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Journal of Experimental Marine Biology and Ecology 352 (2007) 50–64

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Habitat-based submersible assessment of macro-invertebrate and groundfish assemblages at Heceta Bank, Oregon, from 1988 to 1990

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Received 23 March 2006; received in revised form 19 February 2007; accepted 30 June 2007

Abstract

Exploitation of groundfish off the U.S. Pacific coast reached maximum levels during the 1990s, resulting in severe declines in at least nine species of groundfish. From 1988 to 1990, we used the 2-man submersible *Delta* to make 42 dives and run replicate visual belt transects at six stations ranging from 67–360 m in depth at Heceta Bank on the outer continental shelf of Oregon. We identified four major habitats and associated benthic macroinvertebrate and groundfish assemblages: (1) shallow rock ridges and large boulders (<100 m deep) dominated by basket stars, juvenile rockfishes, yelloweye rockfish, and lingcod; (2) mid-depth small boulder-cobbles (100–150 m) dominated by crinoids, brittle stars, rosethorn, pygmy/Puget sound, and canary rockfishes; (3) deep cobble (150–200 m) dominated by crinoids, brittle stars and various small rockfish species, and (4) deep mud slope (>200 m) dominated by fragile urchins, sea cucumbers, shortspine thornyhead, and flatfishes. Although substantial interannual variation in groundfish abundance among seafloor types was evident in the 12 most abundant and/or commercially important fish taxa sampled, high variance resulted in statistically significant differences among years only in juvenile rockfishes. These data provide a baseline for future comparisons exploring long-term change this continental-shelf ecosystem.

Keywords: Groundfish; Invertebrates; Continental shelf; Habitat definition and use; Heceta Bank

1. Introduction

Exploitation of groundfish off the U.S. Pacific coast reached maximum levels during the 1990s, resulting in the depletion of various stocks (Ralston, 1998; Bloeser, 1999; Parker et al., 2000). Suffering particularly severe decline were species of rockfishes (*Sebastes* spp., Scorpaenidae), whose life-history characteristics make them especially vulnerable to overfishing (Leaman and Beamish, 1984; Leaman, 1991). By 2002, seven species of West Coast rockfishes, plus lingcod (*Ophiodon elongatus*) and Pacific hake or whiting (*Merluccius productus*) were declared officially overfished (NMFS, 2003). By 2006, only lingcod and hake had recovered.

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doi:10.1016/j.jembe.2007.06.032

Crucial to developing meaningful recovery plans for groundfish stocks is knowledge of their historical distribution and abundance, as well as past levels of interannual variation in abundance. Populations of rockfishes and other species associated with high-relief rocky bottoms have been difficult to assess using surface-based methods, such as trawl surveys, deep-water tagging, and fishery-dependent catch or observer data (Grimes et al., 1983; O'Connell and Carlile, 1993). Manned submersibles have proven to be useful sampling tools in such natural refuges, and can additionally provide assessments based on seafloor type and associated macroinvertebrates (e.g., Richards, 1986; Butler et al., 1991; Krieger, 1993; O'Connell and Carlile, 1993; Murie et al., 1994; Krieger and Ito, 1999; Yoklavich et al., 2000). However, no studies using submersibles from the Pacific Northwest have examined groundfish abundance over a series of years, thereby precluding analysis of interannual variability. Knowledge of the range of among-year fluctuations in abundance are essential for separating natural and sampling variation from effects of fishing and other human impacts. Moreover, because the distribution and abundance of groundfish are clearly affected by seafloor type and assemblages of benthic macroinvertebrates, assessments useful for among-year and among-site comparisons must be habitat-based.

From 1987 to 1990, before the decline of regional groundfish stocks reached detectably severe levels, a descriptive survey of demersal fish assemblages and associated habitat characteristics at the largest rocky bank on the outer continental shelf of Oregon, Heceta Bank, was conducted using manned submersibles (Pearcy et al., 1989; Hixon et al., 1991; Pearcy, 1992). The impetus for this survey was the mandate of the U.S. Minerals Management Service to produce a baseline description of the bottom-associated communities in this region in anticipation of future offshore oil exploration. In reality, this study provided a habitat-based assessment of groundfish assemblages just before the impacts of overfishing became obvious. The first year of this study (1987) provided an overview of the range of habitats and assemblages at Heceta Bank (Pearcy et al., 1989), as well as the development of standardized observational and statistical designs used in subsequent years (Stein et al., 1992). These methods were later integrated with high-resolution seafloor imagery to provide regional groundfish assessments that are truly habitat-based (Nasby-Lucas et al., 2002; Wakefield et al., 2005). Here, we report habitat-specific assemblages of groundfish and associated macroinvertebrates at Heceta Bank and patterns of interannual variation in the distribution and abundance of groundfish over three years: 1988–1990.

2. Methods

2.1. Data collection

During the month of September in each year from 1988 to 1990, we used the 2-man submersible *Delta* to make 42 dives at Heceta Bank ranging from 67 to 360 m depth (Fig. 1). These dives were made at six representative stations chosen from 16 stations sampled in 1987 (Pearcy et al., 1989). A detailed description of the data derived from each dive is reported in Hixon et al. (1991). At each station, we made three daylight dives in 1988, and two daylight dives in both 1989 and 1990. Dives began and ended at least an hour after dawn and an hour before sunset, respectively, minimizing possible effects of diurnal changes in fish behavior and movements. Each year, almost all dives at each station were made on the same day. To avoid systematic bias among observers, no two dives at the same station during the same year were conducted by the same observer, and the same three observers (Hixon, Stein, and William Barss of the Oregon Department of Fish and Wildlife) participated in all 3 years of the study.

Visual belt transects were adapted from methods long used for SCUBA surveys on shallow reefs (Brock, 1954, 1982; Ebeling, 1982; Sale and Sharp, 1983). The view through the two forward portholes of the sub, which transected the fore ballast tank, provided a visual field width of 2.3 m when the vessel was 2 m off the seafloor. This visual constraint dictated the width of our belt transects for calculating densities of groundfish and macroinvertebrates. During each dive, we ran a single one-hour transect, separated into two 30-minute segments by a 10–15 minute "quiet period" to determine the effect of the sub on fish behavior. Overall, each dive lasted about 2 h, including transit time between the surface and seafloor.

If there was no current, each hour-long transect would measure approximately 2,800 m by 2.3 m. However, most dives encountered currents, and because the pilot could effectively steer the sub only by heading into the current, the currents defined our specific headings from the fixed starting point of each station, and ultimately, the lengths of the transects. For mapping transect paths, we used a Trackpoint II system to position the support vessel directly above the sub every 10–15 min, then noted our latitude and longitude using Loran-C. We calculated the approximate length of each one-hour transect, which averaged 1909 m (SE = 152 m; $n = 42$).

During each transect, the pilot attempted to maintain an altitude of 2 m above the bottom, and radioed depth, temperature, and habitat information to the support vessel.

