Multiscale habitat associations of deepwater demersal fishes off central California

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Abstract—Fish-habitat associations were examined at three spatial scales in Monterey Bay, California, to determine how benthic habitats and landscape configuration have structured deepwater demersal fish assemblages. Fish counts and habitat variables were quantified by using observer and video data collected from a submersible. Fish responded to benthic habitats at scales ranging from cm's to km's. At broad-scales (km's), habitat strata classified from acoustic maps were a strong predictor of fish assemblage composition. At intermediate-scales (m's–100 m's), fish species were associated with specific substratum patch types. At fine-scales (<1 m), microhabitat associations revealed differing degrees of microhabitat specificity, and for some species revealed niche separation within patches. The use of habitat characteristics in ecosystem-based management, particularly as a surrogate for species distributions, will depend on resolving fish-habitat associations and habitat complexity over multiple scales.

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Measuring fish-habitat associations on a number of spatial scales is essential in determining the relative importance of habitat types and landscape configuration in structuring fish assemblages and populations. Many benthic habitat characteristics (e.g., substratum type, depth, relief) are important in explaining the local distribution and abundance patterns of demersal fishes (e.g., Jones and Syms 1998; Stephens et al., 2006). An organism's use of habitat may also change as a function of scale (Wiens, 1989). For example, fishes may make a considerable range of choices about their occupancy of specific habitats and may sample their environment at a range of spatial and temporal scales (Ault and Johnson, 1998; Syms and Jones, 1999). Habitat types (abiotic and biotic), however, are found within a large spatial domain (landscape) in which the configuration and connectivity between neighboring habitat areas may contribute to population structure (Forman, 1995). For example, landscape configuration and the degree of habitat patchiness may modify the distribution and movement of an organism, and the interactions among species (Addicott et al., 1987).

On the U. S. West Coast, demersal fishes, particularly rockfishes (*Sebastes*) are a dominant feature of the benthic ecosystem (Love and Yoklavich, 2006) and are important for both commercial and recreational fisheries (Love, 2006). At broad spatial scales, traditional trawl surveys have documented a range of biogeographical and depth patterns for harvested demersal species (Gunderson and Sample, 1980; Weinberg, 1994; Williams and Ralston, 2002). Less research has been done on the role that benthic habitat variables, such as substratum type and relief, play in explaining the distribution and abundance of either commercial or noncommercial species. Strong relationships between demersal fish species and a range of habitat characteristics, particularly substratum type and abundance of giant kelp, have been identified in shallow (<30 m) coastal waters (Stephens et al., 2006). However, many demersal species in this system, particularly rockfish species, are found over extensive depth ranges beyond those that can safely be investigated with SCUBA (Love et al., 2002). The use of submersibles and remotely operated vehicles (ROVs), with sampling protocols similar to those of nearshore surveys (Stein et al., 1992; Adams et al., 1995; Yoklavich et al., 2000), provides the capabilities to make quantitative *in situ* observations of fish-habitat associations in deepwater (>30 m). Studies in which these tools are employed are also beginning to demonstrate characteristic habitat associations for deepwater demersal fish species (Love and Yoklavich, 2006). The importance of spatial scale in un-

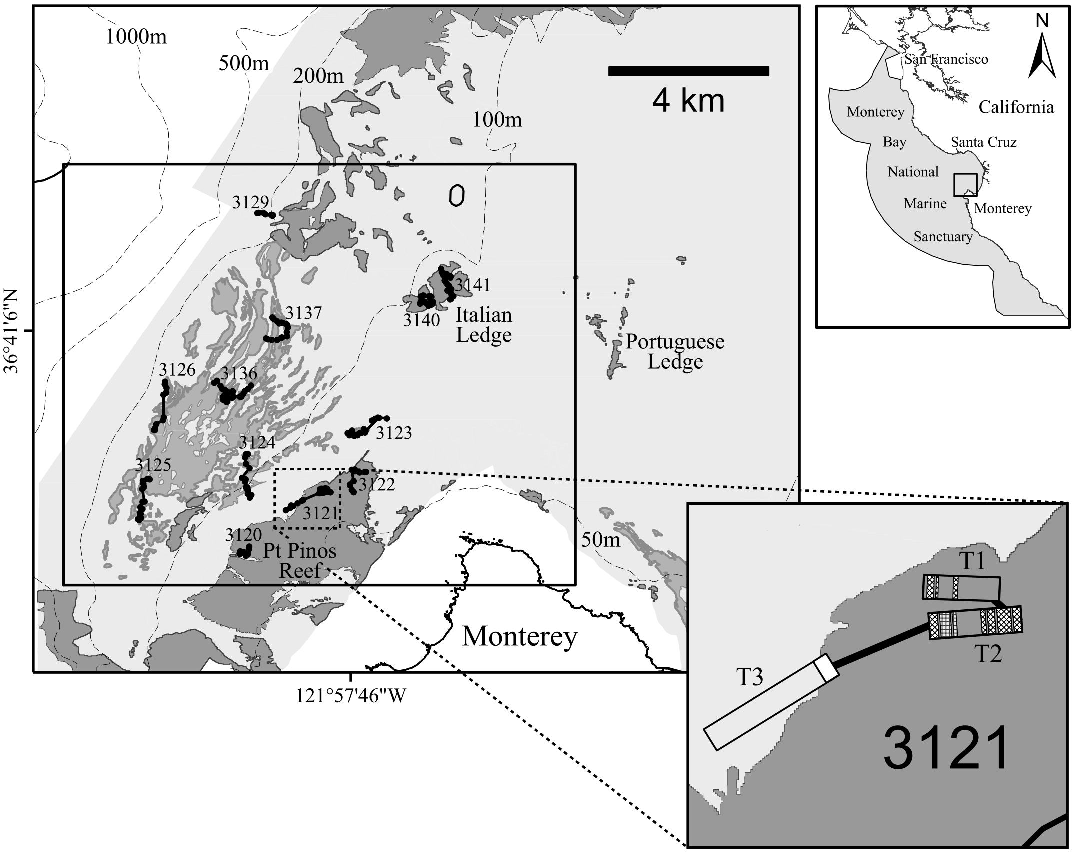

Figure 1

Seafloor map of the continental shelf in southern Monterey Bay, central California, depicting the three acoustically derived broad-scale strata and *Delta s*ubmersible sampling locations (dive numbers 3120–3141). Hard substratum (i.e., complex outcrops) is depicted as dark gray areas. Mixed substratum (areas of hard mixed with soft) is depicted as medium gray areas. Soft substratum (i.e., areas of contiguous soft sediments) is depicted as light gray areas. White areas were not surveyed; box = 10×12 km study area. Bottom insert is an example of the observed intermediate-scale substratum types recorded within the three transects of dive 3121 (depicted by the three rectangles T1=transect 1, T2=transect 2, and T3=transect 3) in relation to the seafloor map of that area. Transects sampled in hard substratum (T1 and T2) were heterogeneous and were composed of mixed patches dominated by rock (dark gray), boulders (diagonal hatching) and cobbles (light gray checks). In contrast, transects run within soft substratum (T3) were more homogeneous, composed of either sand (white) or mud (light gray).

derstanding these associations, however, has received much less attention (Langton et al., 1995).

