



Habitat-based predictive mapping of rockfish density and biomass off the central California coast

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ABSTRACT: Understanding the association between components of habitat and fish distribution and abundance is important in order to achieve accurate stock assessments. We developed generalized additive models (GAM) and spatially predictive maps of rockfish abundance at the individual species level using habitat descriptors collected from visual surveys and fine-scale bathymetry. We advanced beyond presence/absence and presence only models to create predictive maps of fish density (100 m⁻²) and biomass (kg 100 m⁻²) for *Sebastes rosaceus* (rosy rockfish) and *S. constellatus* (starry rockfish), both common species in commercial and recreational fisheries along the central coast of California. Selected models included co-variables of seafloor depth, complexity, substratum type, and heterogeneity. Predicted density and biomass of both species were highest in areas of complex rock on the continental shelf off Points Lobos and Sur at 50–90 (*S. rosaceus*) and 80–120 m (*S. constellatus*) water depth. Our results will be useful both in stock assessments of these data-poor species as well as in allocation of fishing effort, catches, and other space-based management decisions.

KEY WORDS: Visual surveys · Rockfishes · Generalized additive model · Central California

INTRODUCTION

Pacific coast *Sebastes* spp. (rockfishes) are a wide-ranging and diverse genus comprising at least 65 species that occupy most benthic habitats from shallow estuaries and kelp forests to muddy slopes at 1500 m depth (Love et al. 2002). Several life-history characteristics (e.g. slow growth, longevity sometimes >100 yr, and delayed sexual maturity; Love et al. 2002) make most rockfish populations particularly vulnerable to high levels of fishing mortality. Approximately 40 species of rockfishes dominate deep-water fish assemblages in rocky habitats off California (Love & Yoklavich 2006) and support valuable recreational and commercial fisheries that have been ongoing since the mid-1800s (Love 2006, Miller et al. 2014).

Populations of 6 species of rockfishes currently are being rebuilt after having been classified as

overfished by the National Marine Fisheries Service and Pacific Fishery Management Council (PFMC 2011). Rebuilding plans for overfished stocks are required in accordance with the US Sustainable Fisheries Act of 1998 (16 U.S.C. § 1854[e][2]), which highlights the importance of identifying the physical and biological habitat factors that influence the distribution and abundance of these fish species. A number of management actions have been taken to support the rebuilding of rockfish stocks, including time and area closures, fishing gear modifications, minimum stock size thresholds, and catch and size limits. Timely stock assessments are needed to support these management actions (Punt & Ralston 2007, Ralston & MacFarlane 2010), yet only 25 of the 59 federally managed rockfish species have been assessed (www.pcouncil.org/groundfish/stock-assessments/).

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Sedentary rockfishes living in heterogeneous, high-relief, rocky habitats are difficult to appraise accurately with conventional methods such as bottom-trawl gear. Fishery-independent surveys using non-extractive visual methods (e.g. from a submersible) are an effective means to assess and monitor stocks in rebuilding status and provide the opportunity to examine fish-habitat relationships at finer spatial scales (1 to 5 m) than coarse (1 to 2 km) benthic trawl gear (Anderson et al. 2009). For instance, habitat-specific estimates of density and biomass from visual surveys (Yoklavich et al. 2007) are used in current stock assessments of *S. levis* (cowcod).

Advances in seafloor mapping technologies, coupled with recent developments in modeling approaches, support robust predictions of fish assemblages (Moore et al. 2010, Pittman & Brown 2011) and individual species (Young et al. 2010). Rockfishes demonstrate strong affinities to high- and low-relief rocky substrata at specific depths (Yoklavich et al. 2000, Laidig et al. 2009, Love et al. 2009). Additionally, habitat complexity and position relative to the surrounding seabed have further informed spatially predictive models of rockfish distributions (Iampietro et al. 2008, Young et al. 2010). Predicting rockfish density and biomass at the individual species level, based on a variety of seafloor substratum variables, provides important information to improve the assessment of fish stocks in rebuilding status.