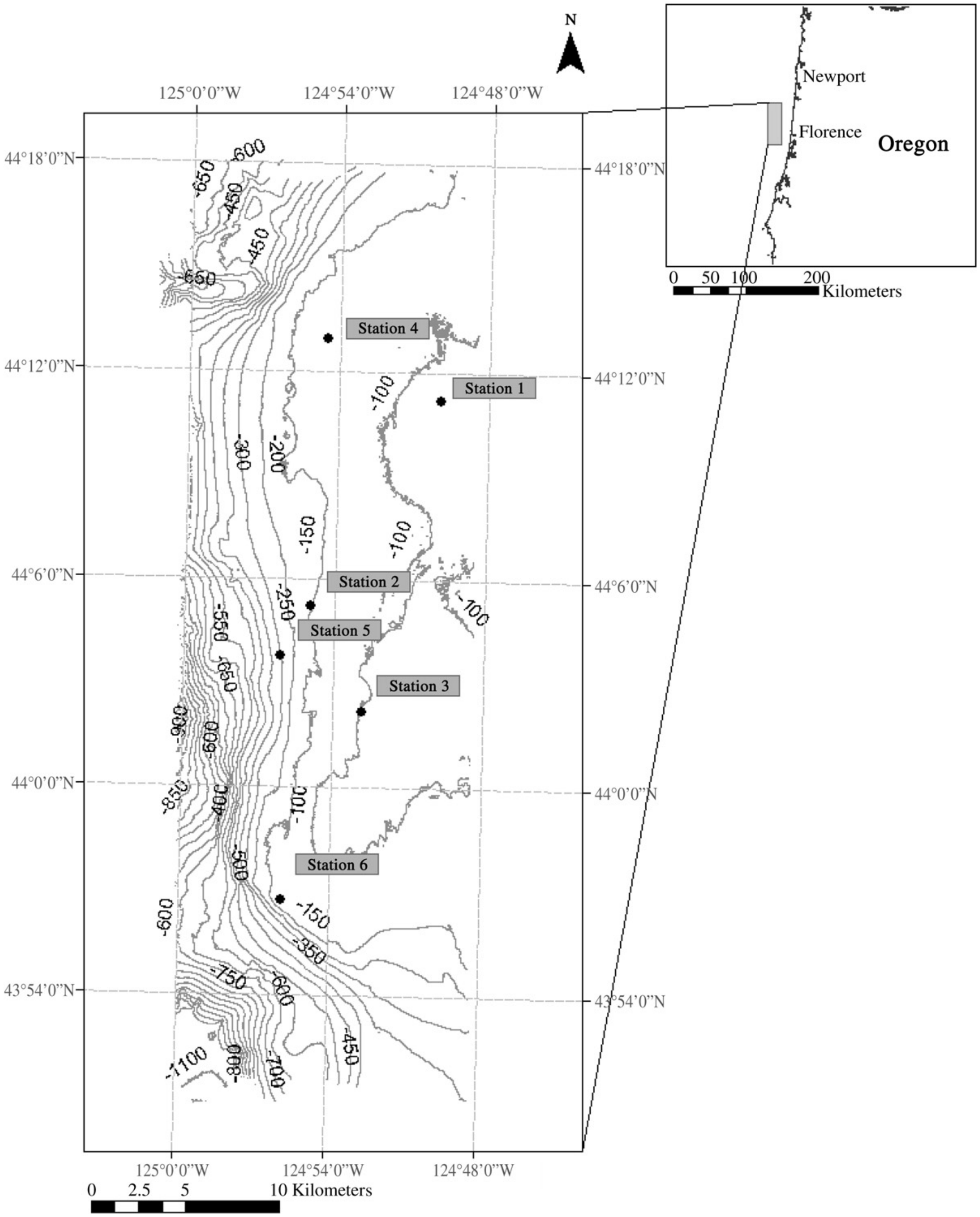

Fig. 1. Location and bathymetric chart of the Heceta bank off the Oregon coast in relation to submersible sampling stations occupied in 1988–1990. Contours in meters.

The observer verbally tape-recorded data on the species, size class (to the nearest dm TL), abundance, and behavior (e.g., schooling vs. non-schooling) of all visible demersal fishes. To accurately estimate fish lengths and to provide an external scale for photography, we suspended a 0.3 m fiberglass rod (marked in decimeter intervals) by a chain into the transect path. A visual record of the transect path was provided by both standard VHS videotape (with timed data logger and audio track) and a Photosea 35-mm camera taking still photos every 30 s. Additional details of transect and photographic methods are described in Stein et al. (1992) and Hixon et al. (1991).

Macroinvertebrate data were collected using transect videotapes, still photos, and the *Delta's* 5 cm diameter slurp gun. Densities of dominant macroinvertebrates (>5 cm in height; see Tissot et al., 2006) were estimated for two transects at each station for each year using the transect videotapes in the same way we counted fishes. Voucher specimens collected by slurp gun were used to verify visual identification wherever possible.

Because the submersible observers needed to concentrate on identifying and counting fishes, we extracted detailed data on seafloor types from our videotape records of each transect. We used 8 different categories of substrata, using standard geological definitions (Greene et al., 1999). In order of increasing particle size and relief, these substrata were: mud (code M), sand (S), pebble (P), cobble (C), boulder (B), continuous flat rock (F), diagonal rock ridge (R), and vertical rock-pinnacle "top" (T). Substrata F and T were seldom encountered. To standardize any inherent bias in this method, one of us (Tissot) reviewed all the videotapes for all dives, recording a two-character code each time a distinct change in seafloor type was noted. We defined each transect segment of uniform seafloor type as a *habitat patch*, which was the sample unit of our multivariate analyses.

We defined *seafloor type* as a two-letter code representing the approximate percent cover of the two most prevalent substrata in a particular habitat patch. The first character represented the substratum that accounted for at least 50% of the patch, and the second represented the second most prevalent substratum accounting for at least 20% of the patch (e.g., "BC" for at least 50% cover by boulders with at least 20% cover by cobble). If the field of view was purely a single substratum, or the second most abundant substratum covered less than 20% of the field, then the observer would enter a single code twice (e.g., "BB" for >80% cover by boulders). We encountered a total of 36 two-way combinations of the 7 substratum codes, defining 36 seafloor types. Although the submersible's video system occasionally failed, we were able to extract seafloor-type data for 97.7% of over 216,145 fishes we counted.

2.2. Data analyses

We examined multivariate associations among fish species abundances, macroinvertebrate species abundances, and seafloor types using canonical correlation analysis (CCA). CCA is a multivariate technique designed to extract a series of interrelations between two related data sets (Pimentel, 1979). In this case, we examined the relationships between fish species abundance (data set 1) and habitat (data set 2), which included both seafloor types and invertebrate abundance data. Our primary goal was to extract meaningful, natural associations between fishes, invertebrates, and habitat factors potentially influencing their distribution and abundance. However, once extracted, these associations served an additional purpose: they estimated the abundance of fishes within a particular habitat type. Thus, in addition to describing basic fish- and invertebrate-habitat associations, the analysis provided an estimate of habitat-specific fish abundances. In effect, CCA allowed us to control for the effects of sampling across a range of different habitats, and thus increased our ability to detect meaningful spatial and temporal variation in fish abundances.

For this community-level multivariate analysis, the sample unit was not an entire transect, but a habitat patch of uniform seafloor type. This approach freed us from the arbitrary nature of station locations and the vagaries of individual transect paths, and allowed us to examine patterns across all stations simultaneously. It also allowed us to integrate our invertebrate data with our seafloor-type data (by combining data sets), providing a more realistic resolution of "habitat" that incorporated both biotic and abiotic variables. Each observation in the analysis represented the density of fishes and invertebrates enumerated on the same seafloor type along a transect. When the seafloor type changed along a transect, a new habitat patch observation was initiated. Thus, the data collected for an individual dive consisted of the sum of the different seafloor type changes occurring along a transect, each observation representing a sample of fish and invertebrate abundances within a particular seafloor type. Because CCA neither assumes nor requires independence of samples, there was no problem posed by the patches along a transect being contiguous.