In this study, we examined the relationship between deepwater demersal fishes and benthic habitat variables at three spatial scales in an area encompassing a proposed marine protected area (MPA) in southern Monterey Bay, California. At the broad spatial scale of km's, habitat strata were identified from acoustic seafloor maps. Within these strata we conducted submersible transects and recorded both benthic habitat variables—such as substratum type, depth, relief, and habitat patchiness—and fish abundance and size. At the intermediate scale of 10–100's of meters, within-transect habitat measures, in combination with fish counts, provided measures of habitat patchiness and fish use of these patches. Finally, we assessed fine-scale or microhabitat (<1 m) fish-habitat associations by recording the habitat type located directly beneath each fish. These multiple spatial scales of habitat association were integrated to examine multiscale habitat and landscape requirements of these species.

Material and methods

Survey of fish habitat

To quantitatively sample demersal fishes and benthic habitats on the continental shelf in southern Monterey Bay (36°E, 121°S) (Fig. 1), *in situ* counts and habitat characterizations were made from the two-person *Delta* submersible. The submersible survey was conducted from 9 through 12 October 1993 (boreal fall), between the hours of 07:30 (1 hour after sunrise) and 17:00 (1 hour before sunset). Thirty-three strip-transects (2 m wide by 10 minutes in duration) were surveyed within a 10 × 12 km study area (Fig. 1). During each transect, the scientific observer made observations from the central starboard porthole while the pilot drove the submersible about 1 m above the seafloor at a speed of 0.4–0.9 knots depending on currents and topography. Three broad-scale strata (hard, mixed, soft substratum), which had been identified from seafloor maps by using geophysical data (Eittreim et al., 2002; Anderson et al., 2005), were sampled at depths ranging from 72 to 252 m.

Within each 10-minute transect, all demersal fishes within 2 m of the submersible were identified to the lowest taxon, measured (total length was visually estimated to 5-cm size classes), and counted vocally by the scientific observer. An external starboard mounted Hi-8 video camera simultaneously recorded the seafloor along each transect and the scientific observers' vocal commentary on the audio track. A hand-held sonar gun was used to gauge transect width, and paired lasers, set 20 cm apart and projected into the observers' field of view, were used to gauge fish size. A *Pisces Video Plus II* data-logger (*Pisces Design*, San Diego, California) superimposed time, date, depth, and altitude of the submersible onto the video image. Final fish sizes and counts were derived from the videotape, by using the audio commentary as supporting information. All video analyses were conducted by the same person to reduce between-observer variability. Individual fish that could not be distinguished to species were assigned to a taxonomic group, for example: to subgenus (e.g., young-of-year *Sebastes* spp. [YOY], *Sebastomus* spp. [rosy-like rockfish species]), genera (e.g., *Citharichthys* spp. [sanddabs], *Zaniolepis* spp. [combfishes]), family (e.g., Agonidae [poachers], Cottidae [sculpins]) or order (e.g., Pleuronectiformes [flatfishes]).

Benthic habitat characteristics within each transect (intermediate scale) were categorized and delineated from the videotape. Substratum composition (rocks, boulders [>25.5 cm], cobbles [6.5–25.5 cm], sand, and mud) within a patch was categorized by using the dominant (primary=>50%) and subdominant (secondary=>20%) percentages of substratum cover used by Stein et al. (1992) and Yoklavich et al. (2000). For example, a patch comprising >50% rock and >20% boulders was classified as rock-boulder (RB); a patch comprising >70% rock was classified as rock-rock (RR). Patches were delineated from videotape where patch duration exceeded 3 seconds of elapsed video time (i.e., where patch size >1.7 m). Habitat relief within each patch was categorized as flat (0–5°), low (5–30°), or high (>30°). These methods adequately defined intermediate scale habitat composition and patchiness within transects (i.e., m's–100's m), yet logistically enabled long transects (max. 585 m) to be quantified. To describe fine-scale (<1 m) microhabitat use by demersal fish species, we recorded the type of substratum (rock, boulders, cobbles, sand, or mud) directly beneath each fish. This multiscale approach enabled habitat associations at each scale to be recorded independently of associations at other scales.

Transect length, independent of submersible speed, was estimated by using the known distance between the lasers (i.e., 20 cm) as a ruler, by counting the number of lengths that occurred sequentially over a 15-s duration within each minute of videotape, and then multiplying by transect duration (i.e., 10 min). Patch lengths were calculated by using the same method but were multiplied by patch duration (elapsed time per patch).

Analysis

The categorical measures of substratum type were recoded as semiquantitative variables. Primary and secondary categories were recoded so that each substratum type within a patch was given a percent cover value of 0%, 20%, 50%, or 70%. For example, rock-rock (RR) was recoded as 70% rock (50%+20%) while all other substratum types scored a value of 0%; similarly boulder-cobble (BC) was recoded as 50% boulder, 20% cobble and all other types scored a value of 0%. Habitat relief was recategorized as an ordinal variable with values of 1, 2, and 3 that corresponded with flat, low, and high relief. The mean and standard error for substratum types and relief, and median depth were then calculated for each transect (broad-scale) and patch (intermediate-scale). Habitat patchiness at the broad-scale was represented by "patch number"—the number of patches within each transect, and "patch size"—calculated as the log(*patch length*) within each transect. Benthic habitat variables, with the exception of patch number and patch size, were $x^{0.5}$ transformed to improve data normality and linearity between variables. Principal components analysis (PCA) was run on the correlation matrix of the transformed transect-level data to evaluate the validity of the broad-scale strata classifications and to describe the relationship between benthic habitat variables over broad spatial scales.

To examine the relationship between fish and habitat, total abundance and species richness were calculated for all fish species and rockfish species at both transect (transect length × 2 m width) and patch (patch length × 2 m) scales: fish densities were then expressed as numbers per 1000 m^2 (transects), and 200 m^2 (patches). To examine the fish assemblage in relation to harvest potential, we classified species as either commercial (e.g., *Sebastes paucispinis* [bocaccio], *S. ruberrimus* [yelloweye rockfish], *S. flavidus* [yellowtail rockfish], *Ophiodon elongatus* [lingcod], and *Microstomus pacificus* [Dover sole]) or noncommercial (e.g., *S. wilsoni* [pygmy rockfish], *Rhinogobiops nicholsii* [blackeyed goby], and *Zaniolepis* spp.). We also categorized fishes as small (≤20 cm) or large (>20 cm). Individual species and taxon groups were included in analyses when they were present in more than 5% of all patches. Consequently, 21 taxa (15 species and six groups) from nine families were retained for analyses. The data on fish distributions were examined by using histograms and Taylor power plots (i.e., log(*variance*) versus log(*mean*)). Data were generally right-skewed and had a positive variance-mean relationship. The slope of the Taylor power plot was used to optimally decouple variance from mean by raising the data to the power of ((2-slope)/2) (McArdle et al., 1990). Consequently, species abundance data were ($x^{0.25}$) transformed, total abundance was transformed by log10(x+1), and a square root ($x^{0.5}$) transformation was applied to species richness. To examine broad-scale relationships between fish species and benthic habitat variables, we ran a canonical correlation analysis on the transect-level data matrix and then plotted the total structure coefficients of the fish in habitat space. The standardized redundancy output values of the model were used to measure the amount of variation for both fish species and benthic habitat variables.

