Abstract. – Heceta Bank is a large reef on the edge of the central Oregon continental shelf that supports a wide variety of commercial fisheries. Using the research submersible *Delta*, we studied fish abundances on Heceta Bank and the relationship between species composition of fish assemblages and bottom types. Cluster analysis indicated that fish assemblages were most unique on mud, boulder, rock ridge, mud and cobble, and mud and boulder substrates. Rockfishes, particularly pygmy *Sebastes wilsoni*, sharpchin *S. zacentrus*, rosethorn *S. helvomaculatus*, and yellowtail *S. flavidus*, were the most abundant fishes and dominated all substrates except mud, where Dover sole *Microstomus pacificus* and zoarcids *Lycodes pacificus* were most abundant.

Principal component analysis (PCA) and canonical correlation analysis (CCA) were used to determine the sources of variation within the data. PCA demonstrated that habitat variability was a fundamental cause of heterogeneity among fish assemblages. In contrast, CCA showed how species occurrences were related to specific substrates.

Ontogenetic shifts in behavior and substrate preference occurred in pygmy rockfish. Small juveniles often formed dense schools above the bank's shallower rocky ridges. Larger individuals occurred in nonpolarized assemblages on the bottom in cobble and boulder fields.

Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf

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Heceta Bank is a major commercial fishery zone off central Oregon. It supports a wide variety of fisheries: a demersal trawl fishery for many species of flatfishes; a longline fishery for halibut *Hippoglossus stenolepis*; midwater trawl and vertical longline fisheries for rockfishes (*Sebastes* spp.); a midwater trawl fishery for hake *Merluccius productus*; and during upwelling, a troll fishery for salmon (*Oncorhynchus* spp). Despite its importance to commercial fisheries, little was known about Heceta Bank prior to our 1987 submersible studies (Pearcy et al. 1989). From those exploratory dives we learned that (1) the bank is composed of diverse substrates, each supporting fish assemblages differing in species composition and relative abundances; (2) shallow areas of the bank act as a nursery for juvenile rockfishes; and (3) commercially valuable species of rockfish are associated with the shallow bank top in untrawlable areas, which thus serve as refugia from most commercial fishing.

Our 1987 studies focused on initial exploration and description of the Bank. Here we report results from our 1988 submersible-based surveys in which we again studied the fishes occurring on the Bank, concentrating specifically on their associations with various bottom types. We selected sampling stations that represented the range of habitats described by Pearcy et al. (1989) (Fig. 1). Our objectives were to (1) further develop methods of collecting and analyzing data that could be gathered from a submersible to study rocky banks; (2) identify the species occurring on Heceta Bank and estimate their relative and absolute abundances; (3) obtain detailed information about the variability of bottom types occurring within each station; and (4) assess the composition of fish assemblages in relation to different bottom types.

Methods

Data collection

We used the submersible *Delta* to make 18 dives at six stations on Heceta Bank in September 1988 (Fig. 1). These stations represented all substrates and depths within range of the submersible (to 366 m).

At each station we made three daylight dives, each by a different observer (DS, MH, WB). Dives began and ended at least an hour after dawn and an hour before sunset, respectively, minimizing the possible effects of diurnal migration by fishes. Almost all dives at each station were made on the same day.

Our methods basically follow those developed for use by scuba divers working on shallow reefs (Brock 1954, Ebeling 1982). Each observer made two 30-minute visual belt transects during each dive, yielding 6 transects per station (i.e., a total of 36 transects, 12 by each observer). To determine if there were any discernible effects from lights or motor noise of the submersible on the fishes, a 10-minute rest was taken with all lights and machinery off between each pair of transects. To minimize variability caused by within-transect substrate changes, all transects within a station started as closely as possible at the same position, as determined by Loran C. However, due to limits in the accuracy of Loran C and variability in current speed and direction, transects within stations were usually 100–300 m apart.

The observer in the submersible viewed the bottom through a single bow port which limited observation to about a 90° view. Submersible altitude above bottom (at height of observers' eyes from the bottom) was held as closely as possible to 2 m, as measured by an altimeter on the vehicle and by a chain suspended from the submersible (see below). Widths of the viewing path at altitudes of 0.5–2.0 m were determined empirically by "flying" the vehicle at right angles across a decimeter-striped 3 m pole placed on the bottom and noting the length of the pole visible to the observer between two fixed points on the submersible. At 2 m altitude, the transect width was 2.3 m. Thus, the density of fishes (no./m²) was calculated as the number of fishes seen along a transect divided by 2.3 times the transect length in meters. To aid in

Figure 1
Bathymetric chart of Heceta Bank, Oregon, indicating locations of the six stations sampled.

estimating fish length and maintaining vehicle altitude, an ~0.4 m long fiberglass rod, striped in alternating black and white decimeters, was hung by chain from the vehicle within the observer's view. Chain length was adjusted so that when the rod was just above the bottom, the observer's altitude was 2 m.

