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SMALL-SCALE ANALYSIS OF FISH AND HABITAT
RELATIONSHIPS OFF CENTRAL CALIFORNIA

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories
and the Department of Biology
San Jose State University

In Partial Fulfillment

of the Requirements for the Degree
Master of Science

by

Jeffrey Michael Field

August 2005

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ABSTRACT

SMALL-SCALE ANALYSIS OF FISH AND HABITAT RELATIONSHIPS OFF CENTRAL CALIFORNIA

by Jeffrey Michael Field

This study compared fish distributions to available habitats at two spatial scales in the Big Creek Ecological Reserve, California. At the microspatial (1 - 10 m) scale, relationships between fishes and habitats were assessed using logistic regression. At the macrospatial (10 - 100 m) scale, Index of Habitat Electivity (IHE) and Habitat Utilization Index (HUI) were used to assess habitat associations and were verified using Habitat Utilization Analysis (HUA). Nine species had significant relationships with specific seafloor substrata. Other habitat parameters, including habitat patch area, depth, and slope, were also identified as important factors affecting fish distributions. Three shallow (<100m) and three deep (>100 m) habitat guilds (Mixed, Hard, and Soft) were developed based on relationships between fishes and their habitat. The above methods detected habitat associations among fishes at both spatial scales and can be used to predict the presence of a species based on the available habitat.

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INTRODUCTION

Many marine fish populations are experiencing severe declines as a result of intensified fishing efforts (Roughgarden and Smith 1996, Jackson *et al.* 2001, Jackson 2001). This trend has prompted review of traditional fishery management plans and regulations, which focus primarily on individual species or small groups of congeneric species and do not address species-specific habitat and the potential impacts of fishing activity to fish habitat (Friedlander *et al.* 1999, NRC 2002). One of the significant impacts of commercial fishing is modification of the seafloor, which reduces complexity and removes structural features (Thrush *et al.* 1998). This alteration of the seafloor results in the loss of habitat and may amplify mortality and emigration rates and decrease fish productivity in an impacted area. Alternative fishery management schemes have been proposed to establish protective measures for fishes and their habitats from some of the fishing impacts listed above.

As an impetus toward alternative management strategies, the 1996 reauthorization of the federal Magnuson-Stevens Fishery Conservation and Management Act requires regional fishery councils and NOAA Fisheries to identify and designate Essential Fish Habitat (EFH) for each managed species (Auster and Langton 1999). The Magnuson-Stevens Act defines EFH as "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity." NOAA Fisheries defines "waters" as aquatic areas and their associated physical, chemical, and biological properties that are used by fish where appropriate, and "substrate" is defined to include sediment, hard bottom, structures, and associated biological communities.

Information on EFH can be used to establish Marine Protected Areas (MPAs). As a general definition, MPAs are geographic regions that are closed to various types of anthropogenic activities, including some or all fishing, and have protected status to enhance marine resources. Theoretically, MPAs may help enhance fish populations by functioning as a source of new recruits to harvested populations, protecting species, genetic, and community diversity, and sheltering specific age classes from over-harvesting (DeMartini 1993, NRC 2001, Roberts *et al.* 2001). In conjunction with traditional management strategies, MPAs can be a valuable management tool because of their potential to protect more than a single species of exploited fish populations (Murray *et al.* 1999), in addition to simultaneously protecting the habitat. However without information on EFH for each species, improperly designed MPAs may endanger a fishery by providing a false sense of protection to fishery managers, and also detract from the expected effectiveness of well-designed MPAs (Carr and Reed 1993).

To accurately interpret EFH and understand fish ecology, it is important to identify the processes that control the relationships between the distribution of fishes and habitat variables (Wilkins and Myers 1992). Primarily the structural complexity of a habitat has direct and indirect influences on the distribution and abundance of fishes (Anderson 1994, Potts and Hulbert 1994, Friedlander and Parrish 1998, Jenkins and Wheatley 1998). For example, habitat can indirectly influence a fish's distribution and abundance by affecting the distribution of its prey and foraging ability (Ebeling and Laur 1985), and directly influence distribution by serving as refuge from predation (Sih *et al.* 1985) and shelter for reproduction (Balon 1985). However, the relationship between

fishes and their associated habitat structures must be studied at a spatial scale appropriate to the organism and the processes of interest (Addicott *et al.* 1987, Sale 1998, Anderson *et al.* in press).

The spatial scale at which habitat ecology is studied has not been thoroughly addressed for many fish species and has important implications relating to how an ecological system is understood (Jackson DA *et al.* 2001). Much of the current knowledge on the relationship between fish distribution and habitat structure has been related to environmental variables on a megahabitat scale (kilometers to tens of kilometers). However megahabitats, such as coral reefs (Sale 1998) and kelp forests (Holbrook *et al.* 1994), are architecturally patchy and can be subdivided into smaller habitat units. Greene *et al.* (1999) defined habitats on a smaller spatial scale as macrohabitats (one to tens of meters) and microhabitats (individual biogenic structures and seafloor materials < 1 meter of horizontal area). Fine-scale structural features, such as those identified by macro- and microhabitats, may more closely influence fish distribution and abundance (Choat and Ayling 1987, Jenkins and Wheatley 1998). Understanding the sources of variation among habitats at macro- and microhabitat scales is critical for interpreting patterns of fish abundance and distribution (Anderson *et al.* in press).

Identifying fish and habitat relationships at small-scales requires direct observation. Recently established survey techniques have standardized assessment of fish habitat in waters depths greater than 30 m through the use of remote sensing technology, habitat classification schemes (Greene *et al.* 1999), and submersible surveys

(Ralston *et al.* 1986, Stein *et al.* 1992, Cailliet *et al.* 1999, Yoklavich *et al.* 2000, Yoklavich *et al.* 2002)). Remote-sensing technology, such as side-scan sonar and multi-beam swath bathymetry, can be used to collect geophysical data and detailed bathymetry. These data are used to identify potential habitat types based on substrate characteristics (Yoklavich *et al.* 1997; Wakefield *et al.* 1998, Friedlander *et al.* 1999), resulting in the generation of detailed habitat maps. Submersible surveys have been used in conjunction with these maps to identify specific fish habitats or EFH for individual species (Jagiello *et al.* 2003).

This study compared fish and habitat relationships off the coast of central California, primarily focusing on rockfishes (Scorpaenidae: *Sebastes*), which dominate the nearshore fish assemblages of the eastern north Pacific (Love *et al.* 2002). Rockfishes are speciose and live in a wide range of habitats and across broad depth and latitudinal ranges. Many rockfishes and their ecological counterparts have remarkable specificity to large-scale structural features, such as *Macrocystis pyrifera* in waters less than 30 m (Ebeling *et al.* 1980, Larson and DeMartini 1983, DeMartini and Roberts 1990, Holbrook *et al.* 1990, Carr 1994). While water depths greater than 30 m may lack the structural complexity provided by macroalgae, rockfishes still demonstrate strong associations with specific demersal macrohabitats and depth zones (Richards 1986, Pearcy *et al.* 1989, Stein *et al.* 1992, O'Connell and Carlile 1993, Yoklavich *et al.* 2000, Yoklavich *et al.* 2002). Many of these rockfishes co-occur and overlap habitat niches (Williams and Ralston 2002) and can be grouped and identified as habitat guilds. A guild

is defined as a group of species that exploit the same class of environmental resources in a similar way (Root 1967).

Rockfishes are some of the most important commercial and recreational fishes off California (Lea *et al.* 1999). Some rockfishes are among the longest living fishes, with slow growth rates and late maturity, which make many of them extremely susceptible to overfishing (Parker *et al.* 2000), especially in deeper dwelling species (Cailliet *et al.* 2001, Andrews *et al.* 2002). Populations of rockfishes are undergoing high fishing mortality, indicated by rapidly decreasing population biomass (Butler *et al.* 2003) and size composition (Mason 1995 and 1998). Additionally, a commercial live fish fishery has increased rockfish mortality rates in nearshore areas. These fishes are ideal species for protection through designation of MPAs, however more detailed habitat assessment is vital to correctly protect this diverse group of fishes.

The objectives of this study were to identify and describe distinct habitats at micro- and macroscales (meter to tens of meters) and associate these habitats with the distribution and abundance of local fish species, in the vicinity of the Big Creek Ecological Reserve (BCER), central California. In addition, statistical techniques were developed to assess fish and habitat relationships. Multivariate statistical techniques were used to: 1) group fish species and their macro- and micro-scale habitats into functional habitat guilds; 2) analyze the relationship between selected fish species and their macro- and microhabitats; and 3) derive an index of habitat electivity to integrate multiple habitat measurements for selected fish species.

MATERIALS AND METHODS

Subtidal fish assemblages and associated habitat variables were surveyed in the vicinity of the Big Creek Ecological Reserve (BCER), central California, using the two-person *Delta* submersible. The reserve boundary extends from the mean high tide zone to the 100 meter contour and is confined by the following points: 36°05.31' N 121°38.24' W, 36°05.31' N 121°37.10' W, 36°03.65' N 121°37.04' W, 36°03.65' N 121°35.50' W (Figure 1). The reserve encompasses 8.09 km², however only 4.8 km² were included in the survey area because the inshore water (< 20 m water depth) was too shallow to safely survey with the submersible. This area was being surveyed concurrently by SCUBA (Ven Tresca *et al.* 1997). Additionally, areas directly adjacent to the western boundary of the reserve were included in the analysis, to a depth of 222 meters (Figure 2). These surveys were completed September 29 through October 4, 1997. The *Delta* was directed to specific dive locations using a detailed habitat map produced from side-scan sonar images collected during a previous cruise (Yoklavich *et al.* 1997), differential Global Positioning System (dGPS), and an acoustic track-point system on board the support vessel.

Each dive consisted of a series of 10-minute video strip transects, recorded with an externally mounted high-8 mm video camera and annotated by the observer with an internally mounted microphone. Two parallel lasers, spaced at 20 cm, were mounted on either side of the video camera to quantify distances traveled by the submersible and to measure the size of habitat patches. The lasers were also used to estimate the size of *Ophiodon elongatus*. The video camera recorded all fishes occurring approximately one

meter off the seafloor and within two meters from the starboard side of the submersible. During each video transect the scientific observer identified and counted all demersal fishes, and described the associated habitats.

Each video transect was subdivided into habitat patches. A habitat patch was identified by a distinct and recognizable change in the substratum type. Substratum type, slope, water depth, and patch area were the independent variables used to describe habitat in the analyses. Substratum categories included fine sediment or sand, shell hash or coarse sand, cobble, boulder, rock, and organic features, defined by the substratum texture or grain size (Greene *et al.* 1999). Fine sediment or sand substrata was composed of grains < 2 mm, shell hash or coarse sand substrata was composed of grains from 2 to 4 mm, cobble comprised grains from 64 to 256 mm, boulder substrata was composed of grains from 0.25 to 3.0 m, and rock substrata was composed of grains greater than 3 m or exposed bedrock. Organic substratum category was classified by the principal biological matter, including understory algae (Laminariales, Desmarestiales, and foliose reds), canopy forming algae (*Macrocystis pyrifera* and *Nereocystis luteana*), anemone (*Metridium* sp.), hydrocoral (*Stylaster californicus*), and seapens (primarily *Stylatula* spp.).