To examine intermediate-scale relationships between fish species and benthic habitat variables, densities of fishes per patch types were examined. However, because all patch types were not equally available, we also standardized patch-use relative to habitat availability (patch selectivity) by subtracting proportional occurrence of each patch type from the proportional abundance for each species. Here, a positive association with a patch type revealed that more individuals were found in that patch type than would be expected given random habitat use (i.e., no selectivity). Conversely, a negative association revealed that fewer individuals were found in that patch type than would be expected by random habitat use. Finally, because microhabitat availability was not measured independently of fish presence, microhabitat use by fishes was restricted to graphical presentation.

Results

Seafloor composition

We sampled 11.15 linear km of seafloor within the 12 × 10 km survey region, using submersible strip-transect methods. At broad-scales, benthic habitat variables were grouped *a posteriori* in order to reliably distinguish hard, mixed, and soft strata (Fig. 2). Hard stratum comprised patchy "high-relief outcrops" of rock, boulders, and sand. In contrast, mixed stratum comprised "low-relief outcrops" of cobbles and mud. Soft stratum comprised "homogeneous mud." The three broad-scale habitat strata also varied in their depth distribution, and strata and depth were strongly collinear. High-relief outcrops were generally shallower (60–100 m) than low-relief outcrops (90–150 m), and although homogeneous mud occurred in most depth ranges, it was the only stratum surveyed in deep offshore locations (80–260 m). Benthic habitat variables within each of the three strata were also strongly collinear. For example, rock always co-occurred with boulders and sand, forming complex high-relief outcrops in shallower water (i.e., <100 m). Therefore, if a species was correlated at broad spatial scales with high-relief outcrops, differentiating the relative importance of substratum composition, depth, or some corequisite would be problematic.

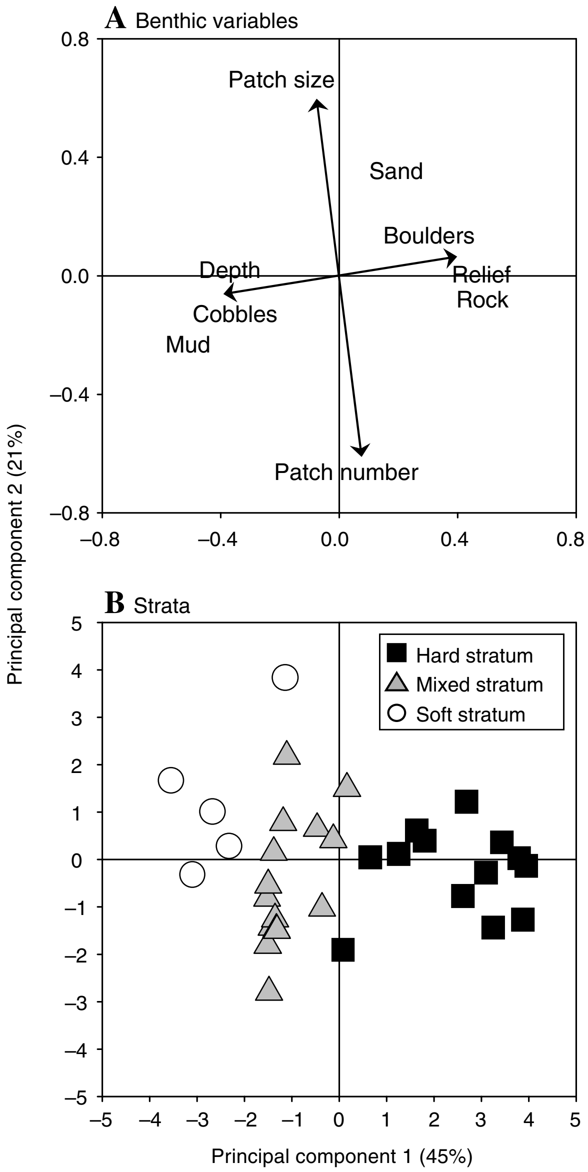

Figure 2

Principal components analysis of broad-scale benthic habitat characteristics: (**A**) correlation matrix of benthic variables; (**B**) projection of strata categories in ordination space.

Variability in intermediate-scale habitat also was discernible (Fig. 3). Five substrata (rock, boulders, cobbles, sand, and mud) were recorded during this survey, which at intermediate scales were present in 21 of 25 possible paired "substratum patch types" (all but mud-sand, cobble-sand, sand-cobble, or sand-mud patches types were recorded). However, the proportional availability of these patch types differed between strata. For example, hard strata contained the highest number of substratum types (n=19), where rock and boulders types were the most abundant (Fig. 3A). Mixed strata also contained a variety of patch types (n=10), but were devoid of rock and contained higher proportions of mud (Fig. 3B). Soft strata contained the fewest patch types (n=3), composed primarily of homogeneous mud, and small amounts of homogeneous sand and mud-cobble patch types (Fig. 3C).

Structure of fish assemblages and broad-scale fish-habitat associations

Sixty-two species of demersal fishes (from 21 families) totalling 21,184 fishes were recorded during this survey. Rockfishes were the most abundant portion of the demersal fish assemblage, representing 93% of all fish sampled (i.e., 24 rockfish species, totalling 19,668 rockfishes). Most fishes recorded (96%) were small (TL ≤20 cm) noncommercial species, dominated by small-bodied (dwarf) rockfishes, such as *S. wilsoni* (n=5857, 28% of all fish sampled), *S. semicinctus* (halfbanded rockfish) (n=5247, 25%), and *S. hopkinsi* (squarespot rockfish) (n=2747, 13%). In comparison, both small (TL ≤20 cm) and large (TL >20 cm) fishes of commercial species and large noncommercial species were uncommon (462 small-size commercial fish (2%); 295 large-size commercial fish (1%); and 79 large-size noncommercial fish (0.4%)).

Fish density and species richness varied between the three broad-scale strata. Hard stratum had the highest density of fish (1357 fishes per 1000 m^2), followed by mixed stratum (862 fishes per 1000 m^2), and both strata were dominated by rockfishes (90%, 98% respectively). Inversely, soft stratum had comparatively few fish (130 fishes per 1000 m^2), dominated by nonrockfish species (63%). Small-size fishes accounted for the majority of demersal fishes within hard (98% of all fish sampled), mixed (99%), and soft (79%) strata. In comparison, large demersal fishes (TL>20 cm) were relatively uncommon in all three substrata; however, the hard stratum had higher densities (27 per 1000 m^2 [2% of all fishes in hard substratum]) than the soft (21 per 1000 m^2 [16%]), or mixed (4 per 1000 m^2 [0.5%]) strata. The mixed stratum had the highest number of species (44 species), where 64% of the species composition comprised nonrockfish species. The hard stratum had slightly fewer species (41 species) but comprised a more even mix of rockfish (54%) and nonrockfish (46%) species. Soft stratum had the fewest species of all three strata (19 species), of which most were nonrockfish species (74%). The number of commercially important species decreased as habitat complexity decreased: 18 commercial species (15 rockfish species) were recorded from hard substratum, compared with 16 (10 rockfish species) in mixed substratum, and 11 (5 rockfish species) in soft substratum.