The goal of the observer during a dive was to identify, count, and estimate the lengths (to the nearest decimeter) of all fishes seen along the transect. Fishes were categorized into "schooling" when five or more individuals formed a polarized group (i.e., all fish
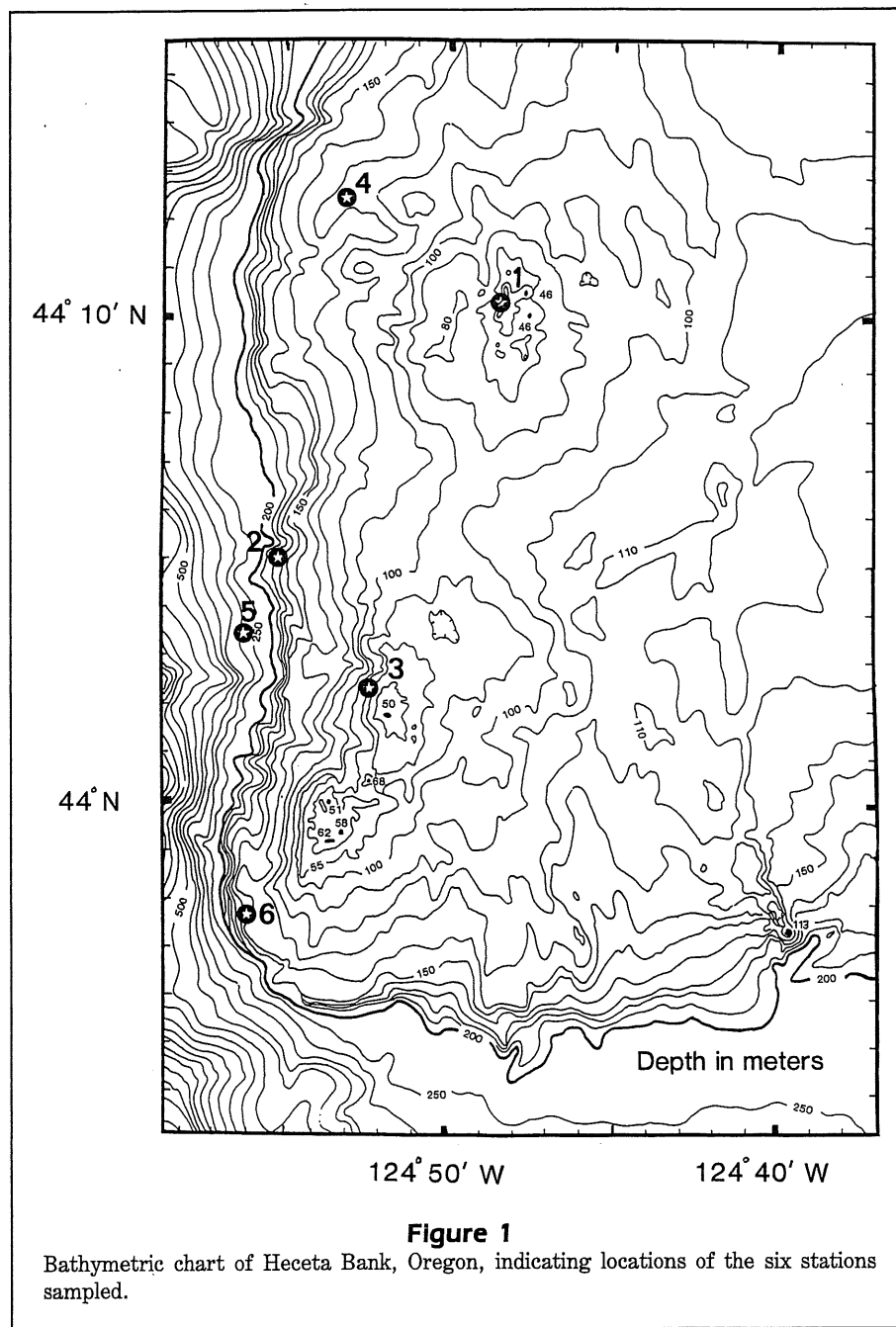
Euclidean distance as a measure of similarity and the group-average clustering method (Pimentel 1979).

To examine specific associations between fish abundance and bottom-type characteristics, data were examined using canonical correlation analysis (CCA). CCA maximizes correlations among two sets of variables while it minimizes correlations within sets (Pimentel 1979). We used CCA to quantify associations between abundances of non-schooling fish species (data set 1) and bottom types (data set 2). Our primary goal was to extract meaningful, natural associations between fishes and habitat factors potentially influencing their distribution and abundance. CCA estimates these associations using four metrics (Pimentel 1979). First, the *canonical correlation* measures the overall association between the two data sets. Second, the *redundancy coefficient* measures the amount of overall variation in one data set as predicted by the other. While the canonical correlation coefficient describes the goodness-of-fit of the two data sets, which can be influenced by a single high correlation between one variable in each data set, the redundancy coefficient measures the extent of overlap in the variation of the two data sets. Third, the *variable loadings* indicate which variables are correlated on a particular axis. The fourth metric, *canonical variate scores*, measures the contribution of each sampling unit (in this analysis, the habitat patch) to the fish-habitat pattern depicted on each axis. Canonical variate scores are derived for each data set: scores for the habitat data indicate the relative cover of specific bottom types on each axis, while scores for the fish data indicate the relative abundance of specific fish on each axis. Canonical variate scores derived from CCA represent a powerful way to measure the abundance of fish in reference to habitat type. In essence, the method controls for the effects of sampling across a range of different habitats, and thus increased our power to detect meaningful spatial variation in fish abundance.

Data for CCA were derived using observations of habitat patches, which were discrete segments of uniform bottom type within each transect (n 524 segments for all transects). For each habitat patch, the abundances of 21 fish species were tabulated relative to the summed total area (in m^2) comprised by the habitat. For mixed bottom types, the total patch area was apportioned 80% to the primary substrate and 20% to the secondary substrate.

Results

The six stations represented a wide variety of substrates, ranging from shallow rocky ridges separated by sand, to intermediate-depth cobble and boulder fields, to deep mud and pebble bottoms (Figs. 1, 2). Stations 1 and 3 (shallow bank tops) were rocky ridges at 60–80 m depth separated by sand and boulder-filled valleys; station 2 (bank saddle) was primarily mud with interspersed cobble at 150–200 m; station 4 was mud, ridge, and cobble at 145–175 m; station 5 was mud at 250–340 m; and station 6 was boulder and cobble grading into mud at 200–270 m. Because transects were always run into the current to insure controlability of the vehicle, distance traveled along the transects was not standardized, but was in the range 467–2367 m ($\bar{x}$ length 1357 m, SE 460 m).

Nested two-way ANOVA of transects and observers, based on the relative abundances of all non-schooling fish species summed, indicated significant differences among stations (F 6.22, df 5,18, $P<0.01$), but not among observers (F 1.39, df 2,18, $P>0.05$), or in interactions among observer transects and stations (F 0.48, df 10,18, $P>0.05$). A Student-Newman-Keuls multiple-range test separated the mean number of non-schooling fish at stations into two subgroups: station 4, where fish were most abundant at 2.09 fish/m^2, and all other stations, which ranged between 1.84 fish/m^2 (station 6) and 0.31 fish/m^2 (station 1).

Species identified: Number and size

We identified 38 taxa to species in our 1988 dives. This represents a 23% increase over the 31 species identified in 1987 (Pearcy et al. 1989). The increase was due primarily to species that were uncommon, suggesting that we identified most or all of the numerically important species on Heceta Bank. There were distinct differences in taxonomic composition and abundances between non-schooling and schooling fishes. About 89% of the non-schooling fishes seen were identified to species; fewer than 2% were not identified to family or genus. All schooling fishes seen were *Sebastes*. Of these, only 49% were identified to species; the remainder were identified to genus only (Table 1). Most of the schooling fish were small or juvenile fish that we could not identify without voucher specimens.

We counted 10,102 non-schooling fish, ranging from 3829 individuals of pygmy rockfish *Sebastes wilsoni* to one individual in each of ten species (Table 1). Schooling fishes comprised 22,470 individuals, over 50% of which (12,820) were unidentified small *Sebastes*. The most abundant identifiable schooling species was again the pygmy rockfish, with 8390 individuals. The least-abundant schooling species was widow rockfish *Sebastes entomelas* with 20 counted. The total number of fish schools seen (all species) was 145, ranging from 70 pygmy rockfish schools to one school of widow rockfish. The number of individuals per school ranged from about 10 to 330.

moving syncronously in the same direction). Non-polarized aggregations or solitary individuals were considered "non-schooling." Data were collected by continuous audio tape recordings of the observer during transects, continuous video records (also including audio, time, and date), and 35mm still photographs automatically triggered every 30 seconds. We used a PhotoSea 1000 35mm still camera and a PhotoSea 2000 video camera, both on fixed mounts outside the vehicle. The video camera was mounted on the starboard bow of the submersible and recorded a field of view that partially overlapped that of the observer within the submersible. The audio track of the videotape recorded the observers comments which allowed real-time integration of fish observations and bottom-type descriptions (see below). Visibility always extended at least to the limits illuminated by the lights (i.e., ~3m or more except where limited by topography). Immediately following each dive, data were entered by computer into a relational database system and verified against the audio tapes.

