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# Impact of habitat structure on fish populations in kelp forests at a seascape scale

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ABSTRACT: Habitat use by a species is a vital component in explaining the dynamics of natural populations. For mobile marine species such as fishes, describing habitat heterogeneity at a seascape scale is essential because it quantifies the spatial extent to which fishes are interacting with their environment. Here, we explored the relationships between habitat metrics and the density and size of kelp forest fishes across a seascape that is naturally fragmented. Multibeam sonar and GIS analysis were employed to create a seascape map that explicitly defined bathymetry and spatial configuration of rocky reefs in southern California (USA). Georeferenced subtidal transects were conducted across this seascape to describe habitat attributes, including the density of macroalgae, and record the number and size of fishes. Multiple regression analyses were conducted to identify which variables of habitat structure were most important in describing numerical density, biomass density, average size, and maximum size for fishes. Responses to different habitat components were dependent on particular species, choice of spatial scale, and the inherent characteristics of the seascape itself. Notably, the relative influence of seascape components was dependent on the configuration of the seascape, where fishes in a more isolated and less connected seascape were more influenced by spatial configuration than fishes in a seascape with greater habitat connectedness. This study demonstrates that explicit habitat maps allow for a more comprehensive understanding of population structure when describing fishes across large spatial scales.

KEY WORDS: Fish populations · Habitat structure · Seascape · Remote sensing · Rocky reefs · Kelp forest

## INTRODUCTION

Seascapes are often a mosaic of habitat patches that are heterogeneous in both habitat composition and spatial configuration. This mosaic can have considerable effects on the distribution and abundances of organisms (Fahrig 2003), and in determining species' habitat use patterns that are vital to understanding the dynamics of natural populations (Turner 1989). Seascape ecology explores how ecological processes such as population dynamics, species interactions, and assemblage structure are related to and altered by marine seascape patterns (Boström et al. 2011, Wedding et al. 2011). This approach is essential for more mobile species such as fishes, because it quantifies habitat heterogeneity at scales that are relevant to the interaction between these organisms and their environment (Grober-Dunsmore et al. 2009, Boström et al. 2011). Responses to seascape structure, however, are often species- or guild-specific and depend on resource use requirements. Consequently, it is important to map seascapes at high resolutions across large spatial extents for a more comprehensive understanding of the distribution and abundance of multiple species (Kendall et al. 2011, Pittman & Brown 2011). Mapping habitat structure at

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a seascape scale and identifying how habitat metrics relate to species-specific responses is critical for assessing population structure. A seascape approach is particularly useful when implementing marine spatial planning methods because the scale of a seascape is often similar to the scale of management practices (Garcia Charton & Perez Ruzafa 1999, Friedlander et al. 2007). Although coral and seagrass habitat maps have been used in many ecological studies, there remains a lack of seascape studies focusing on macroalgae and kelp forest ecosystems (Boström et al. 2011).

A seascape is defined by 2 components: (1) the composition of habitat within patches and (2) the spatial configuration of habitat among patches. The first component considers the variability of habitat within a patch and is described by bathymetric complexity and biogenic structure (e.g. corals and macroalgae). Measures of bathymetry such as depth, slope, and rugosity have shown strong relationships between fish assemblage structure across a range of spatial scales (Connell & Jones 1991, Young et al. 2010, Knudby et al. 2011, Cameron et al. 2014), and the structure of bathymetric habitat can alter ecological interactions (Hixon & Beets 1993, Catano et al. 2016). For example, herbivorous fishes substantially reduce foraging in areas of high vs. low rugosity in the presence of predators (Catano et al. 2016). Biogenic structure, and in particular, foundational species such as macroalgae, have substantial effects on population and community dynamics by providing shelter (Ebeling & Laur 1985) and food (Bray & Ebeling 1975), and by mediating predator-induced mortality (Anderson 2001). Importantly, species-specific responses to habitat structure can differ substantially (Deza & Anderson 2010).

The second component of seascape ecology considers the geometry and spatial heterogeneity of habitat across large spatial extents. The configuration of habitat patches can have significant effects on the distribution and abundances of organisms (With et al. 1997, Tischendorf et al. 2003, Grober-Dunsmore et al. 2009), and the effects on fish population structure and diversity can be more pronounced than those of within-patch habitat structure (Pittman et al. 2007, Grober-Dunsmore et al. 2008, Huntington et al. 2010). For example, the proximity and connectivity of adjacent habitats are often the most important parameters for the distribution of fishes (Olds et al. 2012). Nevertheless, how species perceive and interact with habitat metrics such as isolation distance and habitat connectivity is less well understood (Grober-Dunsmore et al. 2009, Boström et al. 2011). This is particularly relevant for temperate kelp-forested rocky reef fishes, whereby movement patterns and home ranges are known for only a select number of species (Lowe et al. 2003, Topping et al. 2006, McKinzie et al. 2014). To reconcile this gap in knowledge, quantifying a suite of configuration variables at multiple spatial scales allows for a better understanding of habitat use by fishes (Kendall et al. 2011, Pittman & Brown 2011). Moreover, a comprehensive approach to seascape ecology involves both within-patch metrics (rugosity, depth) and among-patch metrics (proximity and connectedness of surrounding habitat) to explore the relative influences of habitat complexity on fish population structure.