Assemblage composition varied between the three broad-scale strata (Fig. 4). High-relief outcrops (hard stratum) were characterized by schools of small-bodied rockfishes (*S. hopkinsi*, *S. wilsoni*, and YOY), a suite of large-bodied rockfish (e.g., *S. paucispinis*, *S. flavidus*, *S. rubrivinctus* [flag rockfish], *S. rosaceus* [rosy rockfish], and *Sebastomus* spp.), and a few nonrockfish species (e.g., *R. nicholsii* and *O. elongatus*). Low-relief outcrops (mixed stratum), in contrast, were characterized by schools of the small-bodied rockfish, *S. semicinctus*, two large-bodied rockfishes (*S. chlorostictus* [greenspotted rockfish] and *S. elongatus* [greenstriped rockfish]), and a variety of nonrockfish species (e.g., *Citharichthys* spp., *Zalembius rosaceus* [pink seaperch], *Zaniolepis* spp. [combfishes], *Argentina sialis* [Pacific argentine], and *O. elongatus*). Homogeneous mud areas (soft stratum) differed from high-relief and low-relief outcrops

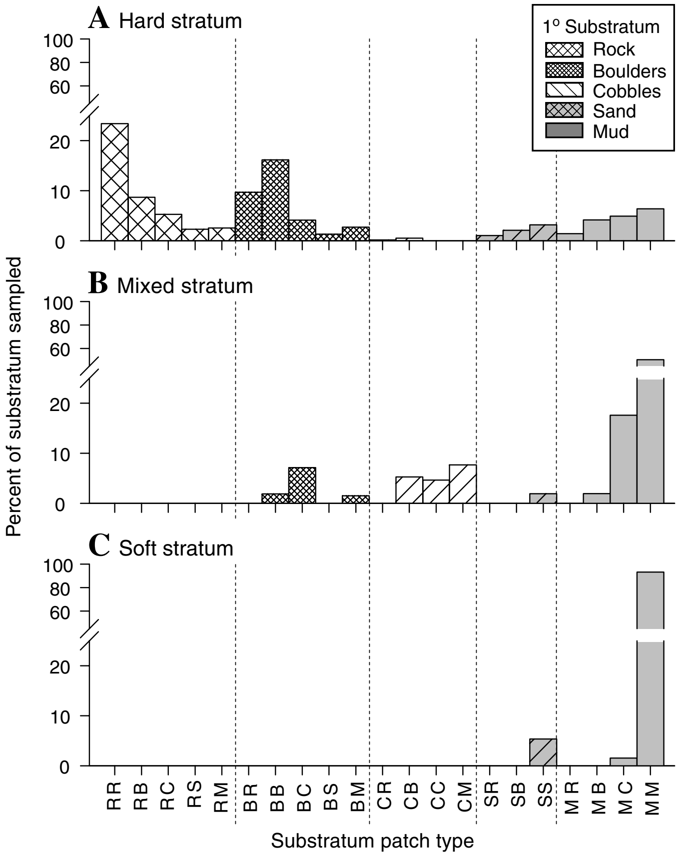

Figure 3

Intermediate-scale habitat characteristics: substratum patch composition within the three broad-scale habitat strata: (**A**) hard stratum, (**B**) mixed stratum, and (**C**) soft stratum. Substratum types recorded were R=rock, B=boulders, C=cobbles, S=sand, and M=mud. The first and second letters of each patch type (e.g., RR, RB, RC, to MM) represent primary (50%) and secondary (20%) substratum types, respectively.

by the characteristic presence of Pleuronectiformes and Agonidae.

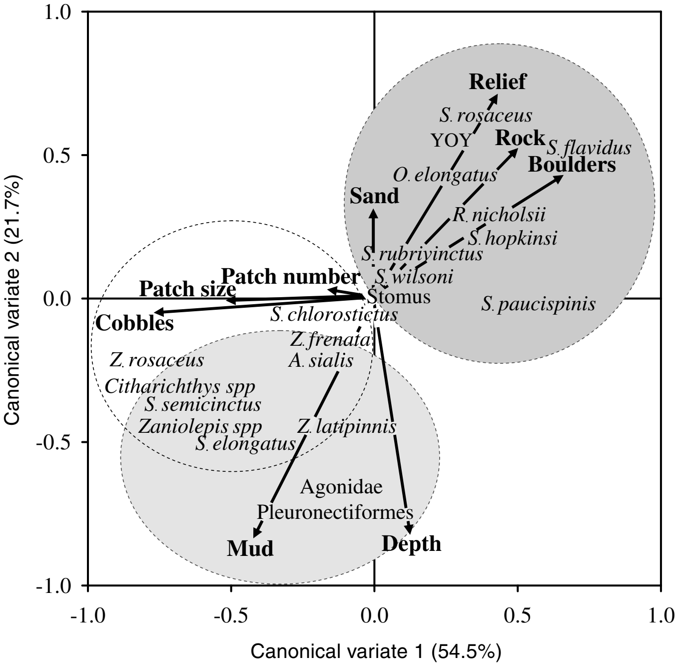

Figure 4

Broad-scale associations of the demersal fish assemblages with benthic habitat variables as discerned from canonical correlation analysis. Circles depict the three broad-scale strata (dark gray=hard, white=mixed, light gray=soft sediment), and are presented to assist in the visual association of species and benthic habitat variables. Vectors are the eigenvectors of the benthic habitat variables. YOY = young-of-year *Sebastes* spp., "Stomus" = *Sebastomus* spp.; *S = Sebastes; R = Rhinogobius; O = Ophiodon; Z = Zaniolepis; and A = Argentina.*

Intermediate- and fine-scale fish-habitat associations

At the level of the individual fish species, a range of benthic habitat variables and spatial scales were important in explaining species-specific distributions. Intermediate-scale information on patch use, patch selectivity, along with fine-scale microhabitat use, revealed four types of species-specific groups (Fig. 5–8).

The first group, rock and boulder associates (e.g., *S. hopkinsi*, *S. flavidus*, and *S. paucispinis*) were species that at the intermediate-scale were strongly associated with patches of rock or boulders (or both) (Fig. 5). At the fine-scale, these three species were found on or above rocks (69%, 76%, and 30%, respectively) or boulders (28%, 24%, and 18%, respectively); *S. paucispinis* also used mud microhabitats (52%).

The second group, generalists (e.g., *S. wilsoni*, *S. rosaceus*, and *O. elongatus*) were species that at the intermediate-scale were associated with a variety of patch types (Fig. 6). However, when standardized by habitat availability, these species were strongly associated with patches of boulders, cobbles, and to a lesser extent, rock, and were negatively associated with patches of homogeneous mud. At the fine-scale, these species were also found on or above all possible microhabitat types and showed a flexibility in habitat use at all three spatial scales. Ontogenetic shifts in habitat use also were indicated. For example, small *O. elongatus*, (<25 cm; *n*=54) were more abundant in patches with mud or cobbles (e.g., 74% in mud-mud [MM], cobble-boulder [CB], and mud-cobble [MC]), whereas medium-size *O. elongatus* (25–50 cm; *n*=57) were found more frequently in patches with boulders (40%) and rock (32%). Larger individuals (>50 cm; *n*=6), on the other hand, were found in patches of rock (83%), indicating that *O. elongatus* move from mixed mud and cobble habitats to more complex rocky outcrops as they grow.

The third group, cobble-mud associates (e.g., *S. semicinctus*, *S. chlorostictus,* and *S. elongatus*) were species that at the intermediate-scale were found in patches containing various mixtures of cobbles, mud, and to a lesser extent, boulders (Fig. 7). At the fine-scale, these species were found over mud (66%, 54%, and 81%, respectively) or low-relief cobbles and boulders (pooled 33%, 47%, and 16%, respectively) indicating that mud habitats adjacent to or within mixed cobble-mud areas had inherent properties above either habitat in isolation.