We used CCA to extract a series of patterns (or axes) from the collection of habitat patches that represent contrasting intercorrelations between fish, invertebrates, and seafloor types. A major asset of CCA is that each axis depicts an orthogonal, or statistically independent, description of the association between data sets. Because axes are independent, each pattern represents a unique association common to both data sets. Each derived axis can be characterized by three different measures. First, the canonical correlation coefficient measures the extent of overall association between fish abundance and seafloor-type/invertebrate abundance on each axis. Second, the redundancy coefficient measures the actual extent of overlap between the two data sets, and varies between 0 (no overlap) to 1 (perfect correspondence). In principle, the redundancy coefficient describes a substantially different aspect of the CCA than the canonical correlation coefficient. 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 overall fit, or overlap in variation, between all variables in both sets.

In our CCA of fish-invertebrate-seafloor data, we typically encountered high canonical correlations and low redundancy. This outcome was consistent with our observations from habitat-specific fish distributions: on each CCA axis some species were abundant within a particular seafloor type while others were not. This pattern resulted in a high goodness-of-fit but low overlap among data sets.

The third and most informative metric in CCA is the loading of each variable on each axis. Variable loadings indicate which fishes are abundant within a particular seafloor type-invertebrate assemblage. Variable loadings represent contrasting associations among fishes, invertebrates, and seafloor types. For example, if muddy bottoms display high positive loadings on an axis and rocky bottoms display high negative loadings, then fishes with high positive loadings are abundant on mud, while those with high negative loadings are abundant on rock.

We tested whether there was significant interannual variation in groundfish abundance by species and seafloor type using two-way repeated-measures analysis of variance (ANOVA) with years and seafloor types as factors. Different observers at the same stations served as repeated measures to minimize the potential for lack of sample independence of multiple transects at the same station. Prior to all ANOVAs, we examined homogeneity of variances by Bartlett's tests, and where necessary, data were log-transformed to ensure equal variances. To evaluate the statistical power of the test to uncover significant interannual differences, the minimum detectable difference was calculated as a percentage of initial (1988) abundance using $\alpha=0.05$ and $\beta=0.10$ (Zar, 1999).

3. Results

3.1. Habitat and invertebrate characterization

During 42 dives over the three-year sampling period, a total of 1058 habitat patches was surveyed, including 129,635 macroinvertebrates representing 44 taxa (30 genera/species and 14 nonspecific categories) and six phyla, as well as 216,145 fish representing 73 taxa (51 species and 22 nonspecific categories) and 24 families. The mean patch size was 173 m^2 with a range from 23 to 3,933 m^2 (SE=7.5). Among the ten most abundant seafloor types (which accounted for nearly 90% of the total cover), there was a strong correlation between depth and seafloor type ranked by degree of relief (Spearman rank

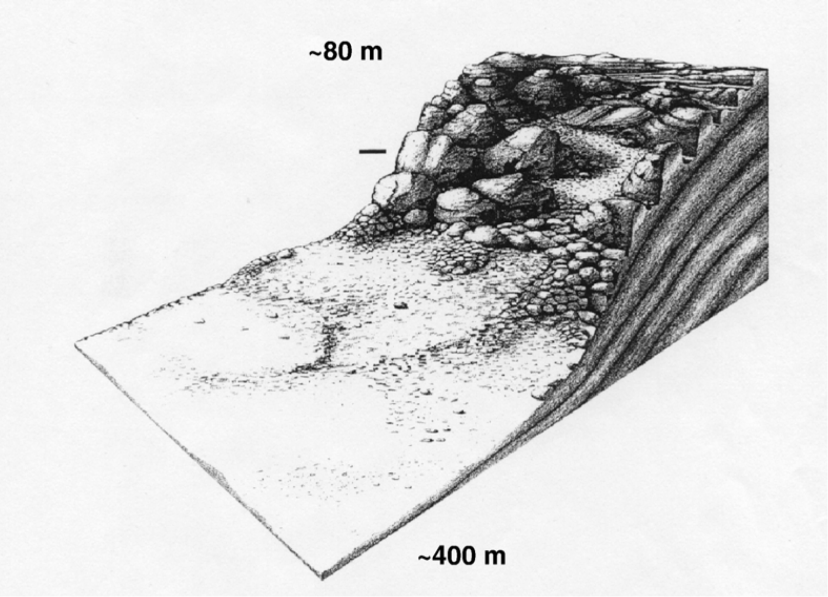

Fig. 2. Artist's conception of the offshore slope profile at Heceta Bank as viewed from the southwest. The illustration is a composite summary of the range of seafloor types observed. Scale bar equals roughly 5 m, the length of the submersible. The scale of the depth profile is condensed.

correlation, $P<0.001$, $r=0.93$, $n=10$). The shallower parts of the bank (<100 m) were strongly dominated by rock ridges (code RR) and contiguous large boulders (BB), intermediate depths by combinations of boulders and cobble (mostly BC, CB, and CC), and deeper areas (>150 m) by mostly mud (MM, MP, MC, MB, and CM). This tight correlation was simply a consequence of Heceta Bank being a rocky outcrop projecting upward from a