Our approach here was to investigate how kelp-forested rocky reefs influence fish population structure at a seascape scale. Temperate kelp forests are among the most productive ecosystems in the world, where rocky reefs are dominated by habitat-forming kelps that create substantial 3-dimensional structure throughout the water column (Dayton 1985). At a within-reef scale, some fishes play a vital role in maintaining a kelp forest ecosystem by consumption of herbivores that can have substantial effects on kelp abundance and recruitment (Cowen 1983, Davenport & Anderson 2007), while also relying on kelp structure for refuge (Ebeling & Laur 1985, Carr 1994, Anderson 2001). Here, we describe how large-scale measures of habitat variables affect reef fish populations by evaluating habitat structure at the reef scale to evaluate the effects of multiple habitat types across a seascape. This reef level seascape approach will allow for direct comparison to other large-scale seascape studies that have been conducted in coral reef systems.

Quantifying seascape metrics requires explicit measurements of habitat across large spatial extents. Remote sensing technology is a valuable tool with which to map marine habitats with great accuracy and efficiency (Mumby et al. 1997, Brown & Blondel 2009, Knudby et al. 2011). High-resolution maps generated from remotely sensed data allow for a multi-scale approach when evaluating the importance of different types of habitat structural complexity. Specifically, multibeam echo-sounders (MBES) have been used for hydro-acoustic mapping of shallow water systems to map physical seafloor characteristics at resolutions less than 1 m (Hughes Clarke et al. 1996) which provide both bathymetry and substratum type maps. Informed by geo-referenced survey data, MBES data are effective tools for habitat classification (Brown et al. 2011). In conjunction with geographic information system (GIS) software, remote sensing is a powerful approach to explore fish populations and communities across large spatial extents

(Hamel & Andréfouët 2010, Brown et al. 2011, Wedding et al. 2011).

To pursue this research, we co-registered remotely sensed seafloor data and habitat maps with *in situ* surveys of habitat structure on southern California (USA) kelp-forested reefs. We also recorded the number and size of fishes to describe their density, biomass, and size in relation to the physical and biological seascape. The size and biomass density of fishes are important variables because there is an exponential relationship between body size and fecundity for many fish species (Love et al. 1996, Claisse et al. 2012) that may result in considerable differences in reproductive output and larval production. Consequently, identifying the seascape components that relate to the distribution and abundance of fishes is instrumental when considering regional population dynamics and conservation management efforts. To our knowledge, this is the first study to evaluate both fine-scale composition and large-scale configuration of habitat across a seascape in a temperate ecosystem (Boström et al. 2011). We aimed to address 3 objectives: (1) the relative importance of habitat composition and configuration on the numerical density, biomass density, and size of fishes across southern California seascapes, (2) the individual habitat structural metrics that explain variability in fish population density and body size, and (3) the scale(s) at which fishes respond to the seascape.

## MATERIALS AND METHODS

### Study area

This study was conducted along the southern California coastline from Laguna Beach (33° 33′ N, 117° 49′ W) to San Diego (32° 40′ N, 117° 15′ W) spanning >100 km of coastline (Fig. 1). This area is ideal for a study of variation in a seascape because it is naturally fragmented with a wide diversity in patch size, configuration, and composition. The seascape is composed of patches of rocky reef substratum dominated by macroalgae including the giant kelp *Macrocystis pyrifera* and areas of unconsolidated sediment. Reefs range from as shallow as a few meters to depths of 40 m. Four focal regions were chosen for surveys: Laguna Beach, Encinitas, La Jolla, and Point Loma. The Laguna Beach and Encinitas regions comprise a network of reefs ranging in size from 0.006 to 222 ha, whereas La Jolla and Point Loma represent large continuous reefs of approximately 1079 and 1768 ha, respectively.

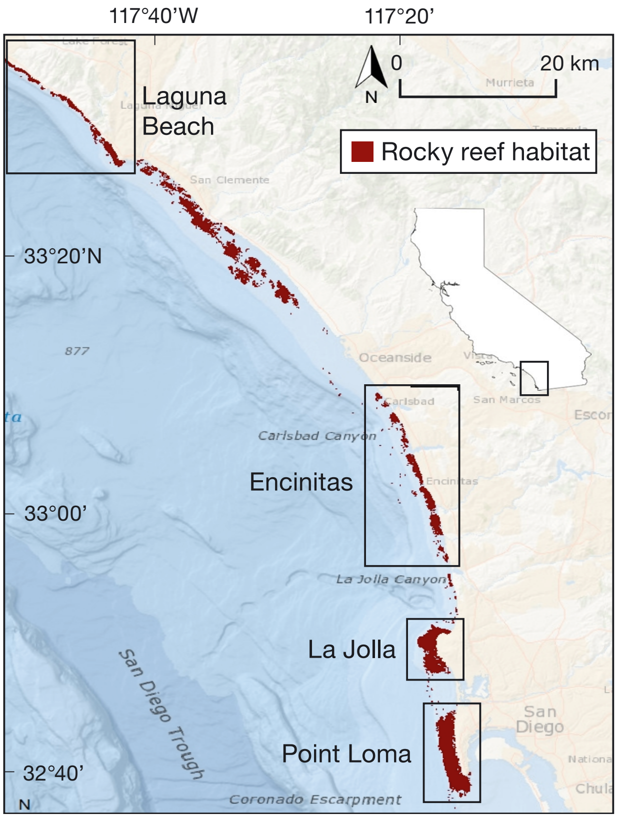

Fig. 1. Survey regions in southern California, USA

### *In situ* surveys

Subtidal surveys were conducted by SCUBA divers at the 4 regions from July to November 2012 and 2013. For each year at Laguna Beach and Encinitas, different reefs of varying sizes were randomly chosen, and a greater number of smaller reefs were surveyed compared to larger reefs to survey a comparable amount of reef area and to account for expected greater variability in the density of fishes (Ault & Johnson 1998). We defined the minimum reef size as 60 $m^2$ (0.006 ha), which is the area of 1 survey transect. Approximation of reef size was made using personal knowledge and the California Department of Fish and Wildlife (CDFW) open source GIS for data on the extent of surface kelp. Point Loma and La Jolla reefs were also surveyed in 2012 and 2013 but at different locations on these large reefs.