In this study, we developed spatially predictive models and maps of abundance for *S. rosaceus* (rosy rockfish) and *S. constellatus* (starry rockfish), typical members of the mid-shelf fish assemblage on rocky substrata off central California, USA (Love & Yoklavich 2006). Rosy rockfish geographically range from the Strait of Juan de Fuca (Washington, USA) to southern Baja California, Mexico, but are most abundant from Cordell Bank off northern California to northern Baja California (Love 2011). Starry rockfish range from northern California to southern Baja California, and are relatively abundant from central California to southern Baja California. Juveniles and adults of both species co-occur in the same depths and substratum types. These are medium-size, mostly solitary species (maximum length 36 and 46 cm for rosy and starry rockfish, respectively), and moderately long lived (likely maximum age at least 40¹ and 32 yr for rosy and starry rockfish, respec-

tively) (Love et al. 2002). Both species are commonly encountered in commercial and recreational fisheries along the central coast of California (Love et al. 2002) and yet are considered to be data-poor stocks (i.e. having only catch data available for assessments; Dick & MacCall 2010).

Our overall goal was to model and map fish density (100 m⁻²) and biomass (kg 100 m⁻²) of *S. rosaceus* and *S. constellatus* based on a variety of seafloor descriptors. The recent availability of detailed and accurate maps of substratum complexity from multibeam-acoustic surveys of the seafloor within California's territorial waters (i.e. those data coming from the California Seafloor Mapping Program) made it possible to produce regional maps of predicted density and biomass at scales that are ecologically relevant to these species. These results will improve our understanding of habitat variables that influence the spatial distribution of these species, advance their stock assessments, and find application in the newly developed California Current integrated ecosystem assessment (Levin & Schwing 2011).

MATERIALS AND METHODS

Study area

Our study area was located largely within state waters (3 nautical miles) off central California, USA, including the southern portion of Monterey Bay, Point Lobos, Point Sur, and Big Creek on the Big Sur coast (Fig. 1). We focused our research efforts in depths from 35 to 150 m, bracketing the depths of occurrence for the 2 species of interest (*Sebastes rosaceus* and *S. constellatus*), and across a range of rocky habitats including extensive rock and boulder fields (e.g. off the Point Lobos and Point Sur headlands), isolated rocky outcrops and pinnacles that can be several meters high and surrounded by flat, sandy seafloor, and on rock talus piles, scarps, and ledges in the heads of submarine canyons along the Big Sur coast. Water is relatively cool and productive along this section of the coast because the California Current flows equatorward year round, and substantial upwelling of cold deep water occurs at the headlands, typically in spring and summer (Hickey 1998). Commercial and recreational fishing with various types of gear has been supported by the diverse habitats on the continental shelf and upper slope in this region for well over 60 yr (Love et al. 2002).

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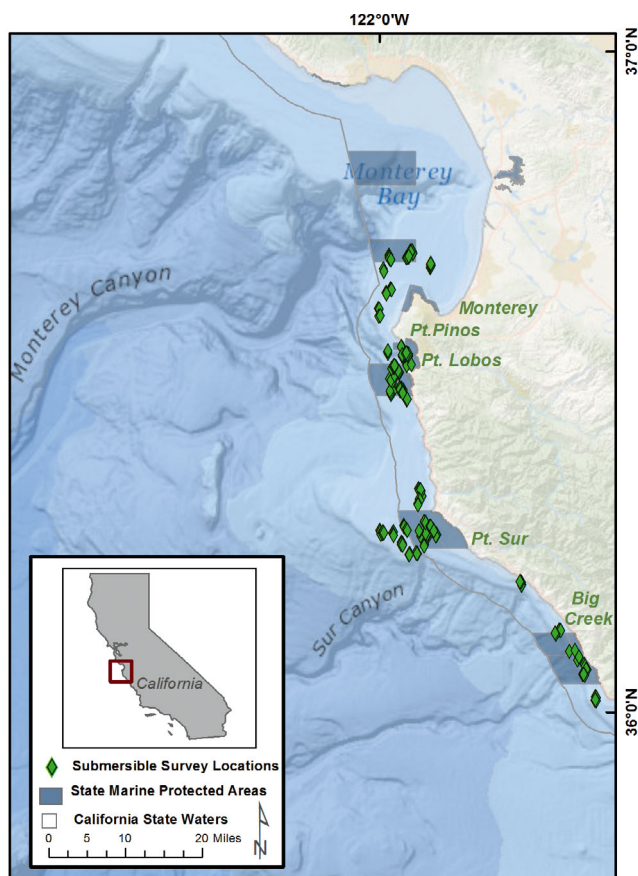