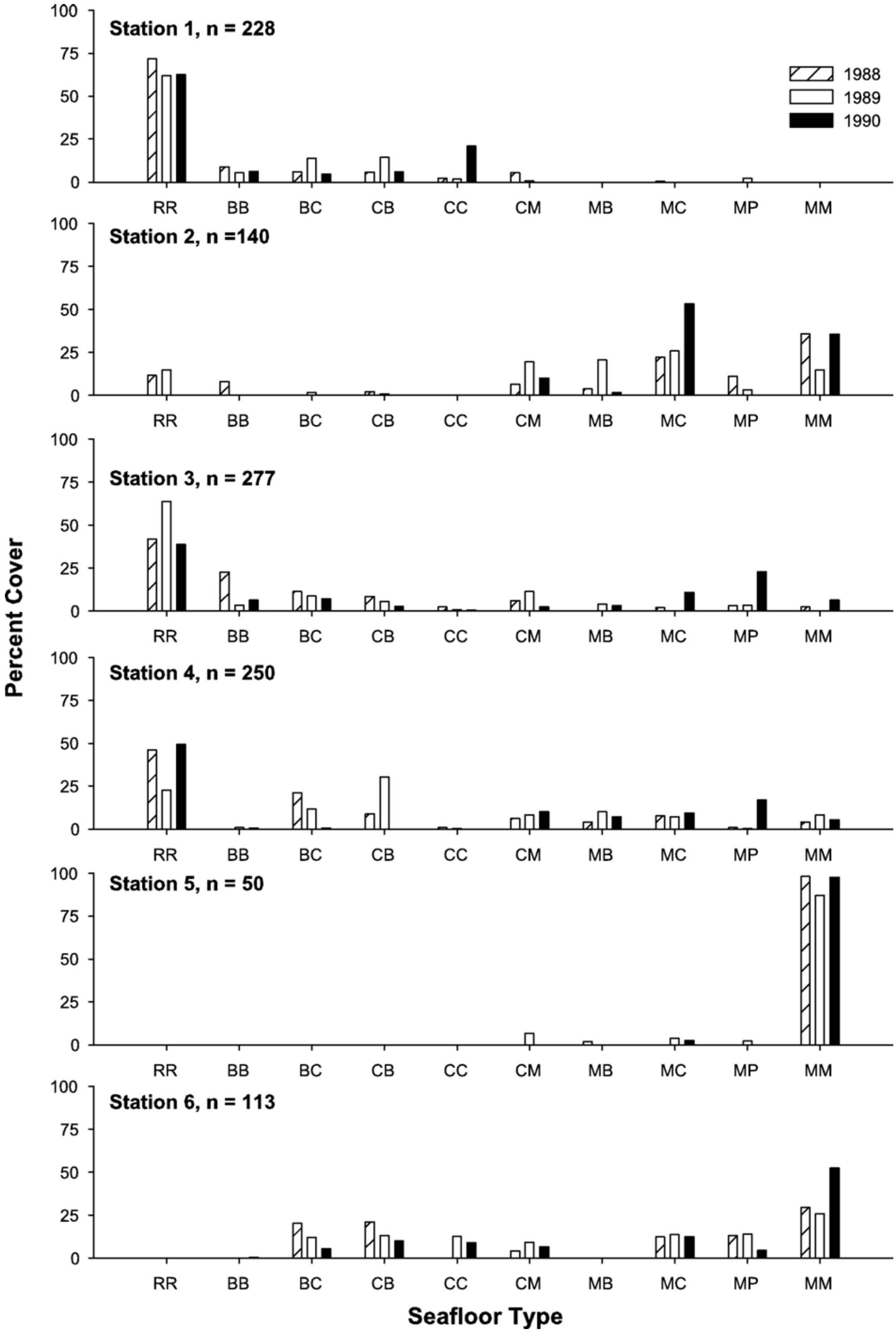

Fig. 3. Percent cover of the ten dominant seafloor types sampled by habitat patch on Heceta Bank by station and year (including total number of patches per station). Seafloor types are listed by decreasing relief and particle size, where the first letter is the dominant substratum and the second letter is the second most prevalent substratum: R = rock ridge; B = boulder; C = cobble; P = pebble; M = mud. Total sample size was $n=1198$ patches.

mud seafloor, with boulders and cobble around its base, much the same as a terrestrial mountain (Fig. 2). This correlation allowed us to use only seafloor type (and not depth) in our multivariate analyses.

To characterize habitat types at the level of sampling station, we examined the relative percent cover of the ten most abundant seafloor types among stations (Fig. 3). This analysis suggested four basic station types: 1) clearly rock-ridge dominated (Stations 1 and 3); 2) heterogeneous but primarily rock-ridge dominated (Station 4); 3) heterogeneous but primarily mud-dominated (Stations 2 and 6); and 4) clearly mud-dominated (Station 5) habitats. Obviously, these were arbitrary distinctions, emphasizing the importance of relying on our multivariate approach to define habitat. This conclusion is especially true given that most transects tended to run from shallow rocky to deep muddy habitats, precluding exclusive habitat distinctions at the scale of entire stations.

The canonical correlation analysis examined 8 invertebrate taxa which accounted for 75% of all macroinvertebrates (Table 1). The first through third axes of the CCA of data pooled among years provided ecologically meaningful contrasts. Seafloor-type and invertebrate loadings on these axes defined four basic habitat types (Fig. 4). The first axis provided a primary contrast between a strongly mud-dominated habitat (mostly deeper than 200 m) and various rock-dominated habitats (mostly shallower than 200 m), which were described by the second and third axes. The "deep mud slope" habitat (positive loadings on axis 1 in Fig. 4) included mostly fragile sea urchins and sea cucumbers, which occurred in isolated patches, as well as occasional sand stars. This is the primary habitat fished by commercial bottom trawlers in this region (Waldo Wakefield, NOAA Fisheries, personal communication, 2006).

Table 1
Total number of macroinvertebrates and fishes observed for taxa statistically analyzed in this study

Taxa	Total number observed
Invertebrates	
Crinoid (*Florometra serratissima*)	65,388
Fragile sea urchin (*Allocentrotus fragilis*)	30,767
Brittle stars (Ophiacanthidae)	26,715
Sea cucumbers (*Parastichopus* spp.)	3,953
Blood stars (*Henricia* spp.)	1,151
Basket star (*Gorgonocephalus eucinemis*)	273
Sand star (*Luidia foliolata*)	195
Sunflower stars (*Rathbunaster / Pycnopodia*)	74
Fishes	
Pygmy/Puget Sound rockfishes (*Sebastes wilsoni/emphaeus*)	115,628
Juvenile rockfishes (*Sebastes* spp.)	55,126
Sharpchin rockfish (*Sebastes zacentrus*)	14,115
Rosethorn rockfish (*Sebastes helvomaculatus*)	6932
Yellowtail rockfish (*Sebastes flavidus*)	5783
Dover sole (*Microstomus pacificus*)	1973
Greenstripe rockfish (*Sebastes elongatus*)	1843
Shortspined thornyhead (*Sebastolobus alascanus*)	1213
Rex sole (*Glyptocephalus zachirus*)	628
Canary rockfish (*Sebastes pinniger*)	508
Lingcod (*Ophiodon elongatus*)	168
Yelloweye rockfish (*Sebastes ruberrimus*)	160

See text for criteria by which these taxa were selected.

Orthogonal to the first axis, the second CCA axis described rocky bottoms dominated by cobbles, yet including small boulders and some ridges. This "*mid-depth small boulder-cobbles*" habitat included mostly crinoids, yet also basket, blood, brittle, and sunflower stars. Cobble-dominated regions of this habitat were of sufficiently low relief to be fished by commercial bottom trawlers (Waldo Wakefield, NOAA Fisheries, personal communication, 2006).

The third CCA axis contrasted two different rocky bottom habitats: those dominated by shallow diagonal rock ridges (positive loadings on axis 3 in Fig. 4), and those dominated mostly by a mixture of deep cobbles and small boulders (negative loadings on axis 3 in Fig. 4). Rock ridges interspersed with large contiguous boulder bottoms were important habitats for some fishes, especially juvenile rockfishes (see below). However, because contiguous boulder bottoms (as opposed to bottoms of boulders mixed with other substrata) were relatively rare (Fig. 3), they failed to load heavily on the CCA. Therefore, we called the mixed habitat defined by positive loadings on CCA axis 3 the "shallow rock ridges and large boulders" habitat. This habitat included mostly basket, blood, and sunflower stars (positive loadings on axis 3 in Fig. 4). The shallow rock-ridge and large-boulder habitat was clearly untrawlable, and thus represented a natural refuge from the bottom-trawl fishery. We called the mixed habitat defined by negative loadings on CCA axis 3 the "deep cobble" habitat and it was dominated mostly by cobbles, crinoids, brittle, and sand stars (Fig. 4). This habitat was of sufficiently low relief to be fished by commercial bottom trawlers (Waldo Wakefield, NOAA Fisheries, personal communication, 2006).

3.2. Fish assemblage characterization

The canonical correlation analysis examined 12 groundfish taxa selected by three criteria (Table 1): 1) the seven species with more than 1000 individuals