For each survey of a reef, transects were 30 m long, and each transect was oriented parallel to shore and separated by no less than 20 m end to end and 10 m side to side for statistical independence. The number of replicate transects within each reef was based on the maximum number of transects that could be surveyed while maintaining minimum separation distances between transects. Transects per reef ranged from a minimum of 1 to a maximum survey effort of 12 transects per reef; 18 transects were conducted at Point Loma and La Jolla because of their large areas. To ensure that surveys between years were independent, a minimum of 200 m distance was required to separate surveys conducted in 2012 and 2013 for larger reefs surveyed in both years. GPS points were recorded at the beginning and end of all transects using buoys deployed at the starting and ending points of each transect. This ensured that biological data were georeferenced to remotely sensed maps with a high degree of confidence.

Two teams of divers conducted 3 survey techniques along a 30 m transect to survey habitat attributes (Table 1) and fish communities . One team performed surveys of fishes while the other team performed benthic composition surveys. Transects to survey fish communities covered 3 depth zones within the water column: bottom, mid-water, and canopy. Each diver identified the species, number, and estimated size of fish to the nearest centimeter within a 2 m wide × 2 m high corridor along the length of the 30 m transect at 3 depth zones for a total volume of 360 $m^3$ per transect. All fish were recorded with the exception of small recruits or highly cryptic species (e.g. blackeye goby *Coryphopterus nicholsii*). The other team of divers recorded macroalgae, benthic habitat type, and vertical relief. One diver performed a swath survey, in which all macroalgae (Table 1) were counted along a 30 m long × 2 m wide corridor. Macroalgae individuals were enumerated to provide a characterization of the density and structural complexity of biogenic habitat. In addition, giant kelp stipes were counted as an estimate of biogenic structure that extends throughout the water column to the water surface. The other diver performed a uniform-point-contact (UPC) survey at discrete 1 m intervals to record depth, substratum type, and vertical relief of the substratum along the transect. Vertical relief was measured as the greatest vertical distance of the benthos recorded within 1 $m^2$.

Table 1. Habitat attributes recorded in subtidal surveys. Substratum type is characterized by rock sizes. UPC: uniform point contact

**Macroalgal species**
*Cystoseira osmundacea*
*Egregia menziesii*
*Eisenia arborea*
*Laminaria farlowii*
*Macrocystis pyrifera* (adult stipes)
*Macrocystis pyrifera* (juvenile)
*Macrocystis pyrifera* stipes
*Pterygophora californica*

**Substratum type categories**
Sand
Cobble (≤10 cm)
Boulder (10–100 cm)
Bedrock (≥1 m)

**Vertical relief UPC categories**
0–10 cm
10–50 cm
50–100 cm
1–2 m
>2 m

### Seafloor data acquisition and processing

Multibeam and backscatter mapping were conducted on the RV 'Point Loma' using a pole-mounted RESON SeaBat 7125 multibeam sonar system equipped with real-time kinematic GPS positioning. After acquisition, data were imported into CARIS Hydrographic Information Processing Software (HIPS) & CARIS Sonar Image Processing Software (SIPS) ver. 8.1, in which data were converted and erroneous data soundings were removed manually using hydrographic data cleaning procedures detailed by CARIS. After cleaning of artifacts, base surfaces were exported as 1 m ASCII files to Fledermaus ver. 6.1 software (QPS). Base surfaces were then exported as a 1 m gridded digital elevation model (DEM), and further benthic terrain analyses were performed in ArcGIS ver. 10.1 (ESRI). Slope was calculated using the spatial analyst tool in ArcGIS, represented as rate of maximum change in the *z*-value for each 1 m cell, reported in degrees. Rugosity was derived using the Jenness extension (Jenness 2004), calculated as the ratio of the surface area to the planimetric area for each 1 m cell. Depth, slope, and rugosity statistics were then averaged for each 30 × 2 m transect survey area using the zonal statistics tool.

### Habitat classification

Backscatter data were collected simultaneously with bathymetry using the Reson SeaBat 7125, and were used to classify habitat substratum type (Brown & Blondel 2009), by classifying geophysical signatures (Le Bas & Huvenne 2009). The acoustic backscatter signal, represented in decibels (dB), is a function of reflection from the seafloor, degree of signal scattering, and the proportion of acoustic signal that returns back to the transducer (Brown & Blondel 2009). Backscatter data were processed in CARIS ver. 8.1 according to the software protocol and then exported to Fledermaus to create a 1 m DEM in which backscatter intensity represents the $z$-value. The DEM was then exported to ArcGIS for habitat classification. Our habitat classification for this research is binary, whereby habitat is defined as rocky reefs dominated by macroalgae and the non-habitat as unconsolidated sandy bottom.

