those data in developing new strategies for managing west coast rockfish fisheries.

Acknowledgments

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