We tried to minimize inherent biases of submersible studies as suggested by Ralston et al. (1986), such as fishes not seen or unidentified, diurnal variability, and effects of vehicle on fishes. Through a detailed analysis of fish and bottom-type observations recorded in the continuous video coverage of each transect, several observer-related factors affecting data collection were discovered. First, the diving observer usually noted fishes first, then bottom type. When fishes were present coincidentally with a substrate change, fish records were frequently correlated with the wrong bottom type. Second, observers tended to record substrate types based upon larger (high-relief) features rather than small (low-relief) ones, even when the smaller ones were preponderant. Apparently, boulders impressed observers more than cobble or mud, even when the latter were most abundant. Neither of these sources of error was intuitively obvious or suspected. If left uncorrected, these errors would have changed the apparent fish-substrate associations.

Due to these inherent biases, we extracted data on bottom types from the videotape record of each transect. In order to standardize any bias in the evaluation of bottom types, a single observer (BT) reviewed all videotapes. Dominant substrates were categorized using a two-code combination of seven possible categories: mud (code M), sand (S), pebble (P, diameter <6.5cm), cobble (C, >6.5 and <25.5cm), boulders (B, >25.5cm), flat rock (F, low vertical relief), or rock ridges (R, high vertical relief). Substrate was noted as either "primary" if it covered at least 50% of the area viewed (the first code), or "secondary" if it covered more than 20% of the area viewed (the second code). For example, a mud-boulder bottom type (code MB)

consisted of at least 50% cover by mud with at least 20% cover by boulders. In contrast, a mud bottom (MM) consisted of >80% cover by mud.

We defined each transect segment of uniform bottom type as a "habitat patch." Transects within stations were therefore represented by a series of habitat patches defined by the frequency of substratum change along a transect. As a result, the size of habitat patches varied both within and among transects in conjunction with the area of uniform bottom types. The average habitat patch measured 150.8m^2 (SE 15.4m^2, n 524).
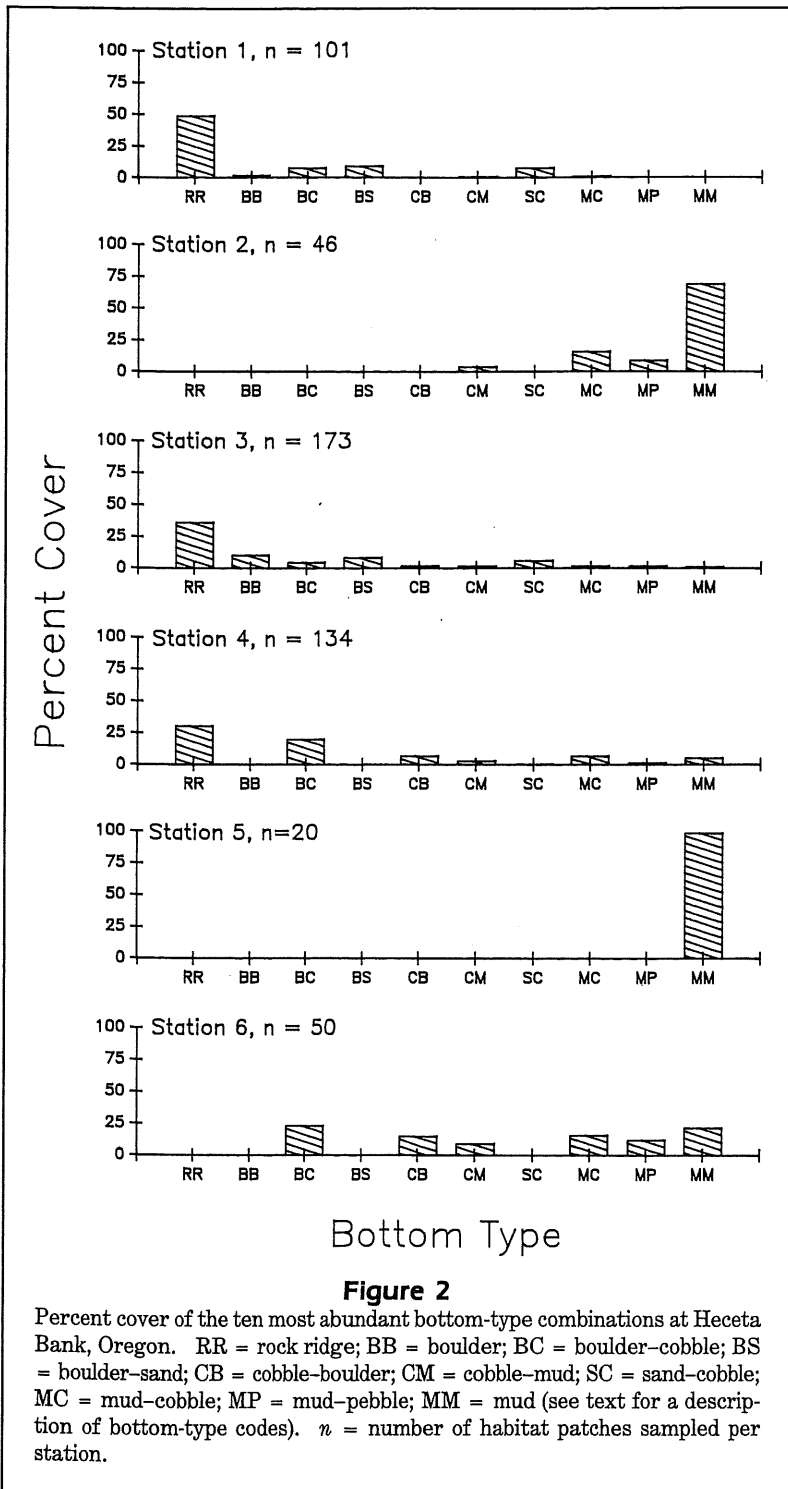
Data analysis

Although data were collected on all observed fish, data analysis focused on the distribution and abundance of non-schooling fishes rather than schooling fishes, because data for the former were more reliable. First, due to the lack of a manipulator on the submersible, we were unable to collect schooling fishes, which were typically small and unidentifiable, to obtain voucher specimens for positive identification. Second, schooling species were generally more abundant above the bottom in midwater and were not common in the transect path.