To classify backscatter data into habitat types, we used UPC substratum data collected on survey transects to inform our classification. For all transects, GPS positions were recorded at the start and end of transects (0 and 30 m points). UPC substratum points were only included as ground-reference points if the adjacent meter substratum point was the same category as the 0 or 30 m substratum point (e.g. the 30 and 29 m UPC substratum points both must have been categorized as sand to use as a sand ground-reference point). Bedrock and sand UPC classifications were used to delineate hardbottom rocky reef habitat from the sandy bottom matrix. For all ground-reference points (n = 218), a 1 m buffer was created in ArcGIS, and backscatter intensity values were acquired using the zonal statistics tool. The mean of the minimum and maximum intensity values for each buffer area were calculated to create the range of values for both bedrock and sand substratum types. The ranges were then used to classify backscatter intensity values into hard and sandy substratum in ArcGIS.

We also used the slope and rugosity DEMs to identify areas of high topographic complexity, indicating rocky reef habitat. Cells exceeding 5° slope and 1.0001 rugosity values, indicating areas of seafloor roughness, were categorized as rocky reef habitat. All lower values were classified as flat sandy bottom. Rocky reef habitat from both the backscatter and bathymetry data were then merged in ArcGIS and used to identify hardbottom rocky reef habitat (Fig. 2).

To assess the accuracy of the habitat classification process, *in situ* substratum UPC data from transects were compared with the classified habitat raster. The middle UPC point (15 m) of an independent set of transects (n = 174) that were not used for habitat classification were used as the comparison validation points. If the classified habitat raster cell overlaid on the 15 m midpoint and at least 3 of the surrounding 8 cells bordering that focal cell matched the *in situ* classification of substratum, the classification was considered successful.

## Spatial analysis

Due to the logistical limitations of multibeam acquisition, additional data sources were used to infer habitat beyond the extent of multibeam data. We used 11 of the years between 1989 and 2012 of kelp forest canopy data at a 0.3 m resolution, publicly available courtesy of the CDFW as a proxy of rocky reef kelp forest habitat for areas where multibeam data were not available. All 11 years were merged in ArcGIS to represent the total potential extent of kelp forest habitat. We further supplemented our dataset

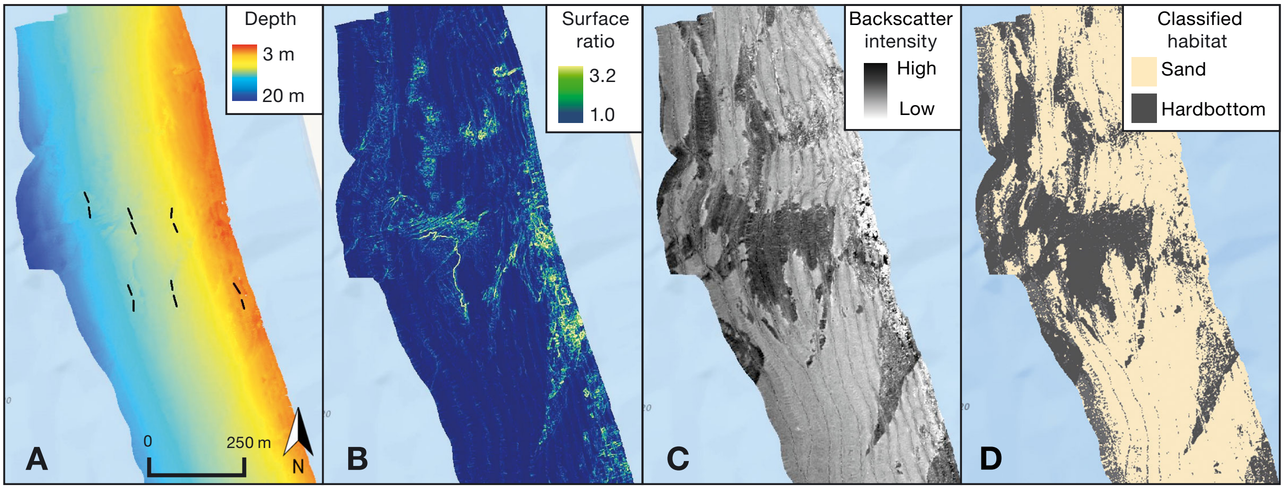

Fig. 2. Results from multibeam sonar for a portion of area in Encinitas, California. (A) Bathymetry, where black lines indicate locations of subtidal transect surveys. (B) Surface ratio (calculated by the Jenness extension in ArcGIS) calculated by the ratio of the surface area to the planimetric area for each raster cell (1 m resolution). (C) Backscatter intensity values. (D) Classified habitat derived from surface ratio and backscatter maps, using *in situ* surveys as georeferenced points to inform classification

with data from the California Seafloor Mapping Project from the Seafloor Mapping Lab at California State University, Monterey Bay (http://seafloor.otterlabs.org/SFMLwebDATA.htm), providing greater spatial extents of bathymetry and the ability to compare and validate our data with other sources. The CDFW kelp layer and multibeam-derived hard-bottom layers were compared using the band collection statistics tool in ArcGIS, providing a Pearson product-moment correlation statistic. Kelp and hard-bottom polygon layers were then combined to create a layer representing the total potential habitat for the entire study region, which then was used as the final output for all spatial analyses of rocky reef kelp forest habitat.