Substratum type was described by a combination of the primary (at least 50% of the area) and secondary (at least 20% of the area) substrata of a patch. For example, a habitat patch could be described as rock-organic if the patch consisted of at least 50% rock substratum and at least 20% organic features. Slope was estimated as the degree of inclination of the seafloor that is flat (0-5°), low (5-30°), or high (>30°). For example, a

habitat patch composed of at least 50% high slope and at least 20% flat slope was described as high-flat. Habitat area was estimated by counting the number of laser intervals (20 cm per interval) along the bottom and multiplying by two (Tusting and Davis 1993). Water depth of each habitat patch was measured to the nearest meter by a sensor located on the submersible.

Data Analysis

Fourteen fish species were analyzed using Logistic Regression Analysis and various Habitat Indices. These fourteen species were selected based on known life history traits and their frequency of occurrence. Only demersal fish species that occurred on at least fourteen habitat patches were selected for use in the analysis. Fourteen occurrences by a fish species seemed to be the minimum sample size for that species to be included in the analysis and produce interpretable results. The species used in various analyses included: *Citharichthys stigmaeus* (speckled sanddab), *Rhinogobiops nicholsii* (blackeye goby), *Ophiodon elongatus* (lingcod), *Oxylebius pictus* (painted greenling), *Sebastes carnatus* (gopher rockfish), *S. chlorostictus* (greenspotted rockfish), *S. crameri* (darkblotched rockfish), *S. elongatus* (greenstriped rockfish), *S. mystinus* (blue rockfish), *S. rosaceus* (rosy rockfish), *S. saxicola* (stripetail rockfish), *S. semicinctus* (half banded rockfish), *S. serranoides* (olive rockfish), and *S. wilsoni* (pygmy rockfish) (Table 1).

Fish and habitat data reflected natural variation of habitat patch size. For the 14 species, the number of fish was plotted against the length of each habitat patch to evaluate the relationship and determine if these data could be standardized using densities (number of fish per area of habitat patch).

Logistic Regression

Logistic regression was used to examine the relationship between binary species data (presence or absence) and both categorical (substratum type and slope) and continuous (depth and patch area) habitat data (Trexler and Travis 1993). Logistic regression models assume a binomial distribution of errors (Agresti 1996). The probability of "success" or the "presence of a species" is fit to the binomial distribution using maximum likelihood. The probability of a species presence increases or decreases as a sigmoid function of habitat variables. The rate of increase or decrease of the sigmoid curve is measured by the parameter β . The null hypothesis for the logistic regression model states that $\beta = 0$, or the probability of species presence is independent of the habitat variables. The Wald statistic was calculated as the squared ratio of the maximum likelihood parameter estimates for β to the asymptotic standard error (Agresti 1996). The significance of the model and the habitat variables were tested by comparing the Wald statistic to a chi-squared distribution with 1 degree of freedom. Habitat variables (substratum type, depth, patch area, and slope) were included in the analysis only if a fish species occurred at least once on that type.

Correlations among substratum types, slopes, depths, and patch areas were tested using Spearman's rank correlation because the data were binary and non-linear (Krebs 1999). Correlated independent variables ($r > 0.60$) were removed from the analysis. Additionally, habitat variables were removed if logistic regression could not compute residual chi-squares due to redundancies. The best-fit logistic regression model was selected based on significance of the model ($p < 0.05$) and its ability to predict species

presence. If previous requirements were equal, the final model with the most variables removed was chosen as the best-fit.

Index of Habitat Electivity/Habitat Utilization Index

Three habitat indices were used to compare habitat affinities of the fourteen fish species from the logistic regression at a larger spatial scale. Substratum types were grouped into general habitat categories based on similar micro-scale features and depth distributions (Yoklavich *et al.* 2002). For example, Rock-rock and Boulder-boulder were grouped together because they represent complex habitats. Six habitat guilds were established by grouping substratum type and depth (Table 2). Habitat categories for the Habitat Utilization Index (HUI) and Index of Habitat Electivity (IHE) included; **1) Shallow (< 100 m) Hard** (Rock-rock, Rock-boulder, Rock-organic, Rock-cobble, Organic-rock, Boulder-boulder, Boulder-organic, Boulder-rock, Boulder-cobble, and Organic-organic), **2) Shallow Mixed** (Cobble-cobble, Cobble-rock, Cobble-sand, Hash-cobble, Boulder-hash, Boulder-sand, Rock-hash, and Hash-rock), **3) Shallow Soft** (Sand-organic, Sand-hash, Hash-organic, Hash-hash, and Organic-hash), **4) Deep (>100 m) Mixed** (Rock-sand and Sand-rock), **5) Deep Hard** (Rock-rock), and **6) Deep Soft** (Sand-sand).

The Habitat Utilization Index (HUI) was based on a resource function described by Manly *et al.* (1993), where probabilities of habitat use were calculated using the following equations:

$$\hat{w}_i = \text{HUI};$$

$$\hat{w}_i = \bar{p}_i / \pi_i;$$

where

$\bar{p}_i$ = proportion of a fish species occurring in the i th habitat category

and

π_i = proportion of habitat area that was surveyed in the i th habitat category.

The difference between the HUI equation and Index of Habitat Electivity is the calculation of available habitat (π_i). Traditional estimates of available habitat used the proportion of habitat area. Alternatively, IHE incorporates the proportion of habitat area in addition to the proportion of frequency of occurrence of that habitat. To calculate IHE, $\pi_i = (\text{proportion of habitat area} + \text{proportion of frequency of occurrence of habitat})/2$. The resultant value approximates an arithmetic mean of habitat availability and weights unequal sample distributions.

To compare IHE and HUI values among species, the values need to be standardized. Manly *et al.* (1993) used the following equation to standardize the selection index;

B_i = Standardized index = IHE;

$$B_i = \hat{w}_i / \sum_{i=1}^I \hat{w}_i$$

The resulting values can be used to rank each Habitat Category according to its use and availability. The standardized values range from 0 to 1, and the highest values represent habitats with low availability and high species use, and the lowest values represent habitats with high availability and low species use. For each Habitat Category, the frequency of occurrence of a species and the amount of available habitat were graphed as

a dual histogram, with the latter plotted on the left side and the prior plotted on the right side. IHE values also were plotted as a scale bar on the right side of the graph.

To assess the validity of the results from the IHE and HUI analysis, a Habitat Utilization Analysis (HUA) was computed and compared with IHE values. This analysis was modified from Neu *et al.* (1974), by using a log-likelihood test with a G statistic instead of a χ^2 analysis because expected values frequently were small and G is likely to result in a more powerful test (Zar 1996). Using the following equation;

$$G = 4.60517 \left[\sum \bar{p}_i \log \bar{p}_i - \sum \bar{p}_i \log \hat{p}_i \right]$$

$\hat{p}_i$ = expected proportion of a fish species in the *i*th habitat category

where $G_{(0.05,5)} = 11.070$

This analysis consisted of a log-likelihood analysis to test if fish species distributions were proportional to habitat category distribution. Additionally, proportions of animals expected in each habitat category were compared with 95% confidence limits generated using Bonferroni statistics using the following equation;

$$\bar{p}_i - Z_{(1-\alpha/2k)} \sqrt{\bar{p}_i(1-\bar{p}_i)/N} \leq p_i \leq \bar{p}_i + Z_{(1-\alpha/2k)} \sqrt{\bar{p}_i(1-\bar{p}_i)/N}$$

where

$Z_{(1-\alpha/2k)}$ = Bonferroni statistic ($\alpha = 0.05$, k = the number of categories, 5),

and

p_i = theoretical proportion of fish expected in the *i*th habitat category,

and

N = the total number of that fish species observed

The resulting confidence intervals can be used to compare the theoretical proportion of occurrence of the multinomial distribution to determine whether expected values lie within the magnitude of the significant effects (Neu *et al.* 1974). For example, expected values of fish proportion that do not lie within the confidence limits can be interpreted as significant differences between observed and expected values and indicate trends of habitat preference or avoidance. Definitions of habitat preference or avoidance were based the observed versus expected fish distributions (higher than expected for habitat preference and lower than expected for avoidance). Ultimately, the trends detected using this technique were compared with the habitat electivity trends illustrated using IHE and HUI values.

Occurrence of Young-Of-Year (YOY) and juvenile *Ophiodon elongatus* were compared with adult *O. elongatus* among different habitat types. Adult and YOY/juvenile fishes were distinguished using total length. *Ophiodon elongatus* less than 30 cm total length were considered YOY/Juvenile and *O. elongatus* greater than 30 cm were considered adult (Miller and Geibel 1973, Smith and McFarlane 1990, Karpov *et al.* 1995). Results were plotted using a histogram comparing abundance of adult and YOY/juvenile *O. elongatus* among different habitat categories.

RESULTS

From ten submersible dives made in 1997, 33 transects were conducted and a total area of 6,319 m² was surveyed inside and west of the BCER. Eight transects were conducted west of the BCER in water depths ranging from 100 to 220 m (Table 3). The remaining 25 transects, accounting for 4650 m² (approximately 64%) of the total area, were conducted inside the BCER in water depths from 20 to 100 m. Twenty-six unique substratum types were identified from 232 habitat patches (Table 2). Habitat patches ranged from 0.3 to 261 m² (mean = 27.2, S.D. = 48.2), however patches under 30 m² were the most frequent (Figure 3).

Soft unconsolidated sediments were the most dominant substratum, accounting for the most total area and the largest patch sizes. The mean patch area was larger in soft unconsolidated sediments (i.e. Sand-sand) than in lithoid substrata (i.e. Rock-rock) (Figure 4). Hash-hash, Sand-sand, Hash-organic, and Sand-organic accounted for 61% of the total substratum (1,658 m², 1204 m², 675 m², and 337 m², respectively) (Table 3). Hard substratum types accounted for 25% of the total substratum and were primarily composed of Rock-rock, Rock-organic, and Organic-rock (560 m², 446 m², and 328 m², respectively). Mixed substratum accounted for the remaining 14% of the total substratum and was primarily composed of Rock-sand, Sand-rock, and Rock-hash (477 m², 145 m², 124 m², respectively). Substrata in water deeper than 100 m accounted for 26% (1,669 m²) of the available habitat and comprised Rock-rock, Rock-sand, Sand-organic, Sand-rock, and Sand-sand (Figure 5). Qualitatively, any soft substrata in water depths greater than 100 m were better described as fine sediment or mud.