Finally, the fourth group, soft-sediment associates (e.g., Pleuronectiformes, Agonidae, *Citharichthys* spp., and *R. nicholsii*) were species that at the intermediate-scale were strongly associated with patches containing mud or sand (Fig. 8). Pleuronectiformes, Agonidae, and *Citharichthys* spp. were all associated with homogeneous soft sediments at all spatial scales (Fig. 8, A–C). In contrast, *R. nicholsii* were found in a range of soft-sediment patch types (e.g., sand-boulder [SB], sand-sand [SS], mud-rock [MR], mud-boulder [MB], etc.) and microhabitats. However, homogeneous soft-sediment areas had few or no *R. nicholsii* (Fig. 8D), indicating that, for this species, sediment gaps within a rocky outcrop matrix had inherent properties above either rock or sediment habitats in isolation.

Discussion

The composition, complexity, and configuration of the seafloor at multiple scales allowed us to predict assemblage structure and species distributions across the continental shelf within southern Monterey Bay. Broad-scale habitat strata, which are routinely mapped by acoustic methods, showed clear distinctions in assemblage structure. Hard stratum, composed of high-relief outcrops, was occupied by a diverse range of demer-

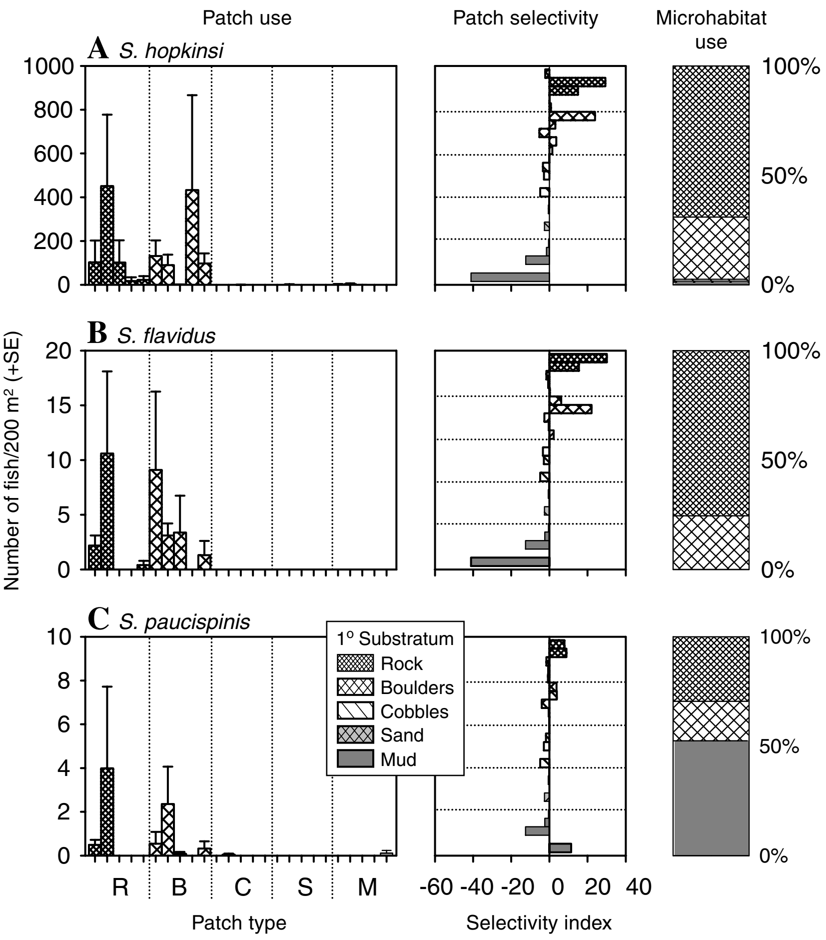

Figure 5

Intermediate and fine-scale habitat use by rock and boulder associates: (**A**) squarespot rockfish (*Sesbastes hopkinsi*) (**B**) yellowtail rockfish (*S. flavidus*), and (**C**) bocaccio (*S. paucispinis*). At the intermediate-scale, patch types (i.e., R=rock, B=boulders, C=cobbles, S=sand, and M=mud) are represented by primary (tick labels and shading) and secondary (sequence of ticks within each primary category R, B, C, S, and M) substratum categories and are ordered from hard (left=rock-rock [RR], rock-boulder [RB], rock-cobble [RC]…) to soft (right = … mud-cobble [MC], mud-sand [MS], mud-mud [MM]) substratum types. "Patch use" depicts the mean number of fish plus standard errors (SE) found in each patch type. "Patch selectivity" depicts the relative patch use by fish, standardized by patch availability: graphs indicate positive (right-hand side of the plot) or negative (left-hand side of the plot) associations with patch types (ordered from hard (top=RR, RB, RC…) to soft (bottom= … MC, MS, MM) substratum types) and the relative strengths of these associations. Fine-scale microhabitat use is represented by the proportion of fish found on or above a particular substratum type.

sal fish species dominated by small rockfish species. Although hard stratum was the least common of the three strata (Anderson et al., 2005), it supported the highest overall densities of fish, including more commercial species, than either mixed or soft strata. High fish densities, a dominance of small rockfish species, and the presence of large commercial species over high-relief outcrops have been recorded in other submersible surveys in California (Yoklavich et al., 2000, 2002), Oregon (Stein et al., 1992), Washington (Jagielo et al., 2003), British Columbia (e.g., Murie et al., 1994), and Alaska (O'Connell and Carlile, 1993). For example, Yoklavich et al. (2000) found high numbers of large commercially important rockfish species (e.g., *S. paucispinis*, *S. ruberrimus*, *S. levis* [cowcod]) associated with discrete rocky outcrops in a submarine canyon