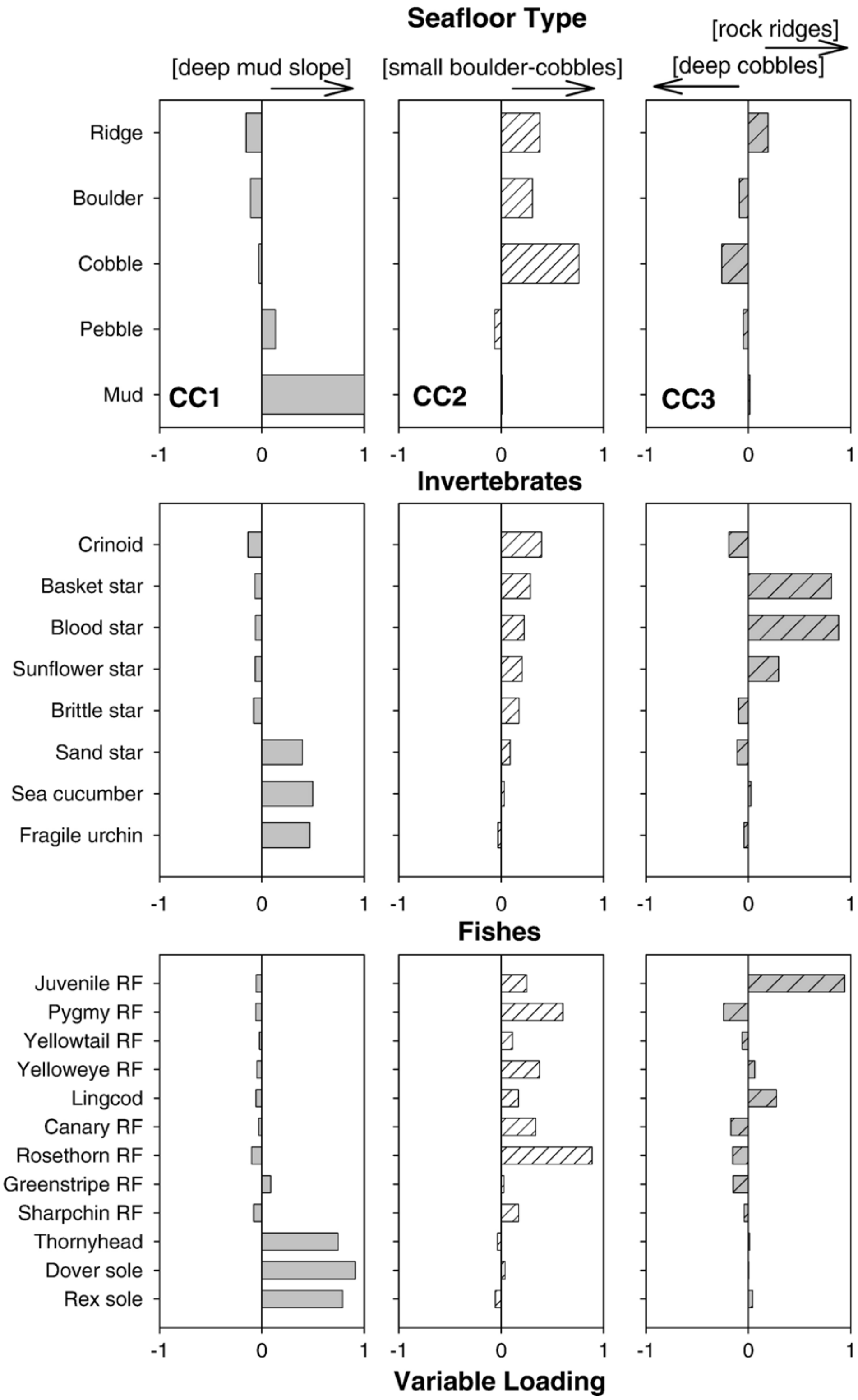

Fig. 4. Variable loadings of seafloor types, invertebrates, and fishes on the two axes of the canonical correlation analysis. The canonical correlation coefficient ($r = 0.89$ for axis 1, $r = 0.68$ for axis 2, $r = 0.59$ for axis 3) measures the overall association between seafloor-type/invertebrate abundance and fish abundance. High positive loadings on axis 1 define a mud habitat with associated invertebrates and fishes. High negative loadings on axis 1 define a general rock habitat, subdivided on axis 2. High positive loadings on axis 2 define a small boulder-cobble habitat with associated species. High positive loadings on axis 3 define a rock ridge habitat with associated species. High negative loadings on axis 3 define a deep-cobble habitat with associated species. Data for analysis were derived from discrete habitat patches for which all variables could be measured ($n = 1058$, see Fig. 3).

observed among all years, excluding cottids and zoarcids (i.e., five rockfishes, shortspine thornyhead, and Dover sole); 2) four commercially harvested and fairly common species (lingcod, canary rockfish, yelloweye rockfish, and rex sole); and 3) juvenile rockfishes (young-of-the-year), none of which could be identified to species (exacerbated by the fact that the submersible's slurp gun could not capture fish). Note that the smallest species of rockfishes, pygmy and Puget Sound, could not be readily distinguished from the submersible and so were pooled. These 12 groundfish taxa accounted for over 94% of all fishes we observed at Heceta Bank from 1988 to 1990.

Considering these key species, the four major habitats defined above were correlated with distinct groundfish assemblages (Fig. 5). In order of generally increasing depth.

3.2.1. Shallow rock ridges and large boulders

This bank-top habitat (less than 100 m deep) supported mostly (in order of decreasing positive loadings on CCA axis 3 in Fig. 4): juvenile rockfishes (<10 cm TL), lingcod, and yelloweye rockfish. Note that most of the juvenile rockfishes in this habitat occurred over patches dominated by boulders (Fig. 5). Over all three years, this habitat supported the highest density of fish (grand average = 2828 fish/hectare), and the second highest species richness (about 51 fish species) of the four major habitats.

When encountered by the submersible, juvenile rockfishes usually were schooled within 2 m of the seafloor and lingcod were usually on the seafloor. Yelloweye rockfish were either on the seafloor or just off the bottom. Schools of juvenile and yellowtail rockfish were huge, sometimes comprising hundreds (if not thousands) of individuals. Yellowtail rockfish did not load strongly on this axis, or any others, due to their broad occurrence across bank seafloor types (Fig. 5). In contrast, lingcod occurred as infrequent individuals averaging 6 dm TL (SD = 2 dm) and ranging up to 1 m TL.

3.2.2. Mid-depth boulder-cobbles

This bank-slope habitat at shallow to intermediate depths (100–150 m) supported mostly (in order of decreasingly positive loadings on CCA axis 2 in Fig. 4): rosethorn rockfish, pygmy/Puget Sound rockfish, yelloweye rockfish, juvenile rockfishes, canary rockfish, lingcod, sharpchin rockfish, and yellowtail rockfish. Over all three years, this habitat supported the second lowest density of fish (grand average = 1451 fish/hectare), and the lowest species richness (about 43 fish species) compared to the other major habitats.

Sharpchin and pygmy/Puget Sound rockfishes sometimes attained nearly uncountable densities in this habitat, occurring in uncommon but dense patches on and within 2 m of the seafloor, often in mixed-species aggregations. In contrast, rosethorn rockfish were rock-habitat generalists, being the most ubiquitous and evenly distributed of all fish species (Fig. 5).

3.2.3. Deep cobbles

This bank-slope habitat at intermediate deep depths (150–200 m) supported mostly (in order of decreasingly negative loadings on CCA axis 3 in Fig. 4): pygmy/Puget Sound rockfish, canary rockfish, rosethorn rockfish, greenstripe rockfish, and sharpchin rockfish. The moderate loadings of mud-bottom associated greenstripe rockfish in this habitat (compare axis 1 positive loadings with axis 3 negative loadings in Fig. 4) was due to the interspersion of mud between patches of cobbles and boulders. Over all three years, this habitat supported the lowest density of fish (grand average = 1369 fish/hectare), and the second lowest species richness (about 45 fish species) compared to the other major habitats.

Greenstripe rockfish were perhaps the most specialized of the rockfishes in terms of microhabitat, almost invariably occurring as one to several individuals sitting on the seafloor near small, isolated rock patches surrounded by mud.

3.2.4. Deep mud slope

This habitat (mostly deeper than 200 m) supported (in order of decreasing positive loadings on CCA axis 1 in Fig. 4): Dover sole, rex sole, shortspine thornyhead, and greenstripe rockfish. Over all three years, this habitat supported the greatest species richness (about 64 fish species), yet the lowest density of fish (grand average = 404 fish/hectare) of the four major habitats.