A total of 16,309 fishes was identified to the lowest possible taxon, including 70 taxa and 56 species (Table 1). Three taxonomic groups were identified only to family level, represented by Agonidae, Cottidae, and Zoarcidae. In addition, five taxonomic groups were identified only to the level of genus or sub-genus, represented by *Citharichthys* spp., *Raja* spp., *Sebastes* spp., *Sebastomus* spp. (subgenus of *Sebastes*) (Chen 1971), and *Zaniolepis* spp. The *Sebastes* genus was additionally classified into groups of Young-Of-Year (YOY) fishes that were recognizable as *Sebastes* spp. YOY or *S. semicinctus* YOY, and into a species complex of *S. miniatus* and *S. pinniger*. A final taxonomic group included fishes that were only recognizable as Pisces or Pleuronectiformes.

Rockfishes (Genus:*Sebastes*) accounted for 87% (14,162 fishes) of the total number of fishes. Twenty-five species of rockfishes were identified, not including the following general rockfish categories: YOY *Sebastes* spp., *Sebastes pinniger*/*S. miniatus* complex, and *Sebastes* subgenus *Sebastomus* spp. Young-Of-The-Year *Sebastes* accounted for 74% (10,503 fishes) of the rockfishes. At the species level, *S. semicinctus* YOY rockfish were the most abundant (2,236 fish) and adult *S. mystinus* were the second most abundant (1,181 fish). *Sebastes hopkinsi*, *S. wilsoni*, and *S. semicinctus* also were very abundant (459, 376, and 261 fishes, respectively). *Sebastes entomelas* (widow rockfish) and *S. serranoides* were the next most abundant rockfishes (134 and 121 fishes, respectively). *Sebastes saxicola*, *S. crameri*, *S. rosaceus*, *S. helvomaculatus* (rosethorn rockfish), *S. chlorostictus*, *S. elongatus*, and *S. carnatus* all had moderate abundance (77, 59, 55, 48, 45, 29, and 23 fishes, respectively).

The remaining rockfish species: *S. jordani* (shortbelly rockfish), *S. miniatus* (vermillion rockfish), *S. caurinus* (copper rockfish), *S. rufus* (bank rockfish), *S. paucispinis* (bocaccio), *S. pinniger* (canary rockfish), *S. atrovirens* (kelp rockfish), *S. rosenblatti* (greenblotched rockfish), *S. ruberrimus* (yelloweye rockfish), *S. ovalis* (speckled rockfish), *S. melanops* (black rockfish, and *S. zacentrus* (sharpchin rockfish) had relatively low abundance (fewer than 15 fishes). However, a category of *S. miniatus*/*S. pinniger* complex had a high abundance (152 fishes) and would have increased the importance of either species if these fishes had been identifiable to each respective species.

Of the 232 habitat patches, *Sebastes mystinus* and *S. serranoides* occurred on the most patches (48 and 31 patches, respectively) (Table 1). *Sebastes crameri*, *S. semicinctus*, and *S. carnatus* occurred on 20, 18, and 17 different patches, respectively. *Sebastes chlorostictus*, *S. elongatus*, and *S. wilsoni* occurred at the same frequency (15 patches), followed by *S. saxicola* and *S. rosaceus* (14 patches each). The remaining rockfishes or species complexes occurred fewer than ten times.

Of the non-rockfish species, *Citharichthys stigmaeus* had high abundance (392 fish) and occurred on 29 different patches. *Citharichthys sordidus* (Pacific sanddabs) had high abundance (135 fish), however they only occurred on eight patches. Additionally, there were 264 fishes identified to the genus *Citharichthys*, which may have been either *C. stigmaeus* or *C. sordidus*. *Rhinogobiops nicholsii* and *Oxylebius pictus* also had high occurrences (148 and 120 fishes, respectively) and occurred on 35 and 54 patches, respectively. *Ophiodon elongatus* had low abundance (30 fishes) and occurred on 20

patches. Several schooling species were not included in the analysis because the submersible was not considered an appropriate tool to assess fishes not primarily associated with the seafloor; these species included, *Argentina sialis* (Pacific argentine), *Aulorhynchus flavidus* (tubesnout), *Cololabis saira* (Pacific saury), *Merluccius productus* (Pacific hake), and *Phanerodon atripes* (sharpnose perch).

Visual assessment of fish abundance versus patch area revealed a positive significant linear relationship for *C. stigmaeus*. There were no other statistically significant linear relationships between abundance and patch area for the other 13 species.

Logistic Regression and IHE/HUI/HUA

The logistic regression analysis was more successful at predicting species absence than species presence. Of the fourteen species analyzed, there was moderate success (47-66% correct) predicting species presence for only five species (*Citharichthys stigmaeus*, *Rhinogobiops nicholsii*, *Sebastes mystinus*, *S. crameri*, and *S. chlorostictus*). There was low success (27-39% correct) predicting species presence for four species (*S. serranoides*, *S. saxicola*, *S. elongatus*, and *Oxylebius pictus*). There was no success (0-14% correct) predicting species presence for the remaining species (*Ophiodon elongatus*, *S. carnatus*, *S. rosaceus*, *S. semicinctus*, and *S. wilsoni*). Only models with moderate or low success of predicting species presence were considered for interpretation.

Comparison of IHE values and HUI values revealed different results based on the Habitat category. The IHE values were higher on **Hard, Soft, Deep Hard, and Deep Soft Habitats**. The HUI values were higher on **Mixed and Deep Mixed Habitats**.

The logistic regression model for *Rhinogobiops nicholsii* included seventeen substratum types, depth, and patch area. The best-fit model retained eight substratum types and depth (Table 4a). The best-fit model predicted absence (95% correct) better than presence (51%). *Rhinogobiops nicholsii* was positively and significantly correlated with Rock-boulder and Rock-hash substratum types. Depth was not significant, however there was a negative correlation with depth indicating *R. nicholsii* was more likely to be absent with increasing depth. The IHE value (0.81) was less than the HUI value (0.87) for **Mixed Habitat** and low for all other categories (Table 5a and Figure 6a). The proportion (0.55) of *R. nicholsii* occurring on **Mixed Habitat** was significantly greater than the proportion expected (0.12), using HUA. The proportion of *R. nicholsii* observed on all **Deep Habitats** was significantly lower than expected using HUA.

The logistic regression for *Sebastes rosaceus* included seven substratum types, depth, patch area, and slope. The best-fit model predicted absence (99% correct), but did not predict presence accurately (14% correct) and was not considered for interpretation. The IHE value (0.83) was less than the HUI value (0.87) for **Mixed Habitat** (0.75). The IHE value (0.17) was greater than the HUI value (0.13) for **Hard Habitat** and low or zero for other categories (Table 5a and Figure 6a). The proportion (0.60) of *S. rosaceus* occurring on **Mixed Habitat** was significantly greater than the proportion expected (0.12), using HUA. The proportion of *S. rosaceus* observed was significantly lower than expected on **Soft** and all **Deep Habitats** using HUA.

The logistic regression for *Sebastes semicinctus* included six substratum types, and patch area, slope, and depth. The best-fit model predicted absence (98% correct) but

did not predict presence accurately (6% correct) and was not considered for interpretation. The IHE value (0.65) was less than the HUI value (0.78) for **Mixed Habitat** (Table 5a and Figure 6a). The IHE value (0.26) was greater than the HUI value (0.16) for **Deep Hard Habitat** (Table 5a and Figure 6a). The proportions of *S. semicinctus* occurring on **Mixed Habitat** (0.73) and **Deep Hard Habitat** (0.08) were significantly greater than the proportions expected (0.12 and 0.02, respectively), using HUA. The proportion of *S. semicinctus* observed was significantly lower than expected on **Hard, Soft, and Deep Mixed Habitats** using HUA.

The logistic regression for *Sebastes wilsoni* included four substratum types, patch area, depth, and slope. The best-fit model predicted absence (100% correct), but did not predict presence (0% correct) and was not considered for interpretation. The IHE value (0.72) was less than the HUI value (0.80) for **Mixed Habitat** and was low or zero for all other (Table 5a and Figure 6a). The proportion (0.65) of *S. wilsoni* occurring on **Mixed Habitat** was significantly greater than the proportion expected (0.12), using HUA. The proportion of *S. wilsoni* observed was significantly lower than expected for **Soft Habitat** using HUA.

The logistic regression for *Sebastes mystinus* included 14 substratum types, patch area, and depth. The best-fit model retained seven substratum types and depth (Table 4a). The best-fit model predicted absence (80% correct) slightly better than presence (66% correct). *Sebastes mystinus* was significantly negatively correlated with Hash-hash and Hash-organic patches, and depth. Additionally, there was a positive non-significant correlation with Organic-rock. The IHE value (0.76) was higher than the HUI value

(0.73) for **Hard Habitat** and low or zero for other categories (Table 5b and Figure 6b).

The proportion (0.85) of *S. mystinus* occurring on **Hard Habitat** was significantly greater than the proportion expected (0.29), using HUA. The proportion of *S. mystinus* observed was significantly lower than expected on **Mixed**, **Soft**, and all **Deep Habitats** using HUA.

The logistic regression for *Sebastes serranoides* included twelve substratum types and patch area. The best-fit model retained five substratum types and patch area (Table 4a). The best-fit model predicted absence (100% correct) better than presence (39% correct). *Sebastes serranoides* was positively and significantly correlated with Organic-rock, Rock-organic, and patch area. The IHE value (0.85) was higher than the HUI value (0.81) for **Hard Habitat** and low or zero for all other categories (Table 5b and Figure 6b). The proportion (0.94) of *S. serranoides* occurring on **Hard Habitat** was significantly greater than the proportion expected (0.29), using HUA. The proportion of *S. serranoides* observed was significantly lower than expected on **Mixed**, **Soft**, and all **Deep Habitats** using HUA.

The logistic regression model for *Sebastes carnatus* included five substratum types, patch area, depth, and slope. The best-fit model predicted absence (99% correct), but did not predict presence accurately (6% correct) and was not interpreted. The IHE value (0.68) was higher than the HUI value (0.60) for **Hard Habitat**. The IHE value (0.32) was less than the HUI value (0.40) for **Mixed Habitat** and low or absent for all other categories (Table 5b and Figure 6b). The proportion (0.87) of *S. carnatus* occurring on **Hard Habitat** was significantly greater than expected (0.29) using HUA. The

proportion (0.13) of *S. carnatus* occurring on **Mixed Habitat** was not significantly different than the proportion expected (0.12), using HUA. The proportion of *S. carnatus* observed was significantly less than expected on **Soft** and all **Deep Habitats** using HUA.