To address our goal of understanding how fishes interact with habitat at the scale of a seascape, all of our configuration calculations were conducted for each reef, where transects were averaged for each reef. We defined reefs as being distinctly isolated by a minimum isolation distance of 30 m. Therefore, if polygons were <30 m from one another they were combined to create 1 reef using the aggregate polygon tool in ArcGIS. Areas <30 m (or 60 m$^2$) are likely functionally acting as small-scale heterogeneity within a reef, and should be classified as part of the reef. To evaluate how fish respond to the surrounding seascape at a reef scale, a suite of configuration variables were calculated for each reef surveyed. Area and fractal dimension were calculated for surveyed reefs, and 3 surrounding seascape configuration variables, viz. percent habitat, proximity index (PI), and connectedness index (CI) using ArcGIS and FRAGSTATS spatial analysis software (Table 2), that describe the habitat surrounding the focal reefs were calculated at 5 spatial scales (100, 250, 500, 750, and 1000 m). The range for radii encompassed available movement data from acoustic tracking studies for a select number of species that were surveyed in this study (Lowe et al. 2003, Topping et al. 2005) and was comparable to other seascape studies in coral reef systems (Pittman et al. 2007, Grober-Dunsmore et al. 2009, Kendall et al. 2011) and temperate systems (Young et al. 2010, Wedding & Yoklavich 2015).

### Data analysis

To evaluate habitat structure and fish responses at the reef scale, fish population variables, macroalgae densities, and bathymetric data for all transects were averaged for an entire reef. Recruits (young-of-year fishes) were eliminated from the analysis. Numerical density, biomass density, mean size (total length, TL), and maximum size (TL), for the 5 most abundant fish species were calculated. Biomass was calculated according to published species-specific length–weight relationships. Prior to analysis, variables were trans-

Table 2. Metrics and descriptions used for best subset analysis with multiple linear regression

| Structural component | Metric | Description | Source |
|---|---|---|---|
| Macroalgae | PCA algae component 1 | *Cystoseira osmundacea, Laminaria farlowii, Pterygophora californica* | *In situ* |
| | PCA algae component 2 | *Macrocystis pyrifera* (adults, juvenile, adult stipe count) | *In situ* |
| | PCA algae component 3 | *Egregia menziesii, Eisenia arborea*, Total algae count | *In situ* |
| Bathymetry | Relief | Total vertical distance within 1 m$^2$, averaged per transect | Multibeam and *in situ* |
| | SD relief | Mean standard deviation of relief per transect | Jenness ext. ArcGIS |
| | Depth | Depth (m), averaged per transect | Multibeam and *in situ* |
| Configuration | Patch area | Area | ArcGIS |
| | Fractal dimension | Patch edge complexity | FRAGSTATS |
| | % habitat[a,b] | Percent rocky reef habitat within radius area | ArcGIS |
| | Proximity index[a,b] | Isolation and area of all patches within radius | FRAGSTATS |
| | Connectedness index[a,c] | Clumpiness or cohesion index: aggregation and fragmentation of habitat | FRAGSTATS |

[a] Metrics were calculated at 100, 250, 500, 750, and 1000 m radius distance from focal patch
[b] Radius distance calculated from edge of focal patch
[c] Radius distance calculated from centroid of focal patch

Table 3. Principal component analysis output for algae variables

| Algae metric | Variable component loading | % Explained<br>All regions | Laguna | Encinitas |
|---|---|---|---|---|
| Component 1 | *Cystoseira osmundacea, Laminaria farlowii, Pterygophora californica* | 29 | 34 | 29 |
| Component 2 | *Macrocystis pyrifera* (adults, juvenile, adult stipe count) | 24 | 26 | 15 |
| Component 3 | *Egregia menziesii, Eisenia arborea*, Total algae count | 21 | 18 | 32 |
| | Total variation explained | 74 | 78 | 76 |

formed when necessary to meet assumptions of normality and heteroscedasticity. To reduce the number of variables and confront collinearity issues, principal components analysis (PCA) was used to combine macroalgae variables to represent community composition groups. PCA revealed 3 components of variation (Table 3), and the variable loading was the same for all regional-level analyses. Resulting factor scores for each component were used in multiple regression analysis.

For configuration variables with multiple radii calculations (percent habitat, PI, CI), only 1 radius was chosen to be included in further analysis. Bivariate regressions were run for all fish response variables against each radius to identify the radius with the highest $R^2$ and a p-value ≤ 0.05. This radius for each configuration variable was included in further analysis, resulting in unique configuration radii variables used for each response variable for each species. Macroalgae PCA components, bathymetry variables, and selected configuration variables were run through the Best Subsets analysis in SYSTAT Version 13.1. This method outputs the top performing multiple linear regression models for each level of variable complexity, and was chosen based on Akaike's information criterion (AIC) values to identify the most parsimonious model. Predictor variables were checked for multicollinearity by calculating Pearson product-moment correlation coefficients and evaluating the variance inflation factor (VIF). Pairs of variables with a correlation coefficient > 0.6 and VIF values > 2.0 were evaluated, and 1 of the collinear variables was removed from the analysis; the final models were then checked to ensure they met the assumptions for multiple linear regression. Multiple linear regressions were conducted for numerical density, biomass density, mean size (TL), and maximum size (TL) for the 5 most abundant fishes. These analyses were conducted for all regions combined (Laguna Beach, Encinitas, La Jolla, Point Loma), and then separately for the Laguna Beach and Encinitas regions, totaling 60 multiple regressions (5 fish species, 4 fish population variables, 3 regional level analyses). Laguna Beach and Encinitas were additionally analyzed independently from the combined region analysis because they had sufficient sample sizes which allowed us to compare potential regional differences from an overall analyses of the entire study. Finally, to evaluate whether any variables explained a significant amount of variation in the response variables, we calculated partial coefficients of determination (partial $R^2$) values for all models (Quinn & Keough 2002). This allowed for an assessment of the relative strength of predictor variables in explaining variation in response variables. Non-parametric tests (Kruskal-Wallace, Mann-Whitney $U$) for differences in means were used to compare the mean partial $R^2$ values between metrics and structural components. To evaluate the relative effects of different structural types, variables were grouped into structural components for the evaluation of partial $R^2$ tests. The macroalgae component was comprised of the PCA algae variables, and the bathymetry component contained vertical relief, standard deviation of relief, and depth; the configuration component grouped reef area, fractal dimension, percent habitat, PI, and CI (Table 2).