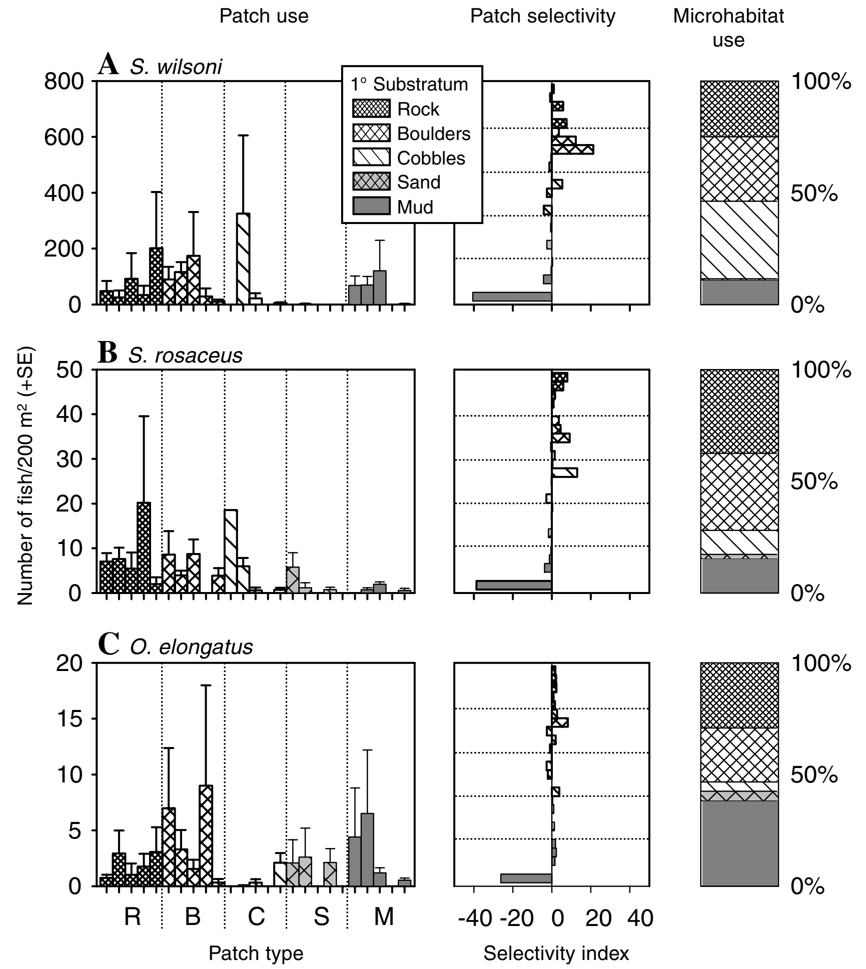

Figure 6

Intermediate and fine-scale habitat use by species that are habitat generalists: (**A**) pygmy rockfish (*Sebastes wilsoni*), (**B**) rosy rockfish (*S. rosaceus*), and (**C**) lingcod (*O. elongates*). Symbols and interpretation are given in Figure 5.

off central California. Jagielo et al. (2003) compared trawlable and untrawlable habitats off Washington and found rockfishes (*Sebastes helvomaculatus* [rosethorn rockfish], *S. rubberimus*, *S. flavidus*, *Sebastes nigrocinctus* [tiger rockfish], and *Sebastes* spp.) were three times more abundant in untrawlable habitats. In more complex habitat systems, Stein et al. (1992) found high densities of juvenile *Sebastes* spp. and *S. flavidus* on the tops of high-relief rocky pinnacles on Heceta Bank, Oregon, whereas in the Gulf of Alaska, O'Connell and Carlile (1993) found the commercially important *S. rubberimus* in highest densities in complex habitats.

Mixed stratum, characterized by lower complexity and relief than areas of hard stratum, also comprised a distinctive demersal fish assemblage with high numbers of species. High diversity in these areas resulted from a combination of species unique to the mixed stratum (e.g., *S. semicinctus*), and species characteristic of both hard (e.g., *S. wilsoni*, *O. elongatus*, *S. rosaceus*) and soft (e.g., Pleuronectiformes and Agonidae) strata. In addition to high diversity, some species (e.g., *S. chlorostictus*, *S. elongatus*, and *Z. frenata*) were also more abundant in the mixed stratum, indicating that some inherent property of heterogeneous habitats (e.g., multiple resource needs, higher levels of habitat fragmentation, and interface zones) may be important to these species. Similar findings have been reported in other submersible surveys. Stein et al. (1992), for example, found more species and higher densities of these species (e.g., *S. chlorostictus*, *S. wilsoni*) in patches with either "mud and boulder" or "mud and cobble" than in patches with mud, boulders, or cobbles in isolation. Species use of interface regions can also be inferred from previous studies even though habitat use at the microscale was not explicitly measured. For example, both Richards (1986) and Pearcy et al. (1989) reported higher numbers of *S. elongatus* in soft sediment areas adjacent to rocks. Similarly, Yoklavich et al. (2002) found that

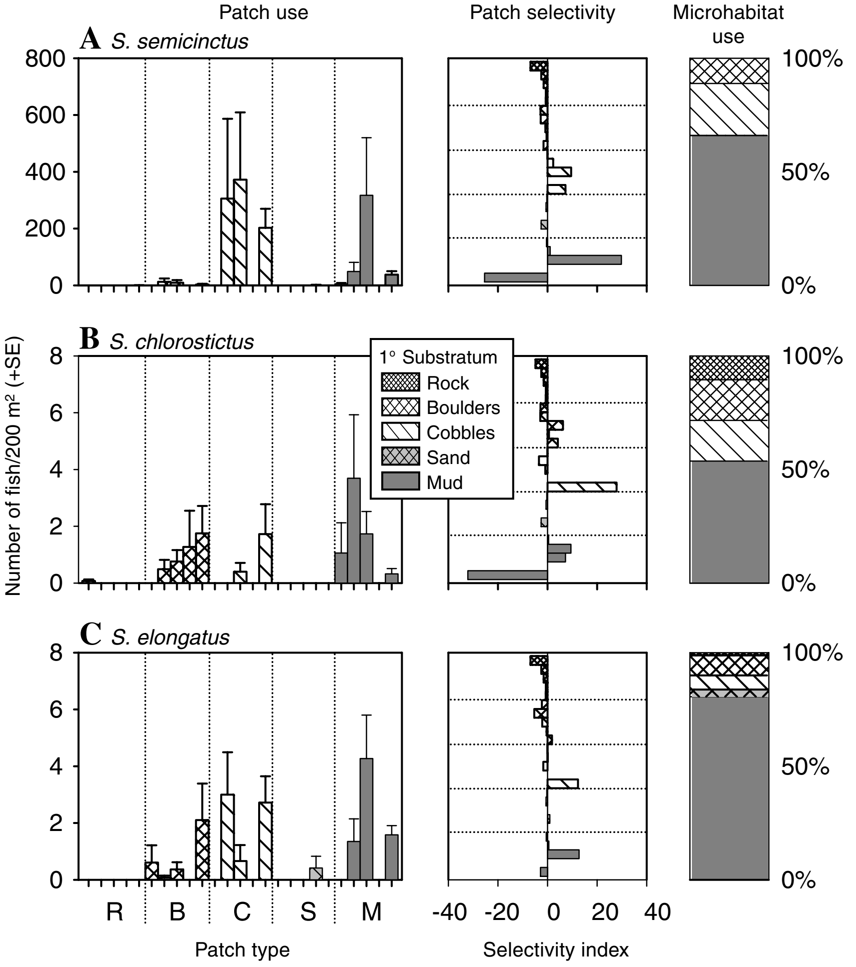

Figure 7

Intermediate and fine-scale habitat use by cobble-mud associates: (**A**) halfbanded rockfish (*Sebastes semicinctus*), (**B**) greenspotted rockfish (*S. chlorostictus*), and (**C**) greenstriped rockfish (*S. elongates*). Symbols and interpretation are given in Figure 5.

S. chlorostictus, along with other species, used habitats comprising a combination of rock and mud.

Soft substratum had the lowest habitat complexity and the lowest diversity and density of fishes of all three strata, although many of these species, particularly the Pleuronectiformes, are important commercial species. Stein et al. (1992), Yoklavich et al. (2000, 2002), and Jagielo et al. (2003) also recorded similar demersal fish assemblages in flat mud habitats (i.e., Pleuronectidae, namely *M. pacificus*, *Glyptocephalus zachirus* [rex sole], and *Lyopsetta exilis* [slender sole]), Agonidae, *Sebastes saxicola* [stripetail rockfish], Zoarcidae [eelpouts], and *Sebastolobus* spp. [thornyhead species]). Although demersal fish assemblages over trawlable habitats have been well documented by traditional fishery methods (e.g., Weinberg et al., 2002), biases in catchability between strata (because trawls may snag in complex habitats) mean that differences in fish assemblage structure between soft, mixed, and hard strata have been difficult to identify. Although *in situ* submersible surveys facilitate these types of comparisons, some biases may still be present. For example, soft-sediment habitats reported in submersible studies (e.g., Stein et al., 1992; O'Connell and Carlile, 1993; Yoklavich et al., 2002) are often adjacent to, at the base of, or in the general vicinity of rock outcrops. As a result, it is unclear how the proximity of hard structure influences demersal fish composition and abundance, or whether these habitats are representative of soft-sediment areas where rock outcrops are not present. The analysis of submersible transects in relation to distance from rocks, or alternatively trawl surveys that include video or acoustic images of the benthos, may help to clarify these patterns.