The logistic regression model for *Oxylebius pictus* included fifteen substratum types and patch area. The best-fit model retained ten substratum types (Table 4a). The best-fit model predicted absence (95% correct) better than presence (37% correct). *Oxylebius pictus* was positively and significantly correlated with Organic-rock, Rock-boulder, Rock-hash, Rock-organic, and Rock-rock. *Oxylebius pictus* was more likely to be absent when Organic-rock, Rock-boulder, Rock-hash, Rock-organic, and Rock-rock were absent. The IHE value (0.61) was higher than the HUI value (0.54) for **Hard Habitat** (Table 5b and Figure 6b). The IHE value (0.37) was lower than the HUI value (0.45) **Mixed Habitat** (0.40), and both measures were zero for other categories. The proportion (0.82) of *O. pictus* occurring on **Hard Habitat** was significantly greater than expected (0.29) using HUA. The proportion (0.16) of *O. pictus* occurring on **Mixed Habitat** was not significantly different than the proportion expected (0.12), using HUA. The proportion of *O. pictus* observed was significantly less than expected on **Soft** and all **Deep Habitats** using HUA.

The logistic regression model for *Ophiodon elongatus* (all age classes) included nine substratum types, patch area, slope, and depth. The best-fit model predicted absence (99% correct), but did not predict presence accurately (5% correct) and was not interpreted. The IHE value (0.40) was higher than the HUI value (0.36) for **Hard Habitat** (Table 5b and Figure 6b). The IHE value (0.34) was less than the HUI value

(0.42) for **Mixed Habitat**, and both measures were low or absent for all other categories. The proportion (0.63) of *O. elongatus* occurring on **Hard Habitat** was significantly greater than expected (0.29) using HUA. The proportion (0.17) of *O. elongatus* occurring on **Mixed Habitat** was not significantly different than the proportion expected (0.12), using HUA. The proportion of *O. elongatus* observed was significantly less than expected on **Soft** and **Deep Hard Habitats** using HUA.

Of the 26 substratum types, the logistic regression for *Citharichthys stigmaeus* included eight substratum types and produced a best-fit model that retained two substratum types (Table 4b). Depth and slope were not included in the model because they were collinear with habitat variables. The best-fit model predicted absence (90% correct) better than presence (48% correct). *Citharichthys stigmaeus* was positively and significantly correlated with Hash-hash and Rock-hash. *Citharichthys stigmaeus* were more likely to be absent when Hash-hash and Rock-hash were absent. The IHE value (0.89) was higher than the HUI value (0.77) for the **Soft Habitat** and low or absent for all other categories (Table 5c and Figure 6c). The proportion (0.96) of *C. stigmaeus* occurring on **Soft Habitat** was significantly greater than the proportion expected (0.36), using HUA. The proportion of *C. stigmaeus* observed was significantly less than expected for **Hard, Mixed**, and all **Deep Habitats** using HUA.

The logistic regression for *Sebastes crameri* included four substratum types, patch area, depth, and slope. The best-fit model retained patch area, depth, and slope (Table 4b). Depth and patch area were significantly and positively correlated. The best-fit model predicted absence (94% correct) better than presence (50% correct). The IHE

value (0.88) was greater than the HUI value (0.83) for **Hard Habitat** (Table 5c and Figure 6c). The IHE value (0.09) was lower than the HUI value (0.14) for Deep Mixed Habitat, and both measures were low or absent for all other categories. The proportion of *S. crameri* occurring on **Hard** (0.58) and **Deep Mixed** (0.31) **Habitats** were significantly greater than expected (0.02 and 0.09, respectively) using HUA. The proportion of *S. crameri* observed was significantly less than expected on all **Shallow Habitats** using HUA.

The logistic regression for *Sebastes chlorostictus* included five substratum types, patch area, slope, and depth. The best-fit model retained three substratum types, patch area, slope, and depth (Table 4c). The best-fit model predicted absence (98% correct) better than presence (47% correct). *Sebastes chlorostictus* was significantly and positively correlated with Rock-sand and Sand-rock, and patch area. Depth and slope were not significant factors. However there was a positive trend with depth and indicating that *S. chlorostictus* were more likely to be absent in shallow waters. The IHE value (0.50) was less than the HUI value (0.61) for **Deep Mixed Habitat** (Table 5c and Figure 6c). The IHE value (0.48) was greater than the HUI value (0.37) for **Deep Hard Habitat**, and both measures were low or absent for all other categories. The proportion (0.80) of *S. chlorostictus* occurring on **Deep Mixed Habitat** was significantly greater than expected (0.09) using HUA. There was not a significant difference between observed (0.16) and expected (0.02) proportions of *S. chlorostictus* on **Deep Hard Habitat** using HUA. The proportion of *S. chlorostictus* observed was significantly less than expected on **Deep Soft** and all **Shallow Habitats** using HUA.

The logistic regression for *Sebastes elongatus* included five substratum types, slope, and patch area. The best-fit model retained three substratum types, slope, and patch area. The best-fit model predicted absence (98% correct) better than presence (27% correct). There were no significant correlations between any habitat variables (Table 4c). The IHE value (0.54) was less than the HUI value (0.66) for **Deep Mixed Habitat** (Table 5c and Figure 6c). The IHE value (0.30) was greater than the HUI value (0.22) for **Deep Soft Habitat** and both measures were low or zero for all other categories. The proportion of *S. elongatus* occurring on **Deep Mixed** (0.59) and **Deep Soft** (0.38) **Habitats** were significantly greater than expected (0.09 and 0.12, respectively) using HUA. The proportion of *S. elongatus* observed was significantly less than expected on all **Shallow Habitats** using HUA.

The logistic regression for *Sebastes saxicola* included five substratum types, depth, and patch area. The best-fit model removed all substratum types, but retained depth and patch area (Table 4c). The best-fit model predicted absence (100% correct) better than presence (36% correct). *Sebastes saxicola* was positively and significantly correlated with depth and patch area. The IHE value (0.49) was greater than the HUI value (0.44) for **Deep Soft Habitat** (Table 5c and Figure 6c). The IHE value (0.20) was lower than the HUI value (0.28) for **Deep Mixed Habitat**, and both measures were low or zero for all other categories. The proportions of *S. saxicola* occurring on **Deep Soft** (0.64) and **Deep Mixed** (0.22) **Habitats** were significantly greater than expected (0.12 and 0.09, respectively) using HUA. The proportion of *S. saxicola* observed was significantly less than expected on all **Shallow Habitats** using HUA.

For all species, there was a significant difference between fish distribution and habitat distribution based on the Habitat Utilization Analysis (Tables 5a, b, and c). The calculated G value was always greater than the critical G value = 11.070 ($G_{\alpha=0.05, n=5}$) for at least one habitat category. Additionally, expected proportions of fish populations were outside estimated confidence limits (one standard deviation), using Bonferroni estimates. However, the results of HUA did not always match interpretation of the IHE and HUI values.

There were discrepancies between HUA and IHE/HUI results with four species (*S. semicinctus*, *S. crameri*, *S. elongatus*, and *S. saxicola*). The remaining species, with one exception (*O. elongatus*), had high IHE/HUI values corresponding with significant HUA results. *Ophiodon elongatus* had moderate IHE/HUI values for multiple habitat categories, however the HUA analysis matched the habitat category with the highest IHE/HUI value. For *S. semicinctus*, the IHE/HUI analyses indicated association with **Mixed Habitat**, however HUA analysis indicated association with **Deep Hard Habitat** as well. For *S. crameri*, the IHE/HUI analyses indicated association with **Deep Hard Habitat**, however the HUA analysis indicated association with **Deep Mixed Habitat** as well. For *S. elongatus*, the IHE/HUI analyses indicated association with **Deep Mixed Habitat**, however the HUA analysis indicated association with **Deep Soft Habitat** as well. For *S. saxicola*, the IHE/HUI analyses indicated association with **Deep Soft Habitat**, however the HUA analysis indicated association with **Deep Mixed Habitat** as well.

In total, 30 *Ophiodon elongatus* were observed in the survey area. Twenty-five of these fish were measured and used for the comparison between abundance of different age classes and habitat. Adults (16 fish) were observed more frequently than YOY/juvenile (9 fish) (Figure 7). Adults occurred more frequently (12 fish) than YOY/juvenile (3 fish) on hard habitats (Boulder-boulder, Organic-boulder, Rock-boulder, Rock-organic, and Rock-rock). YOY/juvenile occurred more frequently (5 fish) than adults (3 fish) on mixed habitat types (Rock-hash, Rock-sand, and Sand-rock). Only one adult and one YOY/juvenile occurred on soft habitat (Sand-sand).

DISCUSSION

The habitats surveyed inside and adjacent to the BCER were highly diverse, with different types of substrata and habitat patch sizes. The wide assortment of substratum types and sizes resulted in a spatially complex and patchily distributed environment. Approximately 26% of the area surveyed was outside of the BCER in water depths greater than 100 m, increasing the diversity of habitats and fishes observed.

The total area surveyed was dominated by soft unconsolidated sediment. However, it is likely the proportion of hard substratum observed in this study was greater than the amount proportionally available in the environment. Using remote sensing technology to characterize the entire BCER and adjacent areas, Yoklavich *et al.* (1997) estimated 8% of the total area in and around the reserve was composed of complex rock bottom types (north, inside and south of BCER). In contrast, approximately 25% of the area surveyed in this study was composed of hard substratum types and 14% of the area was composed of mixed substratum types. This difference is directly related to the intentional targeting of rocky outcrops and other hard substrata by the submersible transects in this survey to record data on rockfishes and their habitat associations.

Rockfishes were the most diverse and abundant genus, dominating the fish assemblages despite the fact that hard and mixed substrata accounted for less than half of the habitat sampled. Of the rockfish species observed in or adjacent to BCER, several are considered to be overfished, including *S. crameri* (Rogers *et al.* 2000), *S. entomelas* (Williams *et al.* 2000), *S. paucispinis* (MacCall 2002), *S. ruberrimus* (Wallace 2001), and *S. pinniger* (Williams *et al.* 1999). While only a few individuals of these species were

found inside of the BCER, the majority of these fishes were found outside the reserve in water depths greater than 100 m. With increasing exploitation of deep-water (>100 m) fisheries (Haedrich *et al.* 2001) and the lack of marine reserves in deep-water (McArdle 1998), expansion of the BCER into deeper waters may help protect many of these species (Yoklavich *et al.* 2002).

The BCER provides protection for several shallow (< 100 m) water rockfish and non-rockfish species with similar life history traits that make them ideal species for protection through marine reserves. Recent stock assessments for *S. carnatus* and *S. miniatus* indicate these species are not overfished (MacCall pers. com), however there is little population information for many of the other rockfish species observed. Additionally, there is particular concern for several species in the Hexagrammidae family, which were commonly observed in the BCER. *Ophiodon elongatus* is already considered overfished (Jagiello *et al.* 2003) and a stock assessment is just beginning for *Hexagrammos decagrammus*.