We tested for statistical differences among stations and observers in non-schooling fish abundance using a nested two-factor analysis of variance (ANOVA). Thirty-minute transect segments served as nested replicates. Sample variances were examined for homogeneity using Bartlett's test (Sokal and Rohlf 1981) prior to using the ANOVA. Because the raw data were heteroscedastic, the analysis examined the log-transformed total abundance of non-schooling fish per m^2.

To examine the variation in fish assemblages among transects, data were analyzed using principal component analysis (PCA). The PCA was an R-mode analysis of the variance-covariance matrix based on the log-transformed abundance of non-schooling fish per m^2. By definition, the axes examined in PCA are statistically independent of on another (Pimentel 1979). Rare species were eliminated from analysis by selecting only species present on at least 10 of the possible 36 transects. A total of 30 taxa met this criterion and were used in the analysis.

To examine the overall similarity of fish assemblages occurring on different substrates, data were analyzed using hierarchical cluster analysis. The analysis was limited to 21 species which were present on at least 12 of the possible 36 transects. The data in this analysis were the log-transformed total number of individuals per m^2 of each species that occurred on each substrate combination. A dendrogram was constructed using

Figure 2

Percent cover of the ten most abundant bottom-type combinations at Heceta Bank, Oregon. RR = rock ridge; BB = boulder; BC = boulder–cobble; BS = boulder–sand; CB = cobble–boulder; CM = cobble–mud; SC = sand–cobble; MC = mud–cobble; MP = mud–pebble; MM = mud (see text for a description of bottom-type codes). *n* = number of habitat patches sampled per station.

varied from 42 cm (yellowtail rockfish *Sebastes flavidus*) to 11 cm (*Sebastes* juveniles).

Ontogenetic habitat changes

Several rockfish species occurred both in schools and singly, including pygmy, yellowtail, sharpchin *S. zacentrus*, redstripe *S. proringer*, and canary *S. pinniger*. Pygmies were the single-most abundant species identified in either category. Schools of pygmy rockfish consisted of significantly smaller individuals, averaging 16.1 cm, whereas non-schooling aggregations and solitary individuals averaged 19.4 cm TL (ANOVA, F 18.0, df 1,699, $P < 0.01$). Furthermore, schools were usually associated with ridge tops shallower than 100 m, while non-schooling fish were on cobble and boulder bottoms at depths of 100–150 m. A similar analysis of the data for yellowtail, sharpchin, redstripe, and canary rockfish showed no significant difference between sizes of individuals in and out of schools (ANOVA, all $P > 0.05$).

Differences among stations: Fish assemblages

Results of the PCA indicated striking differences among stations in both the composition of fish assemblages and the similarity of individual transects within stations (Table 2, Fig. 3). Bartlett's sphericity test indicated that the first two axes described significant non-random patterns of variation among species, and accounted for 70% of the total variation. The first axis, which accounted for 49% of the variation, primarily contrasted transects at station 4 (intermixed mud and rocky ridges) vs. transects at station 5 (mud) (Fig. 3). Transects from stations 1 and 3 (shallow rocky bank tops) formed intermediate homogeneous groups, while transects from stations 2 and 6 (medium-depth boulder and cobble fields) formed intermediate heterogenous groups. Variable loadings indicated that this axis primarily contrasted variation in the relative abundance of rosethorn, pygmy, canary, sharpchin, yellowtail, and greenstriped rockfish, which were abundant at stations 1, 3, and 4 with the relative abundance of thornyhead rockfish, rex sole, sablefish, poachers, and zoarcids, which were abundant at station 5 (Table 2).

Among non-schooling species, the estimated total length ranged from 105 cm (dogfish shark *Squalus acanthias*) to a mean of 12 cm (unidentified small *Sebastes*) (Table 1). Many smaller fishes were seen, but could be identified only to genus (*Sebastes* juveniles) or family (Gobiidae). Among schooling species, average length

Table 1

Numbers of individuals, average total lengths, and standard errors of lengths for schooling and non-schooling fish species identified on Heceta Bank, Oregon, September 1988.

Species	No. seen	Mean length (cm)	SE	Species	No. seen	Mean length (cm)	SE
Schooling				**Non-schooling** (continued)			
Unident. small rockfish (*Sebastes* spp.)	12820	11.1	1.02	Yelloweye rockfish (*S. ruberrimus*)	27	45.4	1.78
Pygmy rockfish (*S. wilsoni*)	8390	16.1	0.72	Petrale sole (*Eopsetta jordani*)	26	27.3	0.55
Yellowtail rockfish (*S. flavidus*)	590	42.3	1.94	Threadfin sculpin	26	23.5	0.52
Sharpchin rockfish (*S. zacentrus*)	320	24.1	2.38	(*Icelinus filamentosus*)			
Redstripe rockfish (*S. proriger*)	220	25.0	4.73	Longnose skate (*Raja rhina*)	23	72.8	40.6
Canary rockfish (*S. pinniger*)	110	41.7	4.70	Sandpaper skate (*R. kincaidii*)	22	30.0	2.77
Widow rockfish (*Sebastes entomelas*)	20	35.0	*	Lingcod (*Ophiodon elongatus*)	20	46.5	9.96
Non-schooling				Blacktail snailfish	15	30.3	0.69
Pygmy rockfish (*S. wilsoni*)	3829	19.4	0.23	(*Careproctus melanurus*)			
Sharpchin rockfish (*S. zacentrus*)	2030	23.7	0.28	English sole (*Parophrys vetulus*)	15	32.3	1.65
Rosethorn rockfish	931	21.6	0.10	Splitnose rockfish (*S. diploproa*)	13	31.9	2.03
(*S. helvomaculatus*)				Black eelpout (*Lycodes diapterus*)	13	28.1	1.10
Dover sole (*Microstomus pacificus*)	436	30.3	0.37	Redbanded rockfish (*S. babcocki*)	11	28.6	3.78
Unident. sculpins (Cottidae)	319	15.8	0.09	Eared blacksmelt	11	15.0	*
Shortspine thornyhead	310	21.7	0.32	(*Bathylagus ochotensis*)			
(*Sebastolobus alascanus*)				Big skate (*R. binoculata*)	10	68.0	32.4
Blackbelly eelpout (*Lycodes pacificus*)	307	25.4	0.29	Hagfish (*Eptatretus* sp.)	10	34.0	3.83
Greenstriped rockfish	288	26.5	0.33	Unident. blennies (Blenniidae)	6	15.0	*
(*Sebastes elongatus*)				Bocaccio (*S. paucispinis*)	5	53.0	3.13
Unident. poachers (Agonidae)	248	22.5	0.15	Sculpin (*Icelinus* sp.)	4	27.5	1.25
Slender sole (*Lyopsetta exilis*)	240	22.5	0.16	Tiger rockfish (*S. nigrocinctus*)	4	40.0	1.67
Unident. small rockfish (*Sebastes* spp.)	130	11.6	1.35	Sanddab (*Citharichthys* sp.)	3	15.0	*
Yellowtail rockfish (*S. flavidus*)	126	43.6	0.62	Unident. blotched rockfish	3	25.0	*
Rex sole (*Glyptocephalus zachirus*)	120	27.3	0.49	(*Sebastes* spp.)			
Unident. flatfish (Pleuronectidae)	93	21.3	1.21	Eelpout (*Lycodapus* spp.)	2	15.0	*
Canary rockfish (*S. pinniger*)	78	46.9	0.98	Arrowtooth flounder	1	45.0	—
Thornback sculpin	57	14.8	0.05	(*Atheresthes stomias*)			
(*Paricelinus hopliticus*)				Darkblotched rockfish (*S. crameri*)	1	35.0	—
Spotted ratfish (*Hydrolagus colliei*)	54	44.1	0.53	Spiny dogfish (*Squalus acanthias*)	1	105.0	—
Unident. fish	47	18.2	1.30	Unident. smelt (Osmeridae)	1	15.0	—
Unident. large rockfish (*Sebastes* spp.)	47	23.1	0.94	Pacific Ocean perch (*S. alutus*)	1	25.0	—
Redstripe rockfish (*S. proriger*)	38	29.0	1.14	Pacific cod (*Gadus macrocephalus*)	1	55.0	—
Ronquils (Bathymasteridae)	33	14.7	0.16	Sand sole (*Psettichthys melanostictus*)	1	35.0	—
Sablefish (*Anoplopoma fimbria*)	33	54.7	3.53	Silvergray rockfish (*S. brevispinis*)	1	55.0	—
Kelp greenling	29	32.2	0.64	Unident. eelpout (Zoarcidae)	1	35.0	—
(*Hexagrammos decagrammus*)				Unident. skate (Rajidae)	1	15.0	—