Fig. 1. *Delta* submersible survey locations in Monterey Bay and along the Big Sur coast, off central California, USA

Data sets

Visual surveys of demersal fishes and components of their habitats were conducted using a manned submersible (*Delta*) during daytime hours from September to November in 2007 and 2008 (see Yoklavich et al. 2000, 2002, 2007 for details on the *Delta* survey vehicle and methods). Dives were positioned randomly in areas of rocky substrata that were identified from maps of bathymetry (Monterey Bay Aquarium Research Institute Mapping Team, Monterey Bay Multibeam Survey; Seafloor Mapping Lab, California State University Monterey Bay [SFML-CSUMB]) and from interpreted seafloor habitats (Yoklavich et al. 1997, Eitrem et al. 2000). Surveys were conducted by traversing haphazardly across substratum types and depth gradients within designated rocky habitats. Soft sediment was not specifically targeted, but was surveyed along with rocky substrata on the quantitative sample transects. The same general areas were surveyed in 2007 and 2008, but transects were not re-sampled from one year to the next. Sen-

sors mounted on the outside of the submersible recorded time, depth (pressure), and altitude at 1 s intervals throughout each dive.


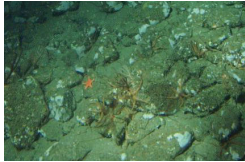

A total of 304 strip transects 2 m wide were conducted for 10 min each along the seafloor. A distance within 1 m of the seafloor and a speed of 0.5 to 1.0 knots were maintained during the transect surveys. The submersible's position was tracked at 1 to 3 s intervals using an ORE Trackpoint II ultra-short baseline (USBL) acoustic system (EdgeTech) and WINFROG software (v3.1; FUGRO). A scientific navigator aboard the support vessel directed the start of a transect once the submersible arrived at the predetermined target depth and location, and tracked the submersible in real time within ArcGIS relative to bathymetric maps. The length (m) of each transect was estimated using a Doppler velocity log (DVL) (NavQuest 600 Micro) and ring-laser gyrocompass (CDL MiniRLG 2) attached to the outside of the submersible. Two video cameras (one outside and one inside the submersible) were used to visually document each transect.

A pilot operated the submersible while an experienced scientist identified, counted, and estimated total length (TL, cm; using paired lasers spaced 20 cm apart) of all fishes within a transect. Fish density (100 m^{-2}) and biomass ($\text{kg } 100 \text{ m}^{-2}$) for *Sebastes rosaceus* and *S. constellatus* were calculated from each transect. To calculate biomass, TL of fish was converted to weight (g) using $W = 0.0052 \times \text{TL}^{3.386}$ ($R = 0.98259$) for *S. rosaceus* and $W = 0.0097 \times \text{TL}^{3.160}$ ($R = 0.97805$) for *S. constellatus* (Love et al. 1990). The relationship between length and weight was identical for males and females for both species.

Seafloor substratum types (mud, sand, gravel, pebble, cobble, boulder, continuous flat rock, rock ridge and pinnacle top) were classified from the video of each transect, based on geological definitions detailed in Greene et al. (1999). Distinct habitat patches, with a minimum duration of 3 s, were defined by assigning primary (at least 50% of the area viewed) and secondary (>20% of the area viewed) substratum types each time a change was noted along the transect.