In addition to protection for adults, the BCER may serve as an area to protect reproduction cycles and recruiting fishes. Schooling YOY rockfishes overall were the most abundant fishes, which may reflect the use of the BCER as a recruitment or nursery area (Yoklavich *et al.* 2002). Both *O. elongatus* and *H. decagrammus* use shallow rocky habitats to establish nesting areas (Cass *et al.* 1990), and small lingcod were observed as potential recruits.

In addition to an abundance of rockfishes, there was a diverse assemblage of non-rockfish species observed in the BCER. The diverse assemblage of fishes observed

reflects reports of high diversities in other subtidal surveys of California rocky reefs (Ebeling *et al.* 1980, Stephens and Zerba 1980, Larson and DeMartini 1983, Yoklavich *et al.* 2002). Only five of 31 non-rockfish species were considered schooling or migratory species. However the submersible surveys were focused on demersal or sedentary species. Speckled (*Citharichthys stigmaeus*) and Pacific (*C. sordidus*) sanddabs dominated the non-schooling species. Sanddabs were highly abundant in shallow soft bottom areas of BCER (Yoklavich *et al.* 2002), and in other areas of California (Stull and Tang 1996, Craig *et al.* 2004). Although pink surfperch (*Zalemnius rosaceus*) occurred infrequently, they were generally observed on soft substrata in association with sea-pens (*Stylatula* spp.). There is little habitat information published for this species.

Despite highly variable habitat patch sizes, density was not used to standardize sample sizes and compare fish distributions among different sized habitat patches. The use of density assumes a linear relationship between habitat patch area and abundance, where larger patches support proportionally larger abundances of fish. In this study, with one exception (*C. stigmaeus*), there were no linear relationships between fish abundance and patch area. Although there are no data to support an explanation, the lack of a relationship between patch area and fish abundance could possibly be tied to specific life history patterns, such as territoriality or home range fidelity. For example, parrotfish density increases on smaller patches and decreases on larger patches because the fish do not defend territories on small patches (van Rooij *et al.* 1996). Territoriality and home range fidelity have been demonstrated for several rockfish species (Larson 1980,

Matthews 1990), lingcod (Starr *et al.* 2005), painted greenlings (DeMartini and Anderson 1980, Elliot 1992), and blackeye gobies (Cole 1984).

Logistic regression & IHE/HUI/HUA

Comparison of the relationship between fishes and their habitats at two spatial scales produced similar results. While only six of 14 species analyzed had relationships identified with a substratum type at the micro-spatial scale using logistic regression, the results were comparable with the macro-spatial scale analysis using various indices. The success of the logistic regression analysis method may have been limited because of the diverse number of habitat variables, resulting in too many categories to detect trends for all species.

Logistic regression analysis also identified several species with significant relationships between depth, slope, and patch length. Two species had a positive (*S. crameri* and *S. saxicola*) and two species had negative (*S. mystinus* and *R. nicholsii*) relationship with depth, matching previously described depth related distribution patterns (Love *et al.* 2002). Depth has been shown to be an important influence for rockfish distribution in the BCER area (Yoklavich *et al.* 2002) and a determinant for rockfish distribution along California and southern Oregon (Williams and Ralston 2002).

The one species (*S. crameri*) correlated with slope was likely to be found more often on habitats with slopes greater than 30 degrees than substrata with lower degrees of slope. This species has been observed on canyon walls (Yoklavich *et al.* 2000). Slope may not have been correlated with more species because it was removed from most logistic regression models due to high correlation with substrata type (e.g. low slope was

often correlated with soft bottom substrata) and with water depth (e.g. high slope was positively correlated with increasing water depth).

Logistic regression analysis indicated that four species (*S. chlorostictus*, *S. crameri*, *S. saxicola*, and *S. serranoides*) were more likely to occur on larger habitat patches. However this relationship was not strong and based only on presence/absence data. The four species with weak, positive relationships to patch size may be an artifact of sampling, where at larger spatial scales the probability of encountering a species increases (Angermeier and Schosser 1989). In addition, at larger spatial scales and on larger patches, there is a higher likelihood of encountering ideal habitat (Rieman and McIntyre 1995), which would account for the higher probability of encountering some of these fishes on bigger patches. Despite extensive work in terrestrial ecology documenting species distribution and habitat size, there is little known about how fish distributions change based on the size of available habitat.

At the macro-spatial scale, *Rhinogobiops nicholsii*, *Sebastes rosaceus*, *S. semicinctus*, and *S. wilsoni* were grouped together as a **Shallow Mixed Habitat Guild**. At the micro-spatial scale, *R. nicholsii* had a positive relationship with two substratum types associated with two different habitat categories at a macro-spatial scale (Rock-boulder from Shallow Hard and Rock-hash from Shallow Mixed). Other studies report *R. nicholsii* uses both of these substrata as habitats (Cole 1984, Csepp and Wing 1999) and occur in similar habitats as *S. rosaceus* and *S. semicinctus* (Yoklavich *et al.* 2002)

Generally, *S. wilsoni* were found at greater depths than the other species associated with **Shallow Mixed Habitat**. In previous research at BCER, *S. wilsoni* was

identified as a unique species, associated with deep rock habitats (Yoklavich *et al.* 2002). In this study, a school of 200 *S. wilsoni* occurred on a very small **Shallow Mixed Habitat** patch (67 m water depth). For the remaining *S. wilsoni*, the highest numbers occurred in water depths around 90 m. There are no size data or age estimates to indicate juvenile or adult fish, however several authors have noted that adult *S. wilsoni* were associated with deeper rocky habitats and juvenile *S. wilsoni* occurred in dense schools on shallower sand and rock mixed habitats (Stein *et al.* 1992, Lea *et al.* 1999).

Sebastes semicinctus had a secondary association with **Deep Hard Habitat** indicated by HUA, however this not likely a significant relationship. Several of the HUA comparisons between individual species and habitat categories were based on very small samples sizes and highly variable data, which make the results difficult to interpret. *Sebastes semicinctus* are commonly found between 60 and 150 m (Love *et al.* 2002), but in this study approximately 60% of *S. semicinctus* were found in three schools at 96, 97, and 99 meters water depth. The results were most likely influenced by the arbitrary use of 100 m water depth to distinguish fish distribution. In reality, these fishes are distributed across a continuous gradient of overlapping depth zones.

Shallow Hard Habitats were composed of five species (*Sebastes mystinus*, *S. serranoides*, *S. carnatus*, *Oxylebius pictus*, and *Ophiodon elongatus*). Four species (*S. mystinus*, *S. serranoides*, *S. carnatus*, and *O. pictus*) were previously shown to co-inhabit similar shallow, high relief rocky habitat associated with macroalgae (Miller and Geibel 1973, Love and Ebeling 1978, DeMartini and Anderson 1980, Ebeling *et al.* 1980, Hallacher and Roberts 1985, Yoklavich *et al.* 2002). However, recent research on

lingcod has suggested broad depth and habitat distributions with seasonal migrations for juveniles and adults (Jagiello 1988, Cass *et al.* 1990, Martell *et al.* 2000, Starr *et al.* 2005).

At the micro-spatial scale, *Oxylebius pictus* were also correlated with one substratum associated with **Shallow Mixed Habitat** (Rock-hash). This habitat use pattern may be explained by ontogenetic habitat segregation. Adults have been shown to inhabit high relief rocks and juveniles occupy sand and rock areas (DeMartini and Anderson 1980, Elliot 1992).

Only one species (*Citharichthys stigmaeus*) was associated with **Shallow Soft Habitat**, which included a positive association with Rock-hash substrata. While there are no data to support an explanation for the relationship between *C. stigmaeus* and the Rock-hash substratum at the micro-spatial scale, this relationship may be an artifact of sampling as a spatial resolution issue. Rock-hash substrata were patches primarily comprised of rock with some low relief hash or soft sediment. *Citharichthys stigmaeus* occurred on the hash or soft sediment, but were classified in association with Rock-hash habitats. There were never any observations of *C. stigmaeus* on rock substrata. Because these surveys were conducted during the fall, prior to the major influence of storm generated sediment transport, low relief rock outcrops may have been partially covered by summer formation of bedforms (Yoklavich *et al.* 1997), explaining the distribution of sanddabs among sandy areas with low lying rocky outcrops.

Deep Mixed Habitats were not overly abundant, representing approximately 10% of the total area of habitat surveyed. However two species (*S. chlorostictus* and *S. elongatus*) had strong associations with this habitat category. *Sebastes chlorostictus* had a

positive relationship with mixed habitats composed of rock and soft sediment. These species have been previously observed on rocky ledges and canyon walls (Yoklavich *et al.* 2000, Yoklavich *et al.* 2002). Both of these species have also been observed in mixed types of habitat (Yoklavich *et al.* 2000, Yoklavich *et al.* 2002). In addition, *S. elongatus* has been described as occurring on soft sediments (Richards 1986) or as not having a strong habitat association with either substratum type (Yoklavich *et al.* 2002).

Two species (*Sebastes elongatus* and *S. saxicola*) were associated with **Deep Soft Habitats**. Previous research found that *S. saxicola* and *S. elongatus* were not definitively associated with either mud or rock habitat (Yoklavich *et al.* 2002), but have been observed in mixed mud and rock habitat (Yoklavich *et al.* 2000, Yoklavich *et al.* 2002, Love *et al.* 2002, Jagielo *et al.* 2003). **Soft** and **Deep Soft Habitats** were widely available (2,715 and 1,204 m², respectively), however only the species listed above were strongly associated with either habitat.

The results of the two habitat indices (IHE and HUI) were similar, but consistently offset depending on the habitat type. IHE values were invariably higher than HUI values for species associated with **Hard, Deep Hard, Soft, and Deep Soft Habitat Guilds**. In contrast, HUI values were consistently higher than IHE values for species associated with **Mixed and Deep Mixed Habitat Guilds**. The difference in these results was directly related to the calculation of each index and the distribution of the habitat in the environment. IHE estimated species relationship with a given habitat based on the proportion of each habitat area and the frequency of occurrence of each habitat. HUI estimated species relationship with a given habitat based only on the proportion of habitat

area. **Soft** and **Deep Soft Habitat Guilds** generally were larger patches with infrequent occurrences. Typically, **Mixed** and **Deep Mixed Habitat Guilds** were smaller patches with frequent occurrence. **Hard** and **Deep Hard Habitat Guilds** had variable distributions, with large and infrequently occurring substrata in combination with small and frequently occurring substrata.

The lack of information on how habitat area or distribution of habitat affects fish distribution necessitates giving equal weight to each of these variables. IHE uses a combination of the two measures, which gives an arithmetic mean distribution (Assis 1995, Duarte and Garcia 1999), resulting in a better estimate of species and habitat relationships. HUI can be biased by overestimating small, but frequently occurring habitats or by underestimating large but infrequently occurring habitats because it only utilizes habitat area.

There was no level associated with either IHE or HUI values that indicated habitat electivity or avoidance by any given species. For each species, the highest IHE value for a given habitat was determined to be the primary habitat elected. The use of HUA was successful and significant results corresponded with the highest IHE values.