*No observed variation; all fish estimated to be same length.

The second axis, which described 20% of the variation of relative fish abundance, presented an additional independent pattern of variation among stations (Table 2, Fig. 3). This axis primarily contrasted transects at stations 1 and 3 (shallow rock ridge) with transects from all other stations. As in the first axis, transects within stations along the second axis were heterogeneous; that is, the relative abundances of the fishes seen varied among transects. Station 1 transects were relatively homogeneous compared with transects at stations 2, 3, and 6, which varied considerably. Variable loadings indicated that this axis represented variation in the relative abundance of kelp greenlings and lingcod, which were abundant on bank tops, versus thornyhead and sharpchin rockfish, zoarcids, threadfin sculpin, and dover, rex, and slender sole, which were abundant at other stations.

Fish-habitat associations

Of the 49 possible combinations of bottom type (7 × 7 types), 27 were encountered. Cluster analysis indicated that habitat types had varying degrees of similarity in fish assemblages (Fig. 4). Mud had the most distinct

Table 2

Results of principal component analysis. Underlined bold characters indicate high variable loadings, with positive and negative loadings being inversely correlated along each axis. Thus, PC1 depicts a gradient from soft-bottom species (negative loadings) to hard-bottom species (positive loadings). PC2 depicts a secondary gradient from hard-bottom species (negative loadings) to soft-bottom species (positive loadings).

	PC1	PC2
Eigenvalue	3.056	1.266
Percent of total variation	49.3	20.4
Chi-square	1778	1557
Degrees of freedom	434	405
Variable loadings		
Canary rockfish (*Sebastes pinniger*)	**0.826**	0.135
Yelloweye rockfish (*S. ruberrimus*)	0.477	−0.230
Yellowtail rockfish (*S. flavidus*)	**0.657**	−0.092
Redbanded rockfish (*S. babcocki*)	−0.552	0.338
Redstripe rockfish (*S. proriger*)	0.411	0.180
Sculpins (Cottidae)	**0.748**	0.036
Threadfin sculpin (*Icelinus filamentosus*)	0.339	**0.447**
Kelp greenling (*Hexagrammos decagrammus*)	0.189	**−0.621**
Lingcod (*Ophiodon elongatus*)	0.203	**−0.525**
Rosethorn rockfish (*S. helvomaculatus*)	**0.888**	−0.296
Pygmy rockfish (*S. wilsoni*)	**0.892**	0.372
Sharpchin rockfish (*S. zacentrus*)	**0.714**	**0.602**
Splitnose rockfish (*S. diploproa*)	−0.595	0.266
Greenstriped rockfish (*S. elongatus*)	**0.670**	0.286
Shortspine thornyhead (*Sebastolobus alascanus*)	**−0.690**	**0.446**
Eelpouts (Zoarcidae)	**−0.701**	**0.606**
Hagfish (*Eptatretus* sp.)	−0.222	0.385
Spotted ratfish (*Hydrolagus colliei*)	−0.326	**0.461**
Poachers (Agonidae)	**−0.751**	**0.519**
Sablefish (*Anoplopoma fimbria*)	−0.668	0.400
Searchers (Bathymasteridae)	0.441	−0.141
Blacktail snailfish (*Careproctus melanurus*)	−0.641	0.198
Dover sole (*Microstomus pacificus*)	−0.503	**0.761**
English sole (*Parophrys vetulus*)	−0.066	0.140
Petrale sole (*Eopsetta jordani*)	−0.005	0.192
Rex sole (*Glyptocephalus zachirus*)	−0.644	**0.448**
Slender sole (*Lyopsetta exilis*)	−0.180	**0.582**
Big skate (*Raja binoculata*)	−0.179	0.115
Longnose skate (*R. rhina*)	0.311	0.021
Sandpaper skate (*R. kincaidii*)	−0.429	0.238

fish assemblage, followed by boulder, rocky ridge, mud and cobble, and mud and boulder habitats. In contrast, habitats involving combinations of boulder, mud, sand, and cobble had comparatively similar fish assemblages.

The results of the cluster analysis provide information relevant to the interpretation of the PCA results (Figs. 3, 4). Stations that displayed little among-transect variability in fish assemblages were composed primarily of rocky ridge (stations 1 and 3), and mud (station 5): habitats that had relatively distinct fish assemblages. In contrast, stations with high among-transect variability (primarily stations 2 and 6) were composed of mixtures of mud, cobble, and boulders: habitats sharing relatively similar fish assemblages.