The length of each patch was determined from the DVL measurements. Primary substrata were grouped based on levels of structural complexity (Table 1). Pinnacle top, rock, and flat rock were classified as high complexity or large structured hard substratum type (Lhard). Boulders, cobble, pebble, and gravel were classified as medium complexity hard substratum (Mhard). Sand and mud comprised a soft substratum group (Soft) of low complexity.

Table 1. Habitat characterization groups from submersible survey video analysis

Habitat image	Habitat type and complexity
	Habitat code: Lhard Habitat description: pinnacle top, rock, flat rock Level of complexity: high
	Habitat code: Mhard Habitat description: boulder, cobble, pebble, gravel Level of complexity: medium
	Habitat code: Soft Habitat description: sand and mud Level of complexity: low

An entire transect was characterized as a weighted sum of the patch substrata (O'Farrell et al. 2009). For substratum type b ($b \in \text{Lhard, Mhard, Soft}$), in transect t , the numerical value describing that substratum's contribution (S) was computed as:

$$S_{b,t} = \sum_p \left[S_{b,t,p} \times \frac{L_{t,p}}{\sum_p L_{t,p}} \right] \quad (1)$$

where $L_{t,p}$ represents the length of patch p in transect t . The resulting transect length-weighted habitat value characterized the 3 main substratum types (e.g. Lhard, Mhard, Soft) for each transect. This value, ranging from 0 (low complexity) to 0.7 (high complexity), was used as a metric of habitat complexity for each visual transect. Habitat heterogeneity was estimated as number of habitat patches per transect (Table 2).

Following our visual surveys, high-resolution multi-beam data were collected throughout the entire study area by the California Seafloor Mapping Program (<http://walrus.wr.usgs.gov/mapping/csmp>). A 5 m resolution bathymetric Digital Elevation Model (DEM) and a derived Rough/Smooth classification of the seafloor were provided in grid format. Slope-of-slope (i.e. habitat complexity) was derived from the bathymetric grids using the ArcGIS Spatial Analyst extension (ESRI) slope function to obtain the rate of change of slope. Bathymetric position index (BPI) was calculated using the Benthic Terrain Modeler extension in ArcGIS. BPI is a second order derivative of the multibeam bathymetry data and characterizes a pixel in the bathymetric DEM as a positive (e.g. pinnacle top) or negative (e.g. canyon) feature of the surrounding seascape (Lundblad et al. 2006, Young et al. 2010). BPI grid creation and classification was applied using a scales of analysis at 5 pixel (25 m) and 50 pixel (250 m) annulus thickness for fine and broad respectively. Finally, the covariates were extracted for each transect using a 100 m radius moving window analysis in GIS.

Statistical analysis

Predictive models of fish density (100m^{-2}) and biomass ($\text{kg } 100\text{m}^{-2}$) of *Sebastes rosaceus* and *S. constellatus* were developed using generalized additive models (GAM; Pinheiro & Bates 2009, Zuur et al. 2009). These species are known to occur at specific depths and on distinct substratum types (Love et al. 2002); we used the flexible GAM to accommodate the expected non-linear responses of both species to our co-variables. Two sets of models were developed: (1) models based on the co-variables depth, a transect length-weighted value for the 3 substratum groups (i.e. Lhard, Mhard, Soft), and habitat heterogeneity, which were collected during the visual surveys, and measures of seafloor roughness, habitat

Table 2. Environmental co-variables collected during visual surveys and used in generalized additive models (GAMs) of rockfish density and biomass