A pattern of habitat use along interfaces or edges was evident at both micro- and macro-spatial scales. Six fish species (*S. rosaceus*, *S. wilsoni*, *S. chlorostictus*, *O. pictus*, *C. stigmaeus*, and *R. nicholsii*) had positive correlations with a mixed substratum habitat, such as Rock-sand in the logistic regression model. Seven species (*S. rosaceus*, *S. wilsoni*, *S. chlorostictus*, *S. elongatus*, *S. semicinctus*, *O. pictus*, and *R. nicholsii*) had high IHE values on **Mixed** or **Deep Mixed Habitat** categories. Habitat edges represent

environmental heterogeneity and have been noted as important features for refuge or feeding (Souza 1984, Pearman 1993, McIntyre and Wiens 1999). *Sebastes chlorostictus* and *S. elongatus* have been previously noted as occurring at sediment and rock interfaces (Yoklavich *et al.* 2002). However, there is little literature on the occurrence of the other species on rock and sediment interfaces. Rock and sand mixed patches can be viewed as habitat edges or interfaces between high relief rocky substrates and low relief non-lithified sediments.

Habitat edges may provide complex structure because of the dramatic change in vertical relief from the soft substratum substrata to rocky habitat. However, this type of assessment was outside the scope of this study and is only identified as an area for future research. Habitat edges have been identified as preferred habitats for other fishes, with more abundant (O'Connell and Carlile 1993) and diverse fish assemblages (Friedlander and Parrish 1998). There is a trend of strong relationships between fishes and mixed habitats and weak relationship between fishes and large patch sizes. If these mixed habitats are representing habitat edges, then larger patches will have fewer edges and be less important than smaller habitats. As patches become larger, the ratio of patch perimeter to patch area decreases, resulting in fewer patch edges (McIntyre and Wiens 1999).

Despite a small sample size, comparison of habitat use between adult and YOY/juvenile *Ophiodon elongatus* supported ontogenetic differences, wherein larger individuals occurred more frequently on rocky substrata and smaller fish more frequently on mixed habitats. Juvenile or YOY *O. elongatus* have been observed on mixed habitats

by several authors (Miller and Geilbel 1973, Cass *et al.* 1990, Karpov *et al.* 1995, Martell *et al.* 2000).

Summary

The Big Creek Ecological Reserve (BCER) provided an ideal system for assessing fish and habitat associations. Due to the remote location of the BCER and the seclusion of fishing activities, major anthropomorphic influences were likely to be absent. Additionally, the BCER has been closed to fishing efforts since January 1994 (Yoklavich *et al.* 2002). While minor residual fishing mortality may still occur (Paddock and Estes 2000), restricted access and local socioeconomic pressures may minimize these affects (Yoklavich *et al.* 2002).

The use of a submersible and video transects provided researchers with direct observation of habitat variables and fish associations while using non-lethal sampling techniques in the BCER. Direct observation of fishes and their habitat associations was salient in the process of identifying habitats at the spatial scale relevant to individual fishes. Non-lethal sampling techniques were essential for surveying protected areas within a reserve. Additionally, this type of research eliminates some of the species-specific biases, such as species selectivity with gear type, that are associated with other sampling techniques (long-line, trawl surveys, etc.) (Ralston *et al.* 1986). It is important to recognize that these survey methods are most effective for demersal fishes and are limited for use with schooling or non-sedentary fish species.

The results of this study provide information on fish distributions at two spatial scales that can be used by fishery managers to establish or evaluate MPAs. At the micro-

spatial scale, only a few fish species were associated with specific substratum types or other habitat variables. Additionally, these associations were not very strong. This may be due to a lack of power to distinguish different habitat use with this technique or because many of these fishes occur on multiple substratum types and do not have an affiliation with a specific substratum type. If the latter is the case, the function of the substratum type is more important than the composition.

The most important habitat variable measured at the micro-spatial scale was water depth. This finding has important implications for the BCER, which does not extend past the 100 m isobath and designation of future marine reserves. Many of the important species that were observed, occurred in water depths greater than 100 m and are not currently protected by the BCER (Yoklavich *et al.* 2002). This concept is compounded by the fact that there are few marine reserves designated in deep water (>100 m) (McArdle 1998) and deep water species are especially vulnerable to fishing activities (Cailliet *et al.* 2001, Haedrich *et al.* 2001).

At the macro-spatial scale, fishes were grouped into habitat guilds based on their co-occurrence on similar habitats using various indices. The IHE proved to be the most successful index for determining habitat electivity. By developing a method to measure and weight two habitat variables, the IHE gives more accurate results on how fish are distributed in relation to how habitat is distributed. Information on which fishes co-occur in habitat guilds is important for selecting EFH for protection.

Finally, the wide range of species encountered in the BCER is likely the result of the structural complexity and wide depth distribution of the habitats surveyed. While

habitat edges were not quantitatively evaluated, they appear to be important habitat characteristics. Ultimately, this information is important for fishery managers, because establishing an MPA in an area with high habitat diversity and variability among substrate types may provide increased habitat edges or structural complexity and provide the most benefits for enhancing fish populations.

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Table 1: An alphabetical list of the fishes recorded in and near the Big Creek Ecological Reserve in 1997. Species in bold and marked with an asterix (*) were used in the logistic regression and IHE/HUI/HUA analyses. The total number of individuals of each taxon is represented by N. The frequency of occurrence (FO) represents the number of patches on which a given taxon occurred.

Scientific Name	Common name	N	FO	Scientific Name	Common name	N	FO
Agonidae	poachers	37	15	<i>Rhinogobiops nicholsii</i>*	blackeye goby	148	35
<i>Argentina sialis</i>	Pacific argentine	39	14	<i>Sebastes atrovirens</i>	kelp rockfish	6	5
<i>Aulorhynchus flavidus</i>	tubesnout	153	3	<i>Sebastes carnatus</i>*	gopher rockfish	23	17
<i>Citharichthys sordidus</i>	Pacific sanddab	135	8	<i>Sebastes caurinus</i>	copper rockfish	10	8
<i>Citharichthys</i> spp.	sanddabs	264	8	<i>Sebastes chlorostictus</i>*	greenspotted rockfish	45	15
<i>Citharichthys stigmaeus</i>*	speckled sanddab	392	29	<i>Sebastes crameri</i>*	darkblotched rockfish	59	20
<i>Cololabis saira</i>	Pacific saury	200	1	<i>Sebastes elongatus</i>*	greenstriped rockfish	29	15
Cottidae	sculpins	15	10	<i>Sebastes entomelas</i>	widow rockfish	134	4
<i>Damalichthys vacca</i>	pile perch	20	9	<i>Sebastes helvomaculatus</i>	rosethorn rockfish	48	10
<i>Embiotoca jacksoni</i>	black perch	6	4	<i>Sebastes hopkinsi</i>	squarespot rockfish	459	8
<i>Embiotoca lateralis</i>	striped seaperch	16	10	<i>Sebastes jordani</i>	shortbelly rockfish	15	1
Embiotocidae	surfperches	10	7	<i>Sebastes melanops</i>	black rockfish	1	1
<i>Enophrys taurina</i>	bull sculpin	4	3	<i>Sebastes miniatus</i>	vermilion rockfish	11	6
<i>Eptatretus stoutii</i>	Pacific hagfish	2	2	<i>Sebastes miniatus/pinniger</i>	vermilion/canary complex	152	5
<i>Errex zacharius</i>	rex sole	1	1	<i>Sebastes mystinus</i>*	blue rockfish	1181	48
<i>Hexagrammos decagrammus</i>	kelp greenling	9	8	<i>Sebastes ovalis</i>	speckled rockfish	2	1
<i>Hydrolagus colliei</i>	spotted ratfish	20	2	<i>Sebastes paucispinis</i>	bocaccio	8	5
<i>Pleuronichthys guttulata</i>	diamond turbot	1	1	<i>Sebastes pinniger</i>	canary rockfish	6	5
<i>Icelinus filamentosus</i>	threadfin sculpin	2	1	<i>Sebastes rosaceus</i>*	rosy rockfish	55	14
<i>Lepidopsetta bilineata</i>	rock sole	2	1	<i>Sebastes rosenblatti</i>	greenblotched rockfish	6	4
<i>Lycodes cortezianus</i>	bigfin eelpout	3	1	<i>Sebastes ruberrimus</i>	yelloweye rockfish	5	3
<i>Lyopsetta exilis</i>	slender sole	13	9	<i>Sebastes rufus</i>	bank rockfish	9	6
<i>Merluccius productus</i>	Pacific hake	129	8	<i>Sebastes saxicola</i>*	stripetail rockfish	77	14
<i>Microstomus pacificus</i>	Dover sole	26	9	<i>Sebastes semicinctus</i> YOY	YOY halfbanded rockfish	2236	7
<i>Ophiodon elongatus</i>*	lingcod	30	20	<i>Sebastes semicinctus</i>*	halfbanded rockfish	261	18
<i>Oxyjulis californica</i>	señorita	3	2	<i>Sebastes serranoides</i>*	olive rockfish	121	31
<i>Oxylebius pictus</i>*	painted greenling	120	54	<i>Sebastes</i> spp.	rockfishes	559	45
<i>Phanerodon atripes</i>	sharpnose seaperch	101	2	<i>Sebastes</i> spp. YOY	YOY rockfishes	8267	64
Pisces	unidentified fishes	35	25	<i>Sebastes wilsoni</i>*	pygmy rockfish	376	15
Pleuronectiformes	flatfishes	86	23	<i>Sebastes zacentrus</i>	sharpchin rockfish	1	1
<i>Parophrys vetulus</i>	English sole	2	2	<i>Sebastomus</i> spp.	<i>Sebastomus</i> rockfishes	63	24
<i>Pleuronichthys</i> spp.	turbots	3	3	<i>Semicossyphus pulcher</i>	California sheephead	8	6
<i>Porichthys notatus</i>	plainfin midshipman	1	1	<i>Zalemibus rosaceus</i>	pink seaperch	36	10
<i>Raja</i> spp.	skates	1	1	<i>Zaniolepis</i> spp.	combfishes	1	1
<i>Rathbunella alleni</i>	stripefin ronquil	1	1	Zoarcidae	eelpouts	9	4

Table 2. Area of patches distributed by depth and bottom type. This distribution was used to combine different substratum types into habitat categories for Index of Habitat Electivity analysis and Habitat Utilization Analysis. Substratum types that had similar composition and occurred in similar depth categories were pooled into habitat categories. The only sea-floor types that occurred primarily in depths greater than 100 m are indicated in bold font.