There were additional habitat patterns evident in the distribution of the most abundant rockfish species (Table 3). Comparing abundances of the four most abundant species *within subhabitats*, pygmy rockfish dominated all except mud, mud and cobble, and flat rock. Sharpchin dominated mud and cobble; rosethorn, the flat rock (Table 3). Comparing abundances for each subhabitat *within species*, it is clear that each species, even though it might not be numerically dominant overall, was most abundant in a particular habitat. Thus, pygmy rockfish were most abundant on mud and boulder; sharpchin and greenstriped rockfish on mud and cobble; rosethorn rockfish on boulder; and yellowtail rockfish on rock ridges.
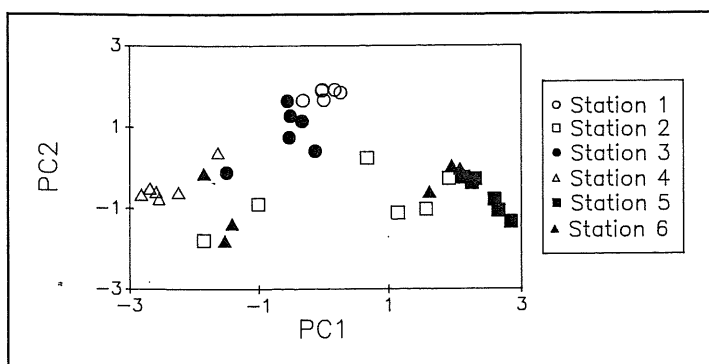
Figure 3

Ordination of first and second principal component scores for 36 transects sampled at six stations on Heceta Bank. The analysis is based on the relative abundances of 30 fish taxa observed (see Table 2 for species list).

Figure 4
Cluster analysis of all observed bottom types based on the relative abundances of 21 fish taxa (see Table 4 for species list).
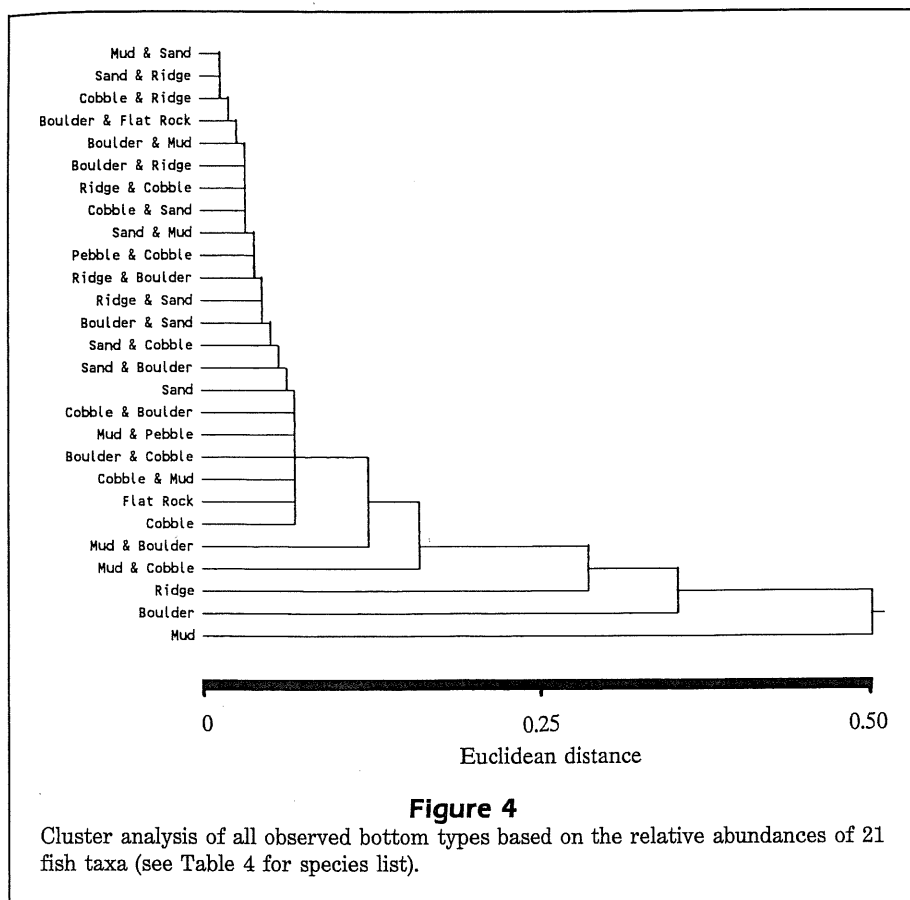
In general, the degree of bottom-type relief varied inversely with depth (Fig. 5). High relief substrates such as rock ridges, boulder, and cobble occurred at relatively shallow 80–100 m depths, while low-relief muddy substrates, such as mud and boulder, mud and cobble, and pure mud, occurred relatively deeper, at 160–240 m depths (Fig. 5).

CCA described associations between species abundance and the distribution of specific habitat types (Table 4, Fig. 6). Bartlett's test indicated that the first three axes represented significant canonical correlations. The low values of the redundancy coefficient for these axes (0.10–0.03, measuring variability in fish abundance explained by habitat variation) demonstrated strong correlations between several species and habitats rather than general associations among all species and all habitats.

Table 3
Average number of fish per hectare ($10^4 m^2$) on the seven most distinct habitat types, as determined by cluster analysis (see Fig. 4). Only the 21 most abundant taxa are listed, these taxa used in the canonical correlation analysis. Most-abundant taxon in each category underlined in bold characters. Species absent from a specific habitat are indicated with dashes.

| Species	Mud	Mud & cobble	Mud & boulder	Cobble	Boulder	Flat rock	Rock ridge
Agonidae	186	464	1122	—	25	—	18
Bathymasteridae	7	7	—	—	—	—	15
Big skate	7	—	51	—	—	—	—
Canary rockfish	—	14	102	—	—	158	82
Cottidae	24	79	51	67	—	158	73
Dover sole	**499**	343	2295	—	—	—	15
Greenstriped rockfish	64	364	204	266	25	—	79
Kelp greenling	—	—	—	67	76	316	27
Lingcod	—	—	—	67	—	—	30
Longnose skate	7	14	51	—	—	—	6
Pygmy rockfish	21	2129	**8926**	**999**	**2772**	—	**1785**
Redstripe rockfish	—	7	—	—	—	—	43
Rex sole	107	57	1887	—	—	—	—
Rosethorn rockfish	26	343	408	933	161	**474**	675
Sharpchin rockfish	60	**2930**	2754	133	—	—	277
Shortspine thornyhead	239	443	2193	—	—	—	—
Slender sole	76	107	408	—	—	—	—
Spotted ratfish	26	14	510	—	—	—	—
Yelloweye rockfish	—	7	—	—	25	—	27
Yellowtail rockfish	—	29	—	67	176	—	191
Zoarcidae	282	279	1887	—	50	—	18
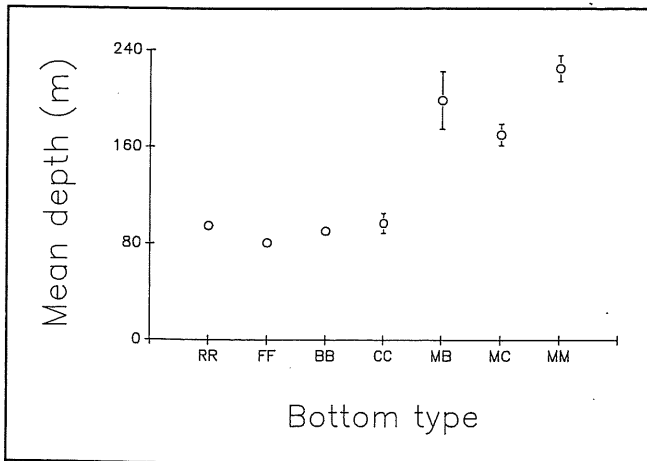
Figure 5
Average depth (±1 SE) of the eight most distinct bottom type combinations on Heceta Bank, Oregon. Bottom codes and sample sizes are as follows: RR = rock ridge (n 109); FF = flat rock (n 4); BB = boulder (n 29); CC = cobble (n 8); MB = mud-boulder (n 11); MC = mud-cobble (n 45); MP = mud-pebble (n 26); MM = mud (n 55) (see text for a description of bottom type codes). n = number of habitat patches sampled per station.