When encountered by the submersible, the dominant mud-bottom groundfish species were sitting on the seafloor. All these species tended to be evenly and sparsely distributed over mud bottoms, except greenstripe rockfish, which were invariably associated with small patches of rock surrounded by mud. Also present yet relatively uncommon over mud were sablefish (*Anoplopoma fimbria*), zoarcids (eelpouts), agonids (poachers), skates (*Raja* spp.), ratfish (*Hydrolagus colliei*), and hagfishes (*Eptatretus* spp.). Sablefish occurred in actively swimming schools. Zoarcids, agonids, and skates sat on the bottom, and ratfish usually swam slowly within a meter of the seafloor. We observed hagfish in burrows with their heads extended, or curled on the seafloor, or occasionally actively swimming (in several instances consuming dead fish).

3.3. Interannual variation

To examine interannual variation in the distribution and abundance of the 12 key taxa of groundfish, we needed to determine whether the submersible transects (none of which followed identical paths) sampled the same relative abundance of seafloor types among years. In fact, there was little interannual variation in the seafloor

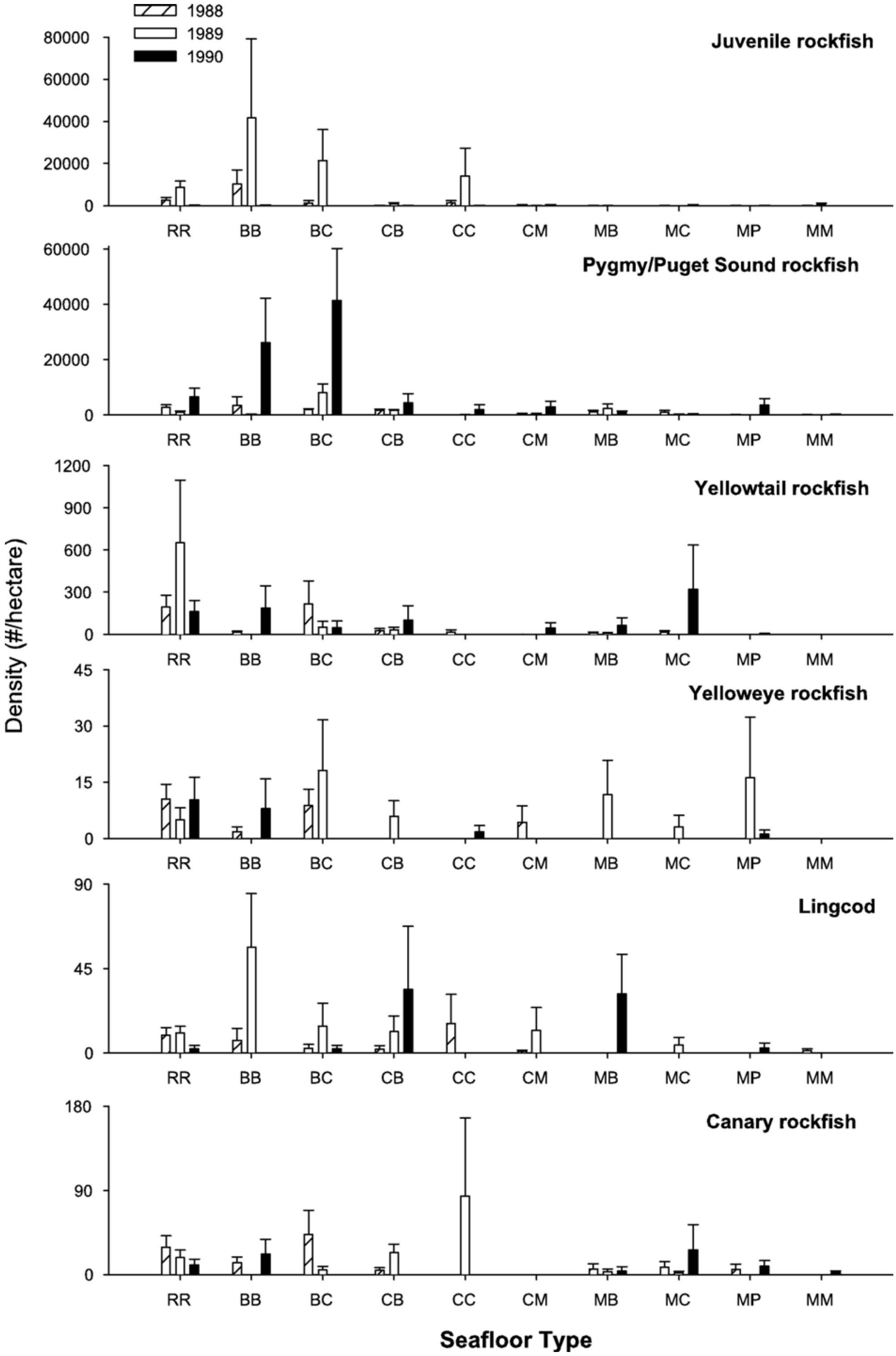

Fig. 5. Densities (mean number/hectare ± 1 SE) of 12 selected fish taxa among the ten dominant seafloor types at Heceta Bank, 1988–1990. Note that the y-axis is scaled differently for each taxa, and that the taxa are ranked by distribution across seafloor types (shallow, rock ridge to deep mud slope). Seafloor types are listed by decreasing relief and particle size, where the first letter is the dominant substratum and the second letter is the second most prevalent substratum: R = rock ridge; B = boulder; C = cobble; P = pebble; M = mud (n = 1058, see Fig. 3).