All three spatial scales provided valuable information on how demersal fish species use benthic habitats.

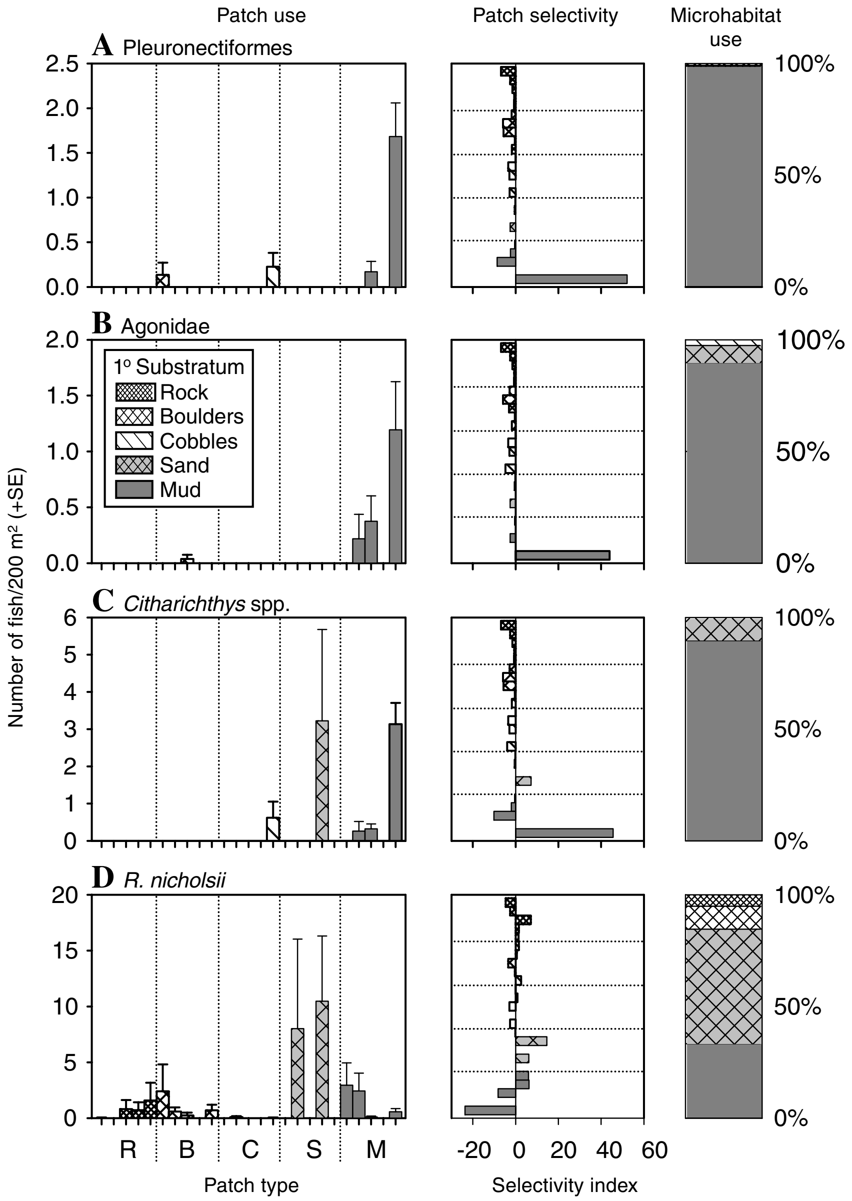

Figure 8

Intermediate and fine-scale habitat use by soft-sediment associates: (**A**) flatfishes, Pleuronectiformes, (**B**) poachers, Agonidae, (**C**) sanddabs, *Citharichthys* spp., and the blackeyed goby (*Rhinogobiops nicholsii*). Symbols and interpretation are given in Figure 5.

For example, broad-scale strata supported characteristic fish assemblages. However, at intermediate scales (within a strata), species distribution varied by patch composition, patch size, and the neighborhood of surrounding patches. At fine scales, microhabitat use by fishes indicated which portions of habitat-patches were actually used (e.g., species A in cobbles and species B in mud, where both species were present within the same cobble-mud patch). A vital aspect of using a multiscaled approach, however, was that information from each spatial scale could then be integrated to examine the relative importance of habitat types and their structural configuration, and this information also indicated that for some species the landscape context was important. For example, *R. nicholsii* was mainly found on sand or at the interface between sand and rock (microhabitat use), but these microhabitats were located within a range of rock and sediment patch types (intermediate-scale), which in turn were located within the complex hard stratum (broad-scale). This structure indicated that for *R. nicholsii* sediment gaps within or adjacent to a rocky landscape were required.

On the other hand, *S. chlorostictus* and *S. elongatus* were both more abundant in the mixed stratum than in the hard stratum (broad scale) and were present together within mixed boulder, cobble, and mud substrata (intermediate scale). At fine scales, however, microhabitat use by these species differed; *S. elongatus* was common in the mud portion of these patches and *S. chlorostictus* was common over boulders and cobbles. These findings indicated that both species were interface associates, but within these interface regions different substratum types were used. The inclusion of microhabitat information within this multiscale approach provided a more comprehensive understanding of how demersal fish use benthic substrata. However, recording microhabitat use for each fish (n=21,184 fishes) was time consuming and therefore would likely negate its use in some studies. A recommended alternative method for recording microhabitat use might be to measure microhabitat use for a subset of fish per species, where subsamples are selected unbiasedly from the overall sample pool.

The ability to describe and predict fish-habitat relationships, as identified in this study, can be used to address area-based management concerns in several ways. For example, species captured by benthic trawl and long-line gear could be used to infer the presence of seafloor substratum types. Although this form of information is not novel, our study provides detailed quantitative species-habitat associations that validate this approach. For example, a benthic trawl that captures Pleuronectidae, Agonidae, *S. semicinctus*, *S. chlorostictus*, and *S. elongatus*, would indicate that the area trawled encompassed multiple strata (e.g., one or more areas of low-relief outcrop and homogenous mud). However, the proportions and spatial configuration of these strata would not be known unless a video camera, for example, was mounted on a benthic trawl (e.g., Abookire and Rose, 2005), or a seafloor substrata map was available for the area (e.g., Bellman et al., 2005).

Conversely, habitat could be used to predict community structure and species distributions. In this study, substratum type was a good indicator of distribution and abundance of many commercial and noncommercial fish species. However, the spatial arrangement and degree of habitat patchiness, in addition to substratum type, also were important predictive variables. Consequently, although areal estimates of substrata are likely to be effective for modeling the abundance and distribution of certain species (e.g., *S. rosaceus* and *S. flavidus*), accurately estimating other species will require additional knowledge of the spatial arrangement of these substrata. For example, species associated with sediment-rock interfaces, such as *S. chlorostictus*, *S. elongatus*, and *Z. frenata,* are likely to be modeled more effectively by estimating the perimeter of either an outcrop or specific habitat type. Likewise, the ability to model gap-associate species, such as *R. nicholsii*, will require information on the availability of sediment-outcrop interfaces and sediment gaps within an outcrop matrix. For other species, such as young-of-year rockfish, a measure of habitat patchiness, in combination with areal estimates of substrata, may be required. The ability to map this level of habitat detail will depend to a large degree on a trade-off between data acquisition and resolution of the mapping tools used, and the amount of seafloor needed to be mapped (Anderson et al., 2005).