## RESULTS

### Habitat classification

When comparing the remotely sensed CDFW kelp layer with the multibeam classified hardbottom habitat layer, the Pearson correlation coefficient was 0.64, representing a 64 % positive correlation between the raster layers at a 1 m resolution. Once the kelp and multibeam layers were combined to create a total potential habitat layer, the validation process confirmed 88 % accuracy with the independent comparison validation points. Informed by the benthic habitat maps, some survey sites that were previously considered as distinct reefs were subsumed into 1 reef. Consequently, 33 total reefs were surveyed, 1 each in La Jolla and Point Loma, 20 in Laguna Beach, and 11 in Encinitas.

### Surveys

In total, we recorded 21 106 older juvenile and adult fish from 50 species. Across all regions, the species present on greater than 50 % of transects included the señorita *Oxyjulis californica* (present on 86.2 % of transects), kelp bass *Paralabrax clathratus* (85.9 %), kelp perch *Brachyistius frenatus* (65.0 %), black surfperch *Embiotoca jacksoni* (56.6 %), and California sheephead *Semicossyphus pulcher* (50.8 %; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m557p051_supp.pdf). These 5 fishes represent a range of trophic levels, home ranges, habitat use, and life histories.

### Relative contribution of predictor variables

Across all 60 models, configuration variables were present in 93 % of models compared with the other 2 components (macroalgae 57 %, bathymetry 48 %), indicating that configuration variables are the most influential in describing fish population variability (Table 4, and see Table S2 in the Supplement).

There were clear differences in component selection between species. Señorita, kelp bass, and California sheephead mirrored the overall trend in which configuration variables were included much more than the other 2 components (macroalgae and bathymetry). Kelp perch, however, exhibited a different pattern with a much lower inclusion of bathymetry variables, indicating a decreased relevance of substratum variables in describing kelp perch dynamics. Black surfperch also demonstrated a deviation from the overall pattern, where bathymetry variables were selected more for black surfperch models compared with the 4 other species. Furthermore, the inclusion of configuration variables in black surfperch models was lower than any other species, and much lower than the general trend. Interestingly, there were no clear indicators that differentiated results among fish population variables, in which density, biomass, and body size were all driven predominately by configuration variables.

The individual seascape configuration variable most used in regression models was the PI (Table 5). This variable is a calculation of the area and distance of all patches within a specified radius. Kelp perch, black surfperch, and señorita generally had higher numerical densities, greater biomass densities, and larger body sizes in more isolated seascapes with less surrounding habitat. By contrast, kelp bass and California sheephead showed the opposite relationship with PI, having greater numerical and biomass densities, and larger mean body sizes, on less isolated, more contiguous reefs.

When evaluating partial $R^2$ values, we found a significant difference in the structural component values for the Laguna Beach region. Configuration variables explained significantly more of the variation compared with bathymetry and macroalgae variables ($\chi^2 = 11.591$, df = 2, p = 0.003; Table 6). When we compared structural components between the Laguna Beach and Encinitas regions, the variation explained by macroalgae and bathymetry in Encinitas were significantly higher when compared to Laguna Beach, but there was no difference in the variation explained by configuration (Fig. 3, Table 6).

Table 4. Summary of variable percentages from each structural component selected for a model output. Results broken into categories representing regional, fish population variable, and species trends

| Grouping | Macroalgae (%) | Bathymetry (%) | Configuration (%) |
|---|---|---|---|
| Overall | 57 | 48 | 93 |
| **Regional** | | | |
| All regions | 55 | 55 | 95 |
| Laguna Beach | 50 | 45 | 100 |
| Encinitas | 65 | 45 | 85 |
| **Fish population variable** | | | |
| Numerical density | 33 | 53 | 100 |
| Biomass density | 60 | 40 | 93 |
| Average size | 80 | 67 | 87 |
| Maximum size | 53 | 33 | 93 |
| **Species** | | | |
| Kelp perch | 67 | 17 | 100 |
| Black surfperch | 83 | 67 | 75 |
| Señorita | 42 | 58 | 100 |
| Kelp bass | 50 | 33 | 100 |
| California sheephead | 42 | 58 | 92 |

Table 5. Percentage that each variable was chosen for model output across all potential models

| Variable | Percent |
|---|---|
| Proximity index | 55 |
| Connectedness index | 45 |
| PCA algae component 3 | 27 |
| Percent habitat | 25 |
| Depth (m) | 23 |
| SD relief | 23 |
| PCA algae component 1 | 20 |
| Patch area | 17 |
| PCA algae component 2 | 10 |
| Relief | 8 |
| Fractal dimension | 7 |