Table 4

Results of canonical correlation analysis. Variables with high loadings are indicated in underlined boldface characters. High negative loadings on the first canonical axis, CC1, indicate fish that were abundant in mud habitats. Similarly, high loadings on CC2 and CC3 indicate fish that were abundant on cobble–boulder bottoms and rock ridge–sand valley bottoms, respectively.

	CC1	CC2	CC3
Canonical correlation	0.849	0.786	0.489
Chi-square	1197	656	249
Degrees of freedom	147	120	95
Fish	Canonical variate loadings		
Canary rockfish (*S. pinniger*)	0.032	**−0.278**	0.090
Yelloweye rockfish (*S. ruberrimus*)	0.035	**−0.382**	−0.139
Yellowtail rockfish (*S. flavidus*)	0.048	−0.021	**0.434**
Redstripe rockfish (*S. proriger*)	0.015	−0.218	−0.098
Cottidae	0.029	−0.200	**0.360**
Kelp greenling (*Hexagrammos decagrammus*)	0.048	−0.140	0.102
Lingcod (*Ophiodon elongatus*)	0.017	−0.134	**0.367**
Rosethorn rockfish (*S. helvomaculatus*)	0.026	**−0.842**	0.295
Pygmy rockfish (*S. wilsoni*)	−0.007	**−0.571**	0.012
Sharpchin rockfish (*S. zacentrus*)	−0.075	**−0.837**	−0.052
Greenstriped rockfish (*S. elongatus*)	−0.155	−0.037	**0.618**
Shortspine thornyhead (*Sebastolobus alascanus*)	**−0.461**	0.066	−0.104
Zoarcidae	**−0.696**	0.077	−0.080
Spotted ratfish (*Hydrolagus colliei*)	−0.337	**−0.504**	−0.172
Agonidae	**−0.678**	0.079	−0.020
Bathymasteridae	0.027	0.043	0.080
Dover sole (*Microstomus pacificus*)	**−0.951**	0.028	−0.005
Rex sole (*Glyptocephalus zachirus*)	**−0.665**	0.065	−0.086
Slender sole (*Lyopsetta exilis*)	−0.088	0.047	−0.081
Big skate (*Raja binoculata*)	−0.324	0.037	−0.059
Longnose skate (*Raja rhina*)	−0.048	0.069	−0.129
Variance extracted	0.132	0.113	0.051
Redundancy	0.095	0.070	0.012
Habitat			
Mud	**−0.998**	0.052	−0.017
Sand	0.037	0.041	**0.665**
Pebble	−0.013	0.070	−0.023
Cobble	−0.041	**−0.514**	0.269
Boulders	0.026	**−0.925**	−0.159
Flat Rock	0.020	0.026	−0.060
Rocky Ridge	0.095	−0.007	**0.529**
Variance extracted	0.144	0.161	0.118
Redundancy	0.104	0.100	0.028

Because bottom-type changes were highly correlated with changes in depth (Fig. 5), the CCA did not confound species associations with bottom types from different depths. Each axis measured associations occurring within the depth range of the habitat indicated by the variable loadings on each axis.

The first axis described variation in fish abundance associated with mud habitats (160–240 m). Variable loadings indicate that thornyheads, zoarcids, poachers, and rex and Dover sole commonly occur on mud (Table 4). Canonical variate scores on this axis were significantly different among stations in both the habitat and fish scores: station 5, the only pure mud station (Fig. 2), was significantly different from all others (Kruskal-Wallis, $p < 0.01$) (Fig. 6A).

The second axis contrasted an additional independent fish-habitat association. Variables loadings indicated that ratfish, and rosethorn, sharpchin, yelloweye, canary, and pygmy rockfish were associated with boulder and cobble fields at 75–100 m depths. Canonical scores for the second axis also differed significantly among stations on both habitat and fish scores: station 6, the station with the highest cover of boulder-cobble (Fig. 2), was significantly different from all other stations (Kruskal-Wallis, $p < 0.01$) (Fig. 6B).

The third axis indicated an additional association between fish and habitat. Variables loadings indicated that greenstriped and yellowtail rockfish, lingcod, and cottids were associated with sand

and ridge habitats at 75–100 m depths. Canonical variate scores among stations differed on the third axis with respect to habitat scores, but not on fish scores. With respect to habitat, stations 1 and 3, which had the highest amount of sand and ridge cover (Fig. 2), were significantly different from stations 2, 4, and 6 (Kruskal-Wallis, $p < 0.01$) (Fig. 6C). In contrast, with respect to fish abundance, stations were highly variable, and not significantly different among stations (Kruskal-Wallis, $p > 0.05$) (Fig. 6C).
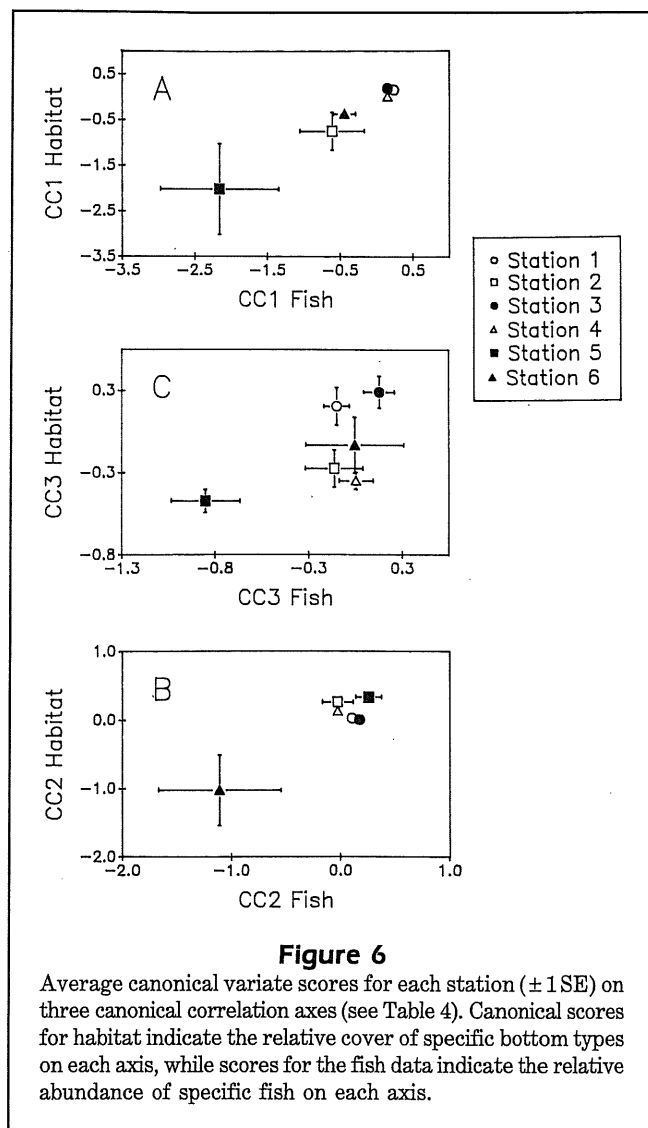
Discussion