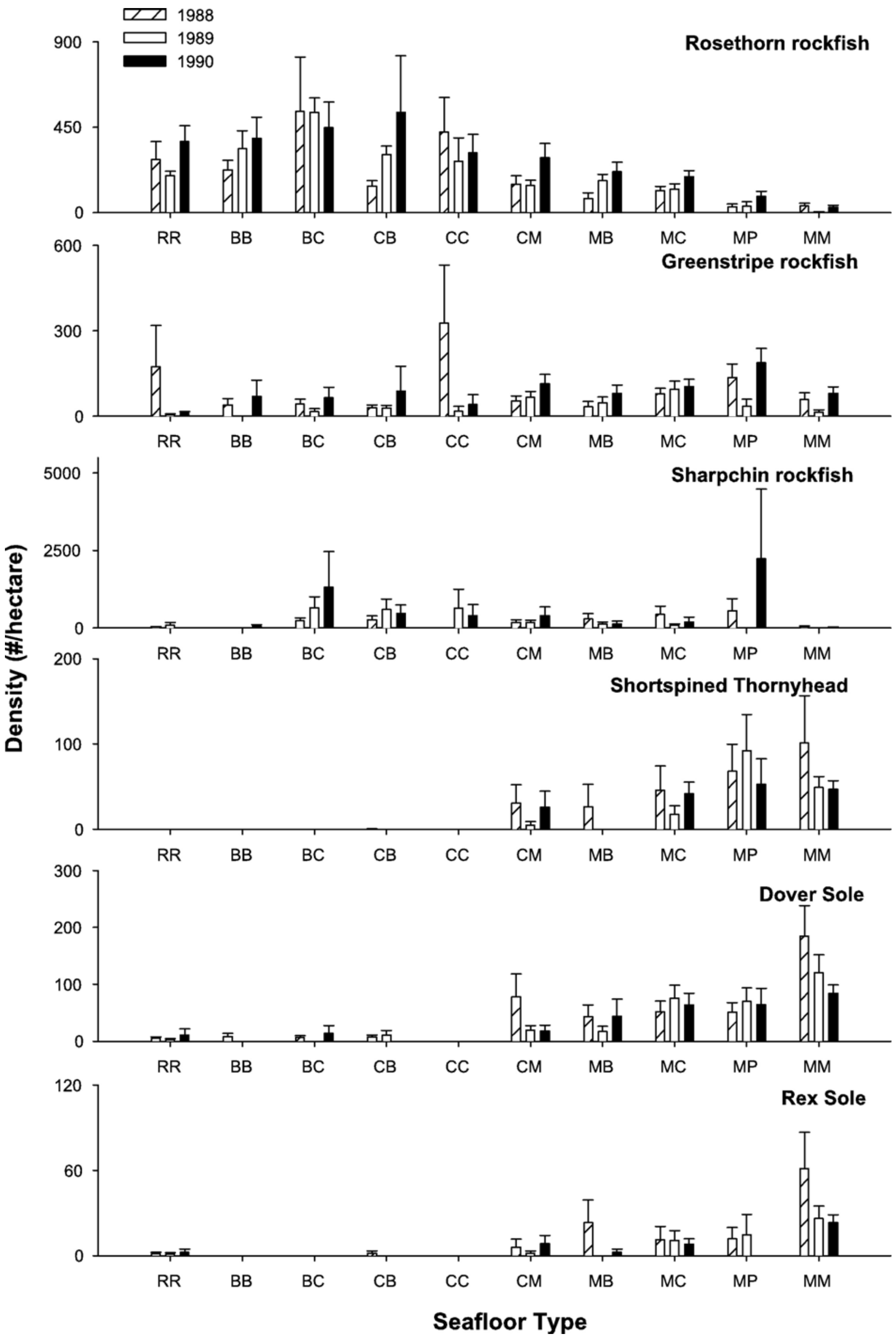

Fig. 5 (*continued*).

types sampled and no significant differences among years in the relative abundances of all 36 seafloor types ($P > 0.05$, Kolmogorov–Smirnov two-sample tests, Fig. 3). Therefore, any among-year differences in fish assemblages we detected could be attributed to interannual variation independent of seafloor type.

Even at a coarse scale of resolution, the overall rank abundances of the 12 key groundfishes (listed in Table 2) were significantly different among years (Kendall's coefficient of rank concordance = 0.271, $P = 0.017$, df = 2). At a finer scale of resolution, due to significant interactions between years and habitats, two-way repeated measure ANOVA of fish densities detected significant differences among years only for juvenile rockfishes (Table 3). Juvenile rockfishes as a group were most abundant in 1989, reaching densities of tens of thousands per hectare, but were nearly absent in 1990. These juveniles occurred mostly over continuous boulders (BB), as well as boulder-cobble (BC) and continuous cobble (CC), all of which appeared to provide numerous refuges. For all other species, there were no other significant interannual differences without habitat interactions, with the minimum detectable difference ranging between 166% (yellowtail rockfish) to 31% of initial abundances (rosethorn rockfish) (Table 3).

In contrast to interannual variation alone, the abundance of pygmy/Puget Sound rockfish, lingcod, and rex sole displayed significant year-habitat interactions, indicating changes in abundance among years associated with changes in distribution across seafloor types (Table 3). Pygmy/Puget Sound rockfish were most abundant in 1990 over boulder-cobble and continuous boulder bottoms. In contrast, they were most abundant on continuous boulders in 1988 and boulder-cobble in 1989 (when they were almost absent on continuous boulders). Lingcod were most abundant on continuous cobbles in 1988, continuous boulders in 1989, and cobble-boulders and mud-boulders (MB) in 1990. Rex sole were most abundant on continuous mud in 1988, but also occurred on mud-boulders. In 1989 and 1990, rex sole were still most abundant on continuous mud, but absent from mud-boulders in 1989 and rare on mud-boulders in 1990 (Fig. 5).

Table 3
Two-way repeated-measure analyses of variance of fish density among years, habitats (seafloor types), and year × habitat interactions at Heceta Bank, 1988–1990 (see Fig. 5), relative to the minimum detectable interannual difference as a percent of initial abundance in 1988

Taxon	*P*-values			% Minimum detectable interannual difference
	Years	Habitats	Years × habitats	
Juvenile rockfishes	0.01	0.05	ns	112
Pygmy/Puget Sound rockfishes	<0.01	<0.01	<0.01	114
Yellowtail rockfish	ns	0.03	ns	166
Yelloweye rockfish	ns	ns	ns	78
Lingcod	ns	0.03	<0.01	83
Canary rockfish	ns	ns	ns	58
Rosethorn rockfish)	ns	0.02	ns	31
Greenstriped rockfish	ns	ns	ns	52
Sharpchin rockfish	ns	ns	ns	174
Shortspined thornyhead	ns	<0.01	ns	58
Dover sole	ns	<0.01	ns	43
Rex sole	ns	<0.01	0.02	55

ns = $P > 0.05$.

Table 2
Mean density (±SE) of fish taxa used in canonical correlation analysis and subsequent analyses, ranked by abundance and pooled across all seafloor types at Heceta Bank over all years

	Total density of fish (number/hectare)		
Taxa	1988	1989	1990
Juvenile rockfishes	2229.9 (960)	6971.7 (2343)	129.4 (64)
Pygmy/Puget Sound rockfishes	1798.9 (539)	1511.0 (433)	6333.7 (1687)
Yellowtail rockfish	97.2 (35)	197.2 (129)	113.8 (54)
Yelloweye rockfish	5.2 (1.5)	5.8 (2.1)	3.5 (1.8)
Lingcod	5.0 (1.7)	9.3 (2.6)	2.8 (1.2)
Canary rockfish	17.9 (5.4)	11.1 (3.4)	9.6 (4.6)
Rosethorn rockfish	199.0 (34.9)	202.5 (15.9)	244.1 (28.4)
Greenstriped rockfish	100.7 (50.1)	27.4 (4.3)	74.9 (9.7)
Sharpchin rockfish	143.0 (31.9)	216.0 (62.5)	391.0 (234)
Shortspine thornyhead	18.0 (5.7)	13.5 (3.2)	22.9 (4.4)
Dover sole	32.9 (6.3)	32.1 (5.9)	39.5 (6.3)
Rex sole	8.1 (2.5)	6.0 (1.7)	7.2 (1.5)

Differences among seafloor types were significant for yellowtail rockfish, rosethorn rockfish, shortspine thornyhead, and Dover sole, indicating significantly different distributions across seafloor types, but no significant interannual variation (Fig. 5). Yellowtail rockfish occurred primarily on rock ridges and mixed boulder bottoms, yet occasional large schools were seen over mud-cobbles (MC). Rosethorn rockfish were very broadly distributed on rocky bottoms, peaking in mixed boulder areas, and were rare in mud-pebble (MP) and continuous mud areas. Shortspine thornyhead and Dover sole were most abundant in mud dominated seafloors that included boulders, cobbles and pebbles. Both also occurred in cobble-mud (CM) areas (Fig. 5).

4. Discussion

The key value of this study is that it serves as a foundation characterizing habitat-specific groundfish assemblages on Heceta Bank in the late 1980s and early 1990s, before the demise of groundfish fisheries in this region became obvious. Shortly after the conclusion of our study in 1990, a report by the Pacific Fisheries Management Council (PFMC, 1991) noted that groundfish catches in the Columbia fisheries area, which includes Heceta Bank, had leveled-off and were increasingly composed of rockfish. Subsequent severe declines in catches and stocks were documented later during the 1990s (Ralston, 1998; Bloeser, 1999; Parker et al., 2000). Therefore, documenting interannual variation in groundfish abundance over specific seafloor habitats at Heceta Bank from 1988 to 1990 provides a valuable basis for future comparisons examining long-term change in this system.