Table 6. Mann-Whitney *U*-test results for each seascape component comparing partial $R^2$ values between Laguna Beach and Encinitas regions. **Bold** p-values indicate significance ($p < 0.05$)

| Component | Region | n | Rank sum | Test statistic | Chi-squared approximation | df | p |
|---|---|---|---|---|---|---|---|
| Macroalgae | Laguna Beach | 12 | 96 | 18 | 7.67 | 1 | **0.006** |
| | Encinitas | 10 | 157 | | | | |
| Bathymetry | Laguna Beach | 12 | 101 | 23 | 4.86 | 1 | **0.027** |
| | Encinitas | 9 | 130 | | | | |
| Configuration | Laguna Beach | 32 | 872 | 343.5 | 0.826 | 1 | 0.364 |
| | Encinitas | 25 | 782 | | | | |

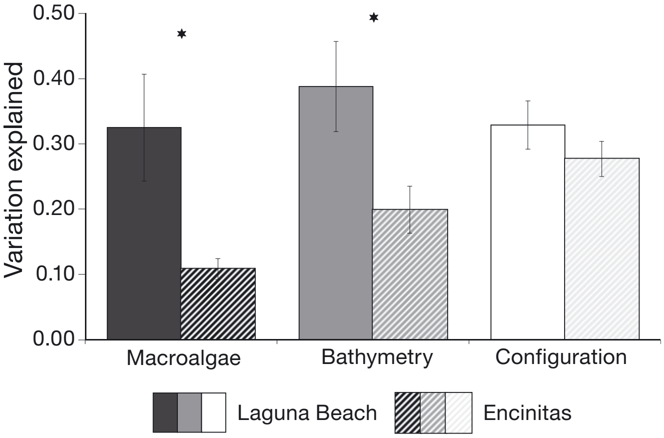

Fig. 3. Mean partial $R^2$ values for each seascape component for Laguna Beach and Encinitas regions. *Indicates significant p-value (≤0.05) for Mann-Whitney *U*-test between regions within each seascape component (see Table 4). Error bars are ± 1 SE and are calculated for all models within each structure component for each region

Interestingly, the relative importance of configuration is greater in the Laguna Beach region, suggesting that configuration is driving population dynamics more in Laguna Beach as compared with Encinitas. This indicates that the relative importance of structural components differs between regions.

## DISCUSSION

This study highlights the importance of remotely sensed habitat maps as a tool in describing fish population structure at a seascape scale. Habitat configuration of the surrounding seascape was the most important factor in describing the density and size structure of fishes on rocky reefs. Interestingly, the relative influence of within-patch and surrounding habitat variables was influenced by the connectedness of the seascape itself. These findings demonstrate that explicit habitat maps are critical for accurate determinations of the density and size structure of fish populations. Our results represent one of the first seascape-level analyses to include multiple structural components and spatial scales across an explicitly mapped seascape in a temperate coastal kelp forest ecosystem.

Within-patch structural habitat complexity, described here by macroalgae and bathymetry, were included less frequently in multiple regression models than configuration when explaining the numerical and biomass density of fishes. This is consistent with other seascape studies that have demonstrated that within-patch variables such as rugosity, benthic complexity, and habitat diversity are less effective at describing the distribution, abundance, and diversity of fishes as compared with the surrounding habitat (Grober-Dunsmore et al. 2007, Huntington et al. 2010, Pittman & Brown 2011, Olds et al. 2012). Although this is a general trend, we found here that the relative influence of seascape structural components varies based on the specific response variable in question.

Black surfperch exhibit strong and consistent relationships across many predictor variables. Within-patch components, specifically macroalgae PCA component 3 representing *Egregia menziesii, Eisenia arborea*, and total algae count, had a stronger influence on black surfperch populations than on other fishes. The resource requirements of black surfperch support these findings, as they are microcarnivorous browsers that are highly associated with understory algae, turf algae, and stipitate subcanopy algae (Schmitt & Holbrook 1984, Ebeling & Laur 1985), predominantly occur in shallow water, and have restrictive movements (Hixon 1981). Because black surfperch and all embiotocids are viviparous, and thus have low dispersal potential (Bernardi 2000), it may contribute to their strong associations to within-patch habitat components, and fewer configuration variables included in models.

By contrast, another embiotocid, the kelp perch, did not exhibit similar relationships to within-patch habitat variables. Bathymetric variables were used less frequently, which is not surprising, as kelp perch are water column foragers and microcarnivorous pickers that are highly associated with *Macrocystis pyrifera* in the upper water column (Bray & Ebeling 1975, Anderson 1994), despite that macroalgae variables were not significant for kelp perch in this study. Perhaps the strong influence of measures such as isolation and connectedness of habitat represent significant barriers to movement, as this species is so strongly attached to kelp which may limit its movements across unvegetated habitat (Anderson 2001).

The 2 variables used most often in model outputs were configuration metrics that describe the connectivity of habitat (PI and CI). Species richness and diversity can be greatly influenced by reef size, isolation, and connectedness (Ault & Johnson 1998, Belmaker et al. 2005). Moreover, habitat area, fragmentation, and isolation can alter predator–prey dynamics (Hovel & Lipcius 2001, Selgrath et al. 2007, Belmaker et al. 2011). For example, isolation of small patch reefs significantly dampens predator aggregation compared with contiguous reef (Belmaker et al. 2005) that could lead to lower predation rates. In this temperate kelp forest system, our results indicate that larger roving predators had negative relationships with the PI, suggesting that these species had lower densities and reduced size on smaller or more isolated reefs. Potentially, piscivores such as the kelp bass may be less likely to traverse large sand gaps, thus decreasing predation pressure on smaller, more isolated reefs which in turn may allow for higher densities of smaller microcarnivorous fishes such as kelp perch and señorita. Configuration measures such as the PI may have substantial influences on fish population structure across a range of species, and we speculate that relative movements of fish due to the configuration of a seascape could alter predation risk.