Bottom Type	Shallow (<100 m)	Deep (>100 m)	Grand Total	Habitat Category
Boulder-boulder	37 m ²		37 m ²	Hard
Boulder-cobble	14 m ²		14 m ²	Hard
Boulder-hash	18 m ²		18 m ²	Mixed
Boulder-organic	20 m ²		20 m ²	Hard
Boulder-rock	12 m ²		12 m ²	Hard
Boulder-sand	5 m ²		5 m ²	Mixed
Cobble-cobble	10 m ²		10 m ²	Mixed
Cobble-rock	5 m ²		5 m ²	Mixed
Cobble-sand	11 m ²		11 m ²	Mixed
Hash-cobble	7 m ²		7 m ²	Mixed
Hash-hash	1658 m ²		1658 m ²	Soft
Hash-organic	675 m ²		675 m ²	Soft
Hash-rock	35 m ²		35 m ²	Mixed
Organic-hash	34 m ²		34 m ²	Soft
Organic-organic	37 m ²		37 m ²	Hard
Organic-rock	328 m ²		328 m ²	Hard
Rock-boulder	74 m ²		74 m ²	Hard
Rock-cobble	34 m ²		34 m ²	Hard
Rock-hash	124 m ²		124 m ²	Mixed
Rock-organic	446 m ²		446 m ²	Hard
Rock-rock	390 m ²	170 m ²	560 m ²	Hard
Rock-sand	78 m²	400 m²	477 m²	Deep Mixed
Sand-hash	11 m ²		11 m ²	Soft
Sand-organic	215 m ²	122 m ²	337 m ²	Soft
Sand-rock	26 m²	119 m²	145 m²	Deep Mixed
Sand-sand	346 m²	858 m²	1204 m²	Deep Soft
Grand Total	4650 m ²	1669 m ²	6319 m ²	

Table 3. Total area of each transect by dive and location. Dives and transects in water depths greater than 100 m were considered west of BCER. Dives inside BCER ranged from 20 to 100 m. Transects labeled with a “C” indicate circular transects.

Total area of each transect		Location	
Dive #	Transect #	Inside BCER	West of BCER
4187	1		188 m ²
	2		187 m ²
	3		246 m ²
4190	2	183 m ²	
4191	1	165 m ²	
	2	245 m ²	
	3	261 m ²	
	4	212 m ²	
	C1	39 m ²	
	C2	73 m ²	
4192	1	167 m ²	
	2	188 m ²	
	3	180 m ²	
	4	170 m ²	
4193	1	238 m ²	
	2	212 m ²	
	3	248 m ²	
	4	236 m ²	
	C	80 m ²	
4194	1	197 m ²	
	2	233 m ²	
4196	1		203 m ²
	2		205 m ²
	3		262 m ²
	C1	44 m ²	
	C2	175 m ²	
4203	1		170 m ²
4205	1	207 m ²	
	2	228 m ²	
	3	194 m ²	
	4	258 m ²	
4206	1		206 m ²
	2	215 m ²	
Grand Total		4650 m ²	1669 m ²

Table 4a. Regression coefficients and significance from the best-fit models for *Rhinogobius nicholsii*, *S. mystinus*, *S. serranoides*, and *Oxylebius pictus*. Statistically significant ($p < 0.05$) substratum types or other variables are in bold type and marked with an asterisk (*). Cells marked with hash marks (---) indicate substratum types that were removed from the logistic regression model. Negative or positive β values indicate negative and positive relationships.

Substratum types	<i>Rhinogobius nicholsii</i>		<i>Sebastes mystinus</i>		<i>Sebastes serranoides</i>		<i>Oxylebius pictus</i>	
	β	Significance	β	Significance	β	Significance	β	Significance
Boulder-boulder	---	---	---	---	---	---	10.476	0.764
Boulder-cobble	10.287	0.865	---	---	9.147	0.803	10.476	0.862
Boulder-hash	---	---	7.181	0.782	---	---	---	---
Boulder-organic	---	---	---	---	---	---	---	---
Boulder-rock	9.739	0.872	---	---	---	---	10.476	0.862
Boulder-sand	10.287	0.865	8.028	0.827	---	---	---	---
Cobble-cobble	10.287	0.865	---	---	9.222	0.801	10.476	0.862
Hash-cobble	---	---	---	---	---	---	---	---
Hash-hash	---	---	-2.819	0.007*	-3.157	0.070	---	---
Hash-organic	---	---	-0.247	0.037*	---	---	---	---
Hash-rock	---	---	-1.699	0.122	---	---	---	---
Organic-hash	---	---	---	---	---	---	---	---
Organic-rock	---	---	1.322	0.067	1.725	0.010*	2.967	0.000*
Rock-boulder	2.423	0.008*	---	---	---	---	2.967	0.002*
Rock-cobble	10.287	0.865	---	---	---	---	10.476	0.862
Rock-hash	2.297	0.000*	-1.119	0.169	---	---	1.986	0.003*
Rock-organic	---	---	---	---	1.759	0.001*	2.178	0.000*
Rock-rock	---	---	---	---	---	---	1.580	0.003*
Rock-sand	---	---	---	---	---	---	---	---
Sand-hash	10.287	0.865	---	---	---	---	---	---
Sand-organic	---	---	---	---	---	---	---	---
Sand-rock	---	---	---	---	---	---	---	---
Sand-sand	---	---	---	---	---	---	---	---
Other variables								
Depth Range	-0.548	0.059	-0.847	0.020*	---	---	---	---
Patch area	---	---	---	---	0.017	0.035	---	---
Slope	---	---	---	---	---	---	---	---

Table 4b. This table shows the results for *Citharichthys stigmaeus* and *Sebastes crameri*, with moderate to low success predicting species presence. Statistically significant ($p < 0.05$) substratum types or other variables are in bold type and marked with an asterisk (*). Empty cells indicate a given species did not occur on that substratum type. Cells marked with hash marks (---) indicate substratum types that were removed from the logistic regression model. Negative or positive β values indicate negative and positive relationships between fish species and habitat features, respectively.

Substratum types	<i>Citharichthys stigmaeus</i>		<i>Sebastes crameri</i>	
	β	Significance	β	Significance
Boulder-boulder				
Boulder-cobble				
Boulder-hash				
Boulder-organic				
Boulder-rock				
Boulder-sand				
Cobble-cobble				
Hash-cobble				
Hash-hash	2.530	0.000*		
Hash-organic	---	---		
Hash-rock	---	---		
Organic-hash				
Organic-rock				
Rock-boulder				
Rock-cobble				
Rock-hash	2.242	0.000*		
Rock-organic	---	---		
Rock-rock	---	---	---	---
Rock-sand			---	---
Sand-hash				
Sand-organic				
Sand-rock	---	---	---	---
Sand-sand	---	---	---	---
Other variables				
Depth Range			1.641	0.013*
Patch area	---	---	0.041	0.010*
Slope			0.687	0.049*

Table 4c. This table shows the results for *Sebastes chlorostictus*, *S. elongatus*, and *S. saxicola*, with moderate to low success predicting species presence. Statistically significant ($p < 0.05$) substratum types or other variables are in bold type and marked with an asterix (*). Empty cells indicate a given species did not occur on that substratum type. Cells marked with hash marks (---) indicate substratum types that were removed from the logistic regression model. Negative or positive β values indicate negative and positive relationships between fish species and habitat features, respectively.

Substratum types	<i>Sebastes chlorostictus</i>		<i>Sebastes elongatus</i>		<i>Sebastes saxicola</i>	
	β	Significance	β	Significance	β	Significance
Boulder-boulder						
Boulder-cobble						
Boulder-hash						
Boulder-organic						
Boulder-rock						
Boulder-sand						
Cobble-cobble						
Hash-cobble						
Hash-hash						
Hash-organic						
Hash-rock						
Organic-hash						
Organic-rock						
Rock-boulder						
Rock-cobble						
Rock-hash						
Rock-organic	1.890	0.148				
Rock-rock	2.529	0.023	-1.629	0.151	---	---
Rock-sand			1.068	0.129	---	---
Sand-hash						
Sand-organic	---	---	106.748	1.000		
Sand-rock	2.418	0.050	---	---	---	---
Sand-sand	---	---	---	---	---	---
Other variables						
Depth Range	0.597	0.278			1.520	0.004*
Patch area	0.038	0.011	0.014	0.334	0.026	0.001*
Slope	7.899	0.828	7.093	0.779		

Table 5a. Observed distribution of fish species on different habitat categories relative to expected distribution based on habitat distribution. Proportion (P_i) of total habitat was calculated using IHE parameters. Expected fish distributions (Fish P_{exp}) greater or less than the upper and lower 95% Confidence Intervals (CI) based on observed fish distributions (Fish P_{obs}) indicate habitat electivity or avoidance. Habitat electivity (+), avoidance (-), or neutrality (=) are indicated in the last column. The following species all primarily elected Mixed Habitats. Habitats indicated with bold had significantly greater fish observed than expected based on the HUA.

<i>R. nicholsii</i>	P_i of total habitat	Observed	Expected	Lower CI	Fish P_{obs}	Upper CI	Fish P_{exp}	IHE Value	HUI Value	Electivity
Hard	0.29	35	42	0.08	0.24	0.39	0.29	0.11	0.09	=
Mixed	0.12	81	17	0.37	0.55	0.73	0.12	0.81	0.87	+
Soft	0.36	32	53	0.07	0.22	0.37	0.36	0.08	0.04	=
Deep Hard	0.02	0	4	0.00	0.00	0.00	0.02	0.00	0.00	-
Deep Mixed	0.09	0	13	0.00	0.00	0.00	0.09	0.00	0.00	-
Deep Soft	0.12	0	18	0.00	0.00	0.00	0.12	0.00	0.00	-
<i>S. rosaceus</i>										
Hard	0.29	22	16	0.24	0.40	0.56	0.29	0.17	0.13	=
Mixed	0.12	33	6	0.44	0.60	0.76	0.12	0.83	0.87	+
Soft	0.36	0	20	0.00	0.00	0.00	0.36	0.00	0.00	-
Deep Hard	0.02	0	1	0.00	0.00	0.00	0.02	0.00	0.00	-
Deep Mixed	0.09	0	5	0.00	0.00	0.00	0.09	0.00	0.00	-
Deep Soft	0.12	0	7	0.00	0.00	0.00	0.12	0.00	0.00	-
<i>S. semitinctus</i>										
Hard	0.29	0	74	0.00	0.00	0.00	0.29	0.00	0.00	-
Mixed	0.12	190	31	0.66	0.73	0.80	0.12	0.65	0.78	+
Soft	0.36	18	94	0.03	0.07	0.11	0.36	0.02	0.01	-
Deep Hard	0.02	20	6	0.04	0.08	0.12	0.02	0.26	0.16	+
Deep Mixed	0.09	6	24	0.00	0.02	0.05	0.09	0.01	0.01	-
Deep Soft	0.12	27	32	0.06	0.10	0.15	0.12	0.06	0.04	=
<i>S. wilsoni</i>										
Hard	0.29	87	50	0.18	0.23	0.28	0.28	0.08	0.07	=
Mixed	0.12	46	21	0.59	0.65	0.71	0.12	0.72	0.80	+
Soft	0.36	0	63	0.00	0.00	0.00	0.36	0.00	0.00	-
Deep Hard	0.02	12	4	0.01	0.03	0.05	0.02	0.13	0.07	=
Deep Mixed	0.09	29	16	0.04	0.08	0.11	0.09	0.07	0.06	=
Deep Soft	0.12	2	22	0.00	0.01	0.01	0.12	0.00	0.00	=

Table 5b. Observed distribution of fish species on different habitat categories relative to expected distribution based on habitat distribution. Proportion (P_i) of total habitat was calculated using IHE parameters. Expected fish distributions (Fish P_{exp}) greater or less than the upper and lower 95% Confidence Intervals (CI) based on observed fish distributions (Fish P_{obs}) indicate habitat electivity or avoidance. Habitat electivity (+), avoidance (-), or neutrality (=) are indicated in the last column. The following species all primarily elected Hard Habitats. Habitats indicated with bold had significantly greater fish observed than expected based on the HUA.