4.1. Habitat-specific fish assemblages

There were four major seafloor habitats and associated macroinvertebrate and groundfish assemblages at Heceta Bank: (1) shallow rock ridges and large boulders, dominated by basket stars, juvenile rockfishes, yelloweye rockfish, and lingcod; (2) mid-depth boulder-cobbles, dominated by crinoids and rosethorn, pygmy/Puget Sound, yelloweye and canary rockfish; (3) deep cobbles, dominated by crinoids, brittle stars and pygmy/Puget Sound, canary, rosethorn and greenstripe rockfish; and (4) deep mud slope, dominated by fragile urchins, shortspine thornyhead, and flatfishes.

Of the 12 taxa of numerically dominant and/or commercially valuable groundfishes analyzed, four species (yelloweye, canary, greenstriped, and sharpchin rockfish) appeared to be habitat generalists because there were no significant differences in the distribution of these species among seafloor types. However, only rosethorn rockfish, and to a lesser extent, greenstripe rockfish, were consistently observed in all 10 seafloor types for all 3 years. The remaining eight key groundfish taxa formed relatively distinct habitat-specific assemblages:

(1) Shallow rock ridges and large boulders: this habitat, occurring at depths less than 100 m, was characterized by supporting most of the juvenile rockfishes, yelloweye rockfish, and lingcod we encountered. We hypothesize that rockfishes utilize shallow boulders as a juvenile nursery that provides: 1) the closest suitable habitat for postlarval/pelagic juvenile settlement from the epipelagic realm; 2) a source of small invertebrate food; and 3) numerous holes, crevices, and large sessile invertebrates for shelter, especially as refuges from predation. This hypothesis is consistent with the observed ontogenetic shift of nearshore rockfish from shallow to deep habitats as they grow (Love et al., 1991). Carlson and Straty (1981), Straty (1987), and O'Connell et al. (1998) also concluded that rocky pinnacles served as nursery habitat for rockfish off southeastern Alaska. Lingcod are overfished piscivores valuable to both commercial and recreational fisheries that may be attracted to shallow boulders because they are likely to feed on the small rockfish that occur there. Tagging studies have revealed that movements of this species are sufficient for such an aggregative response to concentrations of prey (Smith et al., 1990). Given the commercial importance of these species, we conclude that the shallower portions of rocky banks provide truly essential fish habitats that are prime candidates for preservation in marine protected areas (see Yoklavich, 1998; Murray et al., 1999; Parker et al., 2000). Protecting nursery habitats for juvenile rockfish seems especially crucial for replenishing exploited stocks in the region.

(2) Mid-depth boulder–cobbles and (3) deep cobbles: these habitats were characterized by supporting most of the smaller rockfish species we encountered (dominated numerically by pygmy/Puget Sound, rosethorn, greenstripe, and sharpchin rockfish) and the larger canary rockfish. With respect to the smaller species, given that rockfish species occupying shallower reefs typically segregate by depth (Hallacher and Roberts, 1985) and that such segregation has been demonstrated by field experiments to be a result of ongoing interspecific competition (Larson, 1980), there is the question of how four morphologically similar rockfishes can coexist over the same depth range at Heceta Bank. Multivariate analyses have shown that these species tend to partition microhabitats, have divergent jaw morphologies, and consume different prey items (York, 2005). Thus, resource partitioning (sensu Schoener 1974) may possibly be a mechanism minimizing competitive interactions among these species.

(4) Deep mud slope: this habitat was characterized by supporting most of the shortspined thornyhead and flatfishes we encountered. In addition, almost exclusive to this general habitat we observed sablefish, zoarcids, agonids, skates, ratfish, and hagfish. This was the most distinct assemblage of groundfish because of the obvious morphological specializations of most of the resident species, apparent adaptations for exploiting soft bottom habitats.

The first three of the above assemblages comprise subdivisions of the "bottom rockfish assemblage" identified from commercial trawl data by Rogers and Pikitch (1992), whereas our fourth assemblage is directly comparable to their "deepwater Dover sole assemblage." As discussed by Yoklavich et al. (2000, 2002), there is remarkable concordance between the groundfish-habitat assemblages identified off Oregon with those spanning the Pacific coast from Alaska to central California.

4.2. Interannual variation

Although substantial interannual variation in abundance of key groundfish taxa among seafloor types was evident, high variance and significant interaction terms between habitat and year resulted in statistically significant differences among years only in juvenile rockfish. This variance occurred at two levels of resolution: community-level by uniform habitat patches, reported here, and species-level by sampling stations, reported by Hixon et al. (1991). As expected, community-level comparisons by sampling stations were never statistically significant, probably because so many environmental variables were confounded.

Likewise, from the ecologically realistic perspective of community-level analysis of uniform habitat patches using canonical correlation analysis, only variation in the most abundant taxa (juvenile rockfishes) was statistically significant. This variation occurred largely over the boulder-dominated bottoms interspersed between shallow rock ridges where these small fishes were abundant. Juvenile rockfishes were by far most abundant in 1989, whereas the next most abundant rockfish group (pygmy/Puget Sound rockfish) were most abundant in 1990. It is therefore tempting to speculate that the abundant juveniles observed in 1989 grew into the abundant small rockfish species observed a year later, assuming these fish could grow from ca.10 cm TL to ca.20 cm TL in one year. However, the category "juvenile rockfish" almost certainly included more than one species, which we could not separate to species because we could neither identify them visually from the submersible nor capture them. Nonetheless, there was statistically significant order-of-magnitude variation in the recruitment of rockfishes as a group at Heceta Bank during the three years of our study. Such variation in rockfish recruitment has also been noted for inshore species (Love et al., 1991).

Despite high variance precluding significant patterns, there were somewhat concordant habitat-specific temporal trends in the abundance of other shallow rock-ridge and large-boulder groundfishes in that yellowtail rockfish and lingcod were also most abundant in 1989. Because 1989 was not unusual in terms of general oceanographic conditions, it is difficult to speculate on the causes of these trends. Regardless of underlying causation, it appears that interannual variation was most prevalent in the shallower rock-dominated parts of Heceta Bank. Fish assemblages on deeper mud-dominated bottoms appeared to be relatively constant among years.

5. Conclusions

By detecting statistically significant interannual variation in one of the 12 most abundant groundfish taxa sampled, and substantial interannual (and habitat) variation in three of the remaining taxa, there is some evidence of strong interannual variation in some of the major components of the fish assemblages at Heceta Bank, but relatively constancy in others. It is also likely that our low sample sizes, which resulted in relatively large minimum detectable differences, tended to detect no differences among years when additional real differences may have existed. Such interannual variation is typical of demersal fish populations on continental shelves worldwide, despite the fact that the causes of such variability are still elusive (review by Postma and Zijlstra, 1988). Unlike changes in relative abundance, the species composition of the fish assemblages at Heceta Bank did remain constant from year to year. These results provide a valuable measure of natural variation in the densities of the dominant and commercially valuable demersal fishes in the context of the specific geological and biogenic seafloor habitats. As such, these data provide a useful basis of comparison for assessing future trends in regional groundfish stocks.

Acknowledgments

We thank the crews of the Delta and RV William McGaw for logistical support during the surveys. W. H. Barss and S. V. Benech assisted with fish and invertebrate observations, respectively. J. Pirtle created the map in Fig. 1. The manuscript was improved by comments from W. W. Wakefield, H. G. Greene, and three anonymous reviewers. The research was supported by the U. S. Minerals Management Service, Dept. of the Interior, under MMS agreement No. 14-12-0001-30445, and the National Undersea Research Program, West Coast/Polar Programs. **[RH]**

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