In conclusion, the overall success of area-based management strategies will reflect the ability of researchers to accurately measure the functional relationships between organisms and their habitat. Multiscale *in situ* surveys, such as this one, undertaken in multiple locations, in combination with larger-scale fishery surveys can improve our understanding of the role of benthic habitats in structuring demersal fishes across the broader U. S. West Coast. These insights, in turn, improve our ability to characterize and map essential fish habitat, estimate habitat availability, and predict multispecies distributions and habitat associations within specified areas such as marine protected areas. Importantly, this study also provides a quantitative baseline of demersal fish assemblage structure for both commercial and noncommercial species, which is critical for future comparisons of spatiotemporal abundance, diversity, and habitat use. This baseline is also vital for assessing the effects and value of increased protection of West Coast shelf ecosystems.

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Literature cited

Abookire, A. A., and C. S. Rose.
2005. Modifications to a plumb staff beam trawl for sampling uneven, complex habitats. Fish. Res. 71: 247–254.

Adams, P. B., J. L. Butler, C. H. Baxter, T. E. Laidig, K. A. Dahlin, and W. W. Wakefield.
1995. Population estimates of Pacific coast groundfishes from video transects and swept-area trawls. Fish. Bull. 93:446–455.

Addicott, J. F., J. M. Aho, M. F. Antoun, D. K. Padilla, J. S. Richardson, and D. A. Soluk.
1987. Ecological neighbourhoods: scaling environmental patterns. Oikos 49:340–346.

Anderson, T. J., M. M. Yoklavich, and S. L. Eittreim.
2005. Linking fine-scale groundfish distributions with large-scale seafloor maps: Issues and challenges of combining biological and geological data. *In* Benthic habitats and the effects of fishing (P. W. Barnes, and J. P. Thomas, eds.), p. 667–678. Am. Fish. Soc. Symp. 41, Bethesda, MD.

Ault, T. R., and C. R. Johnson.
1998. Spatially and temporally predictable fish communities on coral reefs. Ecol. Monogr. 68:25–50.

Bellman, M. A., S. A. Heppell, and C. Goldfinger.
2005. Evaluation of a US west coast groundfish habitat conservation regulation via analysis of spatial and temporal patterns of trawl fishing effort. Can. J. Fish. Aquat. Sci. 62:2886–2900.

Eittreim, S. L., R. J. Anima, and A. J. Stevenson.
2002. Seafloor geology of the Monterey Bay area continental shelf. Mar. Geol. 181:3–34.

Forman, R. T. T.
1995. Land mosaics: the ecology of landscapes and regions, 632 p. Cambridge Univ. Press, Cambridge, U.K.

Gunderson, D. R., and T. M. Sample.
1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42:2–16.

Jagielo, T., A. Hoffmann, J. Tagart, and M. Zimmermann.
2003. Demersal groundfish densities in trawlable and untrawlable habitats off Washington: implications for the estimation of habitat bias in trawl surveys. Fish. Bull. 101:545–565.

Jones, G. P., and C. Syms.
1998. Disturbance, habitat structure and the ecology of fishes on coral reefs. Aust. J. Ecol. 23:287–297.

Langton, R. W., P. J. Auster, and D. C. Schneider.
1995. A spatial and temporal perspective on research and management of groundfish in the Northwest Atlantic. Rev. Fish Sci. 3:201–29.

Love, M. S.
2006. Subsistence, commercial, and recreational fisheries. *In* The ecology of marine fishes: California and adjacent waters (L. G. Allen, D. J. Pondella, and M. H. Horn, eds.), p. 567–594. Univ. California Press, Berkeley, CA.

Love, M. S., and M. Yoklavich.
2006. Deep rock habitats. *In* The ecology of marine fishes: California and adjacent waters (L. G. Allen, D. J. Pondella, and M. H. Horn, eds.), p. 411–427. Univ. California Press, Berkeley, CA.

Love, M. S., M. Yoklavich, and L. Thorsteinson.
2002. The rockfishes of the northeast Pacific, 405 p. Univ. California Press, Berkeley and Los Angeles, CA.

McArdle, B. H., K. J. Gaston, and J. H. Lawton
1990. Variation in the size of animal populations: patterns, problems and artifacts. J. Anim. Ecol. 59: 439–454.

Murie, D. J., D. C. Parkyn, B. G. Clapp, and G. G. Krause.
1994. Observations on the distribution and activities of rockfish, *Sebastes* spp., in Saanich Inlet, British Columbia, from the *Pisces IV* submersible. Fish. Bull. 92:313–323.

O'Connell, V. M., and D. W. Carlile.
1993. Habitat-specific density of adult yelloweye rockfish *Sebastes ruberrimus* in the eastern Gulf of Alaska. Fish. Bull. 91:304–309.

Pearcy, W. G., D. L. Stein, M. A. Hixon, E. K. Pikitch, W. H. Barss, and R. M. Starr.
1989. Submersible observations of deep-reef fishes of Heceta Bank, Oregon. Fish. Bull. 87:955–965.

Richards, L. J.
1986. Depth and habitat distributions of three species of rockfish (*Sebastes*) in British Columbia: observations from the submersible PISCES IV. Environ. Biol. Fishes 17:13–21.

Stein, D. L., B. N. Tissot, M. A. Hixon, and W. H. Barss.
1992. Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. Fish. Bull. 90:540–551.

Stephens, J. S. Jr., R. J. Larson, and D. J. I. Podella.
2006. Rocky reefs and kelp beds. *In* The ecology of marine fishes: California and adjacent waters (L. G. Allen, D. J. Pondella, and M. H. Horn, eds.), p. 227–252. Univ. California Press, Berkeley, CA.

Syms, C., and G. P. Jones.
1999. Scale of disturbance and the structure of a temperate fish guild. Ecology 80:921–940

Weinberg, K. L.
1994. Rockfish assemblages of the middle shelf and upper slope off Oregon and Washington. Fish. Bull. 92:620–632.

Weinberg, K. L., M. E. Wilkins, F. R. Shaw, and M. Zimmermann.
2002. The 2001 Pacific west coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, and length and age composition. NOAA Tech. Memo. NMFS-AFSC-128, 140 p.

Wiens, J. A.
1989. Spatial scaling in ecology. Funct. Ecol. 3:385–397.

Williams, E. H., and S. Ralston.
2002. Distribution and co-occurrence of rockfishes (family: Sebastidae) over trawlable shelf and slope habitats of California and southern Oregon. Fish. Bull. 100:836–855.

Yoklavich, M. M., G. M. Cailliet, R. N. Lea, H. G. Greene, R. M. Starr, J. de Marignac, and J. Field.
2002. Deepwater habitat and fish resources associated with the Big Creek Marine Ecological Reserve. CalCOFI Rep. 43:120–140.

Yoklavich, M. M., H. G. Greene, G. M. Cailliet, D. E. Sullivan, R. N. Lea, and M. S. Love.
2000. Habitat association of deep-water rockfishes in a submarine canyon: an example of a natural refuge. Fish. Bull. 98:625–641.