These assumptions of restricted movement are based on the premise that the amount of sandy bottom habitat acts to influence fish movement. Linking seascape connectedness measures to functional connectedness of an organism requires an understanding of not only the spatial arrangement of habitat, but how organisms perceive the risk of traveling through unfavorable habitat (Tischendorf et al. 2003, Grober-Dunsmore et al. 2009). We lack a mechanistic understanding of how fishes perceive habitat configuration, particularly across larger spatial scales. As one of the few studies to investigate how fishes perceive barriers to movement, Turgeon et al. (2010) translocated damselfish S*tegastes diencaeus* and found that they were deterred by sand gaps, traveling up to 6 times greater distances along hardbottom habitat when presented with a patchy seascape. Nevertheless, this small, strongly site-attached coral reef damselfish was responding to the seascape at a scale of only a few meters. This suggests that configuration variables such as isolation and connectedness can alter fish movement, and therefore influence population level effects such as density and abundance. Lowe et al. (2003) used telemetry data to demonstrate that large kelp bass had greater movement rates when their home range was in a sandy cove interspersed with artificial reef habitats compared with a natural contiguous reef. They suggested that although these species are categorized as residing in sandy habitat, they are in fact present near artificial reef habitat such as mooring blocks and that the greater home range size in the cove may be due to their need to visit multiple mooring blocks to access prey. Thus large adult predatory fish are able to move between sand gaps at the scale up to 200 m. However, the same telemetry data suggest that both kelp bass and California sheephead can be significantly deterred by deep sand channels that potentially act as a barrier to movement. Furthermore, responses to habitat for kelp bass and California sheephead are extremely variable in that they both exhibit a wide range in home range size (33–11 224 $m^2$ and 938–82 000 $m^2$, respectively; Lowe et al. 2003, Topping et al. 2005). This highlights the importance of considering rocky habitat configuration and variability across multiple spatial scales. Notably, the only configuration variable to show a relationship for a specific radius was the PI to the 100 m spatial scale, suggesting that isolation distances of the surrounding habitat within 100 m are most influential to fish movement across all species.

Whether habitat configuration or composition is more influential in explaining variation in the density and size of an organism is dependent on the species of interest, the choice of spatial scale, and the characteristics of the seascape itself. Here we found that the relative effect of seascape components of structural habitat complexity is mediated by the type of configuration structure. When evaluating partial $R^2$ values for the Laguna Beach region, we found that configuration describes significantly more variation in fish population dynamics as compared to macroalgae and bathymetry. This relationship also significantly differs from the $R^2$ results for the Encinitas region, with no differences in variation explained between the 3 structure components. Laguna Beach is comprised of smaller, more isolated and fragmented reefs (mean reef area 19.0 ha) compared to the larger interconnected arrangement of reefs in the Encinitas region (mean reef area 41.7 ha). Moreover, the characteristic scale of choice for Encinitas is larger than for Laguna Beach, indicating that fishes are responding to a greater extent of habitat in Encinitas. These patterns may be driven by differences in functional habitat connectedness of different seascapes, where larger, connected reefs may not restrict the movement of fishes as much as a seascape comprised of smaller, more isolated reefs. American lobsters *Homarus americanus*, for example, move 10 to 15% more within contiguous habitat as compared to patchy habitat (Hovel & Wahle 2010). These results indicate that the relative effect of configuration is influenced by the seascape itself and is determined by the relative connectedness of the seascape. Therefore, an appropriate estimation of the level of connectedness in the surrounding seascape is paramount when evaluating how organism movements are influenced by habitat structure over a large spatial extent.

Seascape ecology is a means of quantifying habitat structural metrics in an effort to describe biological patterns and ecological processes. The findings of this study are similar to other studies that demonstrate an overall greater influence of the surrounding seascape in describing the density and size structure of fishes as compared to within-patch metrics (Grober-Dunsmore et al. 2007, Pittman et al. 2007, Olds et al. 2012). However, the strength of the relationship and the relative influence of seascape structure varies when evaluating individual species, specific variables, and spatial scales. If variables of structural habitat complexity considered only particular seascape components (e.g. biogenic habitat, bathymetric complexity, or habitat configuration), there is a risk that the assessment of variables that influence patterns may be incomplete. Consequently, a range of structural habitat complexity variables across a range of spatial scales is critical for a more complete understanding of relevant drivers that structure fish populations. We have demonstrated that the relative influence of seascape structural components is dependent on the seascape itself, which has significant implications for marine spatial planning and management practices. The surrounding seascape should be critically evaluated when designing a place-based marine protected area to ensure alignment with management objectives. For example, if the goal of a reserve is to enable spillover of large adult species that replenish surrounding habitats, then consideration of the structural connectedness and potential restriction of adult movement and home ranges is critical. Furthermore, explicit understanding of adult fish distribution and body size across a seascape provides some evaluation of potential reproductive output and will allow for better estimation of the reproductive 'value' of reefs in a seascape (Claisse et al. 2012). The incorporation of adult home range movements can increase the predictability and certainty of population models and reserve performance (Moffitt et al. 2009). Our data suggest that the abundance of adult fishes may be mediated by the surrounding seascape, and consideration of configuration of a seascape is paramount when creating such models. The relative influence of within-patch and surrounding habitat variables varies across species and seascapes. Therefore, incorporation of explicit habitat maps into marine conservation management practices is necessary to improve the accuracy and predictability in describing fish population structure at ecologically relevant spatial scales.

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