The principal objective of our study was to develop methods to estimate spatial variation in fish abundance on Heceta Bank. However, the high variability of bottom types encountered required that we understand the effects of bottom-type variation on fish abundance and distribution.

Fish-habitat associations

The principal components analysis showed that stations with the least variability in fish abundance among replicate transects were those at stations composed of rock ridge, such as the bank tops (stations 1 and 3), and of mud (station 5). In contrast, high variability in fish abundance among replicate transects occurred at stations having combinations of mud, cobble, and boulders (stations 2, 4 and 6). Moreover, canonical correlation analysis indicated that fish assemblages associated with these habitats were unique. Mud, cobble–boulder, and ridge–sand habitats displayed different species composition and relative abundance.

In most sampling situations, such as use of a bottom trawl or bottom-set gillnet, analysis would be limited to a fish-only PCA-type appproach. Within-station variability, such as that documented here, would be largely unaccounted for without detailed information about bottom type. In the present study, canonical correlation analysis of fish abundance relative to bottom type provided key information on a major source of within-station variability.

The ability to estimate bottom-type composition and determine the relationships of species with each substrate is a critical advantage of submersible studies. In shallow water, this has been done using scuba (e.g., Hixon 1980, Larson 1980, Hallacher and Roberts 1985). However, there are few such studies below scuba depths. In the northeastern Pacific, Carlson and Straty (1981) and Straty (1987) used a submersible to study habitat and nursery areas for rockfishes in southeastern Alaska. Straty (1987) concentrated on species of juvenile rockfishes and their occurrence in relation to

Figure 6
Average canonical variate scores for each station (± 1 SE) on three canonical correlation axes (see Table 4). Canonical scores for habitat indicate the relative cover of specific bottom types on each axis, while scores for the fish data indicate the relative abundance of specific fish on each axis.

substrate type and relief; he did not attempt to quantify abundances. Richards (1986) similarly investigated distributions of deep rockfishes at 21–140 m and related their occurrence to bottom type. Although she was able to show substrate associations for three species (*Sebastes elongatus*, *S. maliger*, and *S. ruberrimus*), only three substrate categories were used, and abundances of fishes were determined on the basis of distance of maximum visibility. Nevertheless, she recognized the importance of such studies and developed initial methods for obtaining data on this subject.

Abundances of species

We know of no comparable data to that presented here for fish abundances on Heceta Bank. However, similar studies have been done on inshore reefs in central California. Miller and Geibel (1973), using scuba tech-

niques similar to our submersible methods, estimated abundances of juvenile and adult rockfishes along transects on an inshore reef supporting an extensive kelp forest. Their estimates of juvenile abundances are much higher than ours: more than 46,000 fish/ha compared with our maximum of 15,039 fish/ha (station 3). Comparing abundances of adults at the same stations, they estimated 3133–5046 fish/ha vs. 558–1724 fish/ha at our station 3. The maximum estimated number of adult fishes at any of our stations was 9635 fish/ha (station 4). However, our estimates at the shallow bank top stations (1 and 3) are low because they did not include most of the schooling fishes, which were above the submersible. We have no accurate estimates of the abundances of these fishes, primarily yellowtail and widow rockfish. They occurred in schools of thousands.

Availability of comparative data

There are few data sets comparable with ours that were obtained by other methods. Rough bottoms are untrawlable, reducing usable gear to longlines or set nets. Even where these are used, if substrate varies over the length of the longline or net, they "integrate" the fishes over those different bottom types, preventing association of species with specific substrate types. Using otter trawls with foot rope rollers, Barss et al. (1982) studied fish assemblages associated with "rough" (rocky bottom fishable with nets using rollers) and "smooth" bottom on the west (offshore) side of Heceta Bank. The areas with most relief were unfishable (including our stations 1 and 3). They found distinct differences in catches between the two types of areas, but admitted that their results were biased by the type of gear they were forced to use in order to trawl on rough bottom.

Recently, Matthews and Richards (In press) used gillnets to compare fish assemblages on trawlable and untrawlable bottoms west of Vancouver Island. Their goal was to determine whether, as commercial fishermen believe, untrawlable bottom west of Vancouver Island provides refuges for commercially exploited fishes (primarily Pacific Ocean perch) caught nearby. They concluded there were no reservoir populations. However, given the mesh size of their bottom-set gillnets, they were unlikely to sample either juveniles or semipelagic species such as yellowtail and widow rockfish. Thus, given our current and previous observations of juvenile and yellowtail rockfish associated with shallow, high-relief rocky ridges (Pearcy et al. 1989), we suggest that these unfished areas could still provide refuges for fishes in either of those categories.

Habitat shifts

Ontogenetic habitat shifts, such as those desribed here for pygmy rockfish, are common among rockfish species. Westrheim (1970), Carlson and Haight (1976), and Straty (1987) found that juvenile Pacific Ocean perch *Sebastes alutus* were usually shallower than adults. Carr (1983) described the growth-related migration of juvenile *S. atrovirens*, *S. carnatus*, *S. chrysomelas*, and *S. caurinus* to the bottom in a central California kelp forest. However, Hallacher (1977), studying adults and juveniles of *S. mystinus* and *S. serranoides* in Monterey Bay at depths of ~25 m or less, found that abundances of both increased with depth, maxima occurring at the greatest depths sampled. This difference could be related to degree of association with the bottom as adults. The species Carr (1983) studied were benthic as adults, whereas the latter two species occur in the water column.

Conclusions

The results presented here show the utility of using a submersible rather than bottom set nets, traps, or longlines to study fish-substrate associations in deep water areas where substrate is heterogeneous. Other methods, such as Remote Operated Vehicles, rely on video and still camera images, which are not as adequate for accurate identification as the human eye. Moreover, other types of gear do not allow detailed characterization of the substrate sampled, but rather integrate the catch from a variety of habitats. We believe that the methods presented here, in addition to describing basic fish-habitat associations, allowed us to control the effects of sampling across a range of different habitats, and increased our ability to detect meaningful spatial variation in fish abundance.

Acknowledgments

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