<i>S. serranoides</i>	P_i of total habitat	Observed	Expected	Lower CI	Fish P_{obs}	Upper CI	Fish P_{exp}	IHE Value	HUI Value	Electivity
Hard	0.29	114	34	0.89	0.94	0.99	0.29	0.85	0.81	-
Mixed	0.12	6	14	0.00	0.05	0.10	0.12	0.14	0.19	-
Soft	0.36	1	44	-0.01	0.01	0.03	0.36	0.01	0.00	-
Deep Hard	0.02	0	3	0.00	0.00	0.00	0.02	0.00	0.00	-
Deep Mixed	0.09	0	11	0.00	0.00	0.00	0.09	0.00	0.00	-
Deep Soft	0.12	0	15	0.00	0.00	0.00	0.12	0.00	0.00	-
<i>S. mystidinus</i>										
Hard	0.29	1000	336	0.82	0.85	0.87	0.29	0.76	0.73	+
Mixed	0.12	71	139	0.04	0.06	0.08	0.12	0.17	0.23	-
Soft	0.36	110	425	0.07	0.09	0.11	0.36	0.07	0.04	-
Deep Hard	0.02	0	29	0.00	0.00	0.00	0.02	0.00	0.00	-
Deep Mixed	0.09	0	107	0.00	0.00	0.00	0.09	0.00	0.00	-
Deep Soft	0.12	0	145	0.00	0.00	0.00	0.12	0.00	0.00	-
<i>S. carinatus</i>										
Hard	0.29	20	7	0.70	0.87	1.04	0.29	0.68	0.60	-
Mixed	0.12	3	3	-0.04	0.13	0.30	0.12	0.32	0.40	=
Soft	0.36	0	8	0.00	0.00	0.00	0.36	0.00	0.00	-
Deep Hard	0.02	0	1	0.00	0.00	0.00	0.02	0.00	0.00	-
Deep Mixed	0.09	0	2	0.00	0.00	0.00	0.09	0.00	0.00	-
Deep Soft	0.12	0	3	0.00	0.00	0.00	0.12	0.00	0.00	-
<i>O. pictus</i>										
Hard	0.29	98	34	0.68	0.82	0.96	0.29	0.61	0.54	+
Mixed	0.12	19	14	0.03	0.16	0.29	0.12	0.37	0.45	=
Soft	0.36	3	43	-0.03	0.03	0.08	0.36	0.02	0.01	-
Deep Hard	0.02	0	3	0.00	0.00	0.00	0.02	0.00	0.00	-
Deep Mixed	0.09	0	11	0.00	0.00	0.00	0.09	0.00	0.00	-
Deep Soft	0.12	0	15	0.00	0.00	0.00	0.12	0.00	0.00	-
<i>O. elongatus</i>										
Hard	0.29	19	9	0.46	0.63	0.81	0.29	0.40	0.36	+
Mixed	0.12	5	4	0.03	0.17	0.30	0.12	0.34	0.42	=
Soft	0.36	1	11	-0.03	0.03	0.10	0.36	0.02	0.01	-
Deep Hard	0.02	0	1	0.00	0.00	0.00	0.02	0.00	0.00	-
Deep Mixed	0.09	3	3	-0.01	0.10	0.21	0.09	0.15	0.15	=
Deep Soft	0.12	2	4	-0.02	0.07	0.16	0.12	0.09	0.05	=

Table 5c. Observed distribution of fish species on different habitat categories relative to expected distributions based on habitat distribution. Proportion (P_i) of total habitat was calculated using IHE parameters. Expected fish distributions (Fish P_{exp}) indicate greater or less than the upper and lower 95% Confidence Intervals (CI) based on observed fish distributions (Fish P_{obs}) indicate habitat electivity or avoidance. Habitat electivity (+), avoidance (-), or neutrality (=) are indicated in the last column. The following species all primarily elected Hard Habitats. Habitats indicated with bold had significantly greater fish observed than expected based on the HUA.

<i>C. stigmaeus</i>	P _i of total habitat	Observed	Expected	Lower CI	Fish P _{obs}	Upper CI	Fish P _{exp}	IHE Value	HUI Value	Electivity
Hard	0.29	5	112	-0.03	0.01	0.05	0.29	0.01	0.02	-
Mixed	0.12	11	46	-0.03	0.03	0.09	0.12	0.10	0.21	-
Soft	0.36	376	141	0.89	0.96	1.03	0.36	0.89	0.77	-
Deep Hard	0.02	0	9	0.00	0.00	0.00	0.02	0.00	0.00	-
Deep Mixed	0.09	0	36	0.00	0.00	0.00	0.09	0.00	0.00	-
Deep Soft	0.12	0	48	0.00	0.00	0.00	0.12	0.00	0.00	-
<i>S. crameri</i>										
Hard	0.29	0	17	0.00	0.00	0.00	0.29	0.00	0.00	-
Mixed	0.12	0	7	0.00	0.00	0.00	0.12	0.00	0.00	-
Soft	0.36	0	21	0.00	0.00	0.00	0.36	0.00	0.00	-
Deep Hard	0.02	34	1	0.42	0.58	0.73	0.02	0.88	0.83	-
Deep Mixed	0.09	18	5	0.16	0.31	0.45	0.09	0.09	0.14	+
Deep Soft	0.12	7	7	0.02	0.12	0.22	0.12	0.03	0.03	=
<i>S. chlorostictus</i>										
Hard	0.29	0	13	0.00	0.00	0.00	0.29	0.00	0.00	-
Mixed	0.12	0	5	0.00	0.00	0.00	0.12	0.00	0.00	-
Soft	0.36	0	16	0.00	0.00	0.00	0.36	0.00	0.00	-
Deep Hard	0.02	7	1	0.02	0.16	0.29	0.02	0.48	0.37	=
Deep Mixed	0.09	36	4	0.65	0.80	0.95	0.09	0.50	0.61	+
Deep Soft	0.12	2	6	-0.03	0.04	0.12	0.12	0.02	0.02	-
<i>S. elongatus</i>										
Hard	0.29	0	8	0.00	0.00	0.00	0.29	0.00	0.00	-
Mixed	0.12	0	3	0.00	0.00	0.00	0.12	0.00	0.00	-
Soft	0.36	0	10	0.00	0.00	0.00	0.36	0.00	0.00	-
Deep Hard	0.02	1	1	-0.05	0.03	0.12	0.02	0.16	0.12	=
Deep Mixed	0.09	17	3	0.36	0.59	0.81	0.09	0.54	0.66	+
Deep Soft	0.12	11	4	0.16	0.38	0.60	0.12	0.30	0.22	+
<i>S. saxicola</i>										
Hard	0.29	0	22	0.00	0.00	0.00	0.29	0.00	0.00	-
Mixed	0.12	0	9	0.00	0.00	0.00	0.12	0.00	0.00	-
Soft	0.36	6	28	0.00	0.08	0.15	0.36	0.02	0.02	-
Deep Hard	0.02	5	2	0.00	0.06	0.13	0.02	0.29	0.26	=
Deep Mixed	0.09	17	7	0.11	0.22	0.34	0.09	0.20	0.28	+
Deep Soft	0.12	49	9	0.50	0.64	0.77	0.12	0.49	0.44	+

Figure 1: Map of Big Creek Ecological Reserve and adjacent areas (B) along the central coast of California (A). The reserve boundary extends from the mean high tide zone to the 100 meter contour and is confined by the following points: 36°05.31' N 121°38.24' W, 36°05.31' N 121°37.10' W, 36°03.65' N 121°37.04' W, 36°03.65' N 121°35.50' W.

Figure 2. Distribution of transects inside and west of the Big Creek Ecological Reserve. The small black lines represent transects over different habitat types. Colored areas represent different substrata types. Black triangles and black shapes represent rock outcrops and pinnacles. Light shaded areas are soft unconsolidated sediments.

Figure 3. Frequency of patch area inside and west of BCER in 1997.

Figure 4. Mean patch area and standard error for each substratum type. BB=Boulder-boulder, BC=Boulder-cobble, BH=Boulder-hash, BR=Boulder-rock, BS=Boulder-sand, CC=Cobble=cobble, CR=Cobble-rock, HC=Hash-cobble, HH=Hash-hash, HO=Hash-organic, HR=Hash-rock, OH=Organic-rock, OO=Organic-organic, RB=Rock-boulder, RC=Rock-cobble, RR=Rock-rock, RS=Rock-sand, SH=Sand-hash, SO=Sand-organic, SR=Sand-rock, and SS=Sand-sand

Figure 5. Total area of patches per substratum type. BB=Boulder-boulder, BC=Boulder-cobble, BH=Boulder-hash, BR=Boulder-rock, BS=Boulder-sand, CC=Cobble=cobble, CR=Cobble-rock, HC=Hash-cobble, HH=Hash-hash, HO=Hash-organic, HR=Hash-rock, OH=Organic-rock, OO=Organic-organic, RB=Rock-boulder, RC=Rock-cobble, RR=Rock-rock, RS=Rock-sand, SH=Sand-hash, SO=Sand-organic, SR=Sand-rock, and SS=Sand-sand.

Figures 6 a-c. Index of Habitat Electivity (IHE) for Habitat Guilds. Available habitat is plotted on the left and is composed of percent area of each habitat type (black) and percent frequency of each habitat patch occurrence (white). The percent frequency occurrence of each species (grey) and IHE (scale bar) are plotted on the right.

6a. Shallow Mixed Habitat Guilds

6b. Shallow Hard Habitat Guilds

6c. Shallow Soft, Deep Mixed, Deep Soft, and Deep Hard Habitat Guilds

Figure 7. Total abundance of adult and YOY/juvenile *Ophiodon elongatus* on different habitat types. Adult and YOY/juvenile fish were distinguished based on 30 cm total length. Five lingcod were not able to be measured and were not included in this histogram.