Co-variable	Description	Units	Source	Range	Mean (SD)
Depth	Depth at start of transect	meters	Submersible sensor	25–315	137.4 (83.1)
Lhard*	Pinnacle top, rock, flat rock	length-weighted habitat value	$S_{b,t} = \sum_p [S_{b,t,p} \times L_{t,p} / \sum_p L_{t,p}]$	0–0.7	0.4 (0.2)
Mhard*	Boulder, cobble, pebble, gravel	length-weighted habitat value	$S_{b,t} = \sum_p [S_{b,t,p} \times L_{t,p} / \sum_p L_{t,p}]$	0–0.7	0.1 (0.1)
Habitat heterogeneity	Measure of seascape patchiness	# habitat patches on transect line	Video analysis	1–57	18.2 (9.8)

*The length-weighted habitat value was calculated using $S_{b,t} = \sum_p [S_{b,t,p} \times L_{t,p} / \sum_p L_{t,p}]$ based on O'Farrell et al. (2009)

complexity, and BPI derived from the high-resolution multibeam bathymetry; and (2) models based only on the co-variables derived from the multibeam bathymetry. Calculations were computed using R software and the *mgcv* package (Wood 2004) with a Gaussian error distribution and an identity link. Data exploration followed protocols described by Zuur et al. (2010). Cleveland dotplots and boxplots were used to determine the presence of outliers. Collinearity was investigated between covariates using Pearson correlation coefficients, multi-panel scatterplots, and variance inflation factors (VIF) (Montgomery & Peck 1992).

Akaike's information criterion (ΔAIC) and Akaike weights (w_i) were used to select the most parsimonious models among all possible covariate combinations (Burnham & Anderson 2002). We selected models based on lowest AIC values using the MuMIn package (Barto 2011) and models having $\Delta AIC < 2$ were combined using a weighted (w_i) model average. We used *k* fold cross validation in which we split the data into equal sized parts and then iteratively used part of the data to fit the model and a different part to test it (Hastie et al. 2009). We repeated each *k*-fold cross validation process 500 times and examined the distribution of coefficient of determination. Validation of the optimum model was accomplished by inspecting homogeneity (plotting residual vs fitted values) and independence (variogram of residuals and plotting residuals versus each covariate).

Spatially predictive mapping was conducted in ArcGIS 10.1 using the Marine Geospatial Ecology Tool (MGET; v0.8a48) (Roberts et al. 2010), which integrates ArcGIS with the R statistical package (R Development Core Team 2011). In MGET, the GAM tool was applied to derive spatially predictive rasters for rockfish density and biomass. Prior to predictive mapping of the data for this analysis, data were randomly split into 'test' (1/3) and 'training' (2/3) sets to assess map accuracy. The training data sets were used to create the predictive maps, and the test data sets were applied to evaluate map accuracy assessment using Kendall's τ and Spearman's ρ .

RESULTS

Spatial patterns of rockfish density and biomass

Sebastes rosaceus and *S. constellatus* density and biomass data were used in our modeling efforts based on a total of 304 transects covering 146 000 m² of seafloor that comprised 70% LHard (pinnacle top,

rock, and flat rock), 15% Mhard (boulder, cobble, pebble, and gravel), and 15% Soft (sand and mud) substrata at depths of 35 to 150 m. Average density for *S. rosaceus* and *S. constellatus* was 3.42 (SE = 0.16) and 0.74 (0.06) fish 100 m⁻², respectively. On transects, the average biomass was 0.26 kg 100 m⁻² (SE = 0.01) for *S. rosaceus*, and 0.14 kg 100 m⁻² (0.01) for *S. constellatus*. Density of both species was relatively high on transects at Carmel Canyon, Point Sur, and Sur Canyon sites (Figs. 2a & 3a). Spatial pattern of *S. rosaceus* biomass was similar to that of density along the Central California coast, with higher biomass coincident with areas of greater habitat structural complexity off the Monterey Peninsula, Point Lobos, and Point Sur (Fig. 2d). There were several pockets of relatively high biomass of *S. constellatus* along the central Californian coast, from the Monterey Peninsula to Big Creek, the most southern reaches of our study area (Fig. 3d).

Modeling of *Sebastes rosaceus* density and biomass

The GAMs to predict fish density and biomass were based on habitat co-variables from *in situ* visual surveys and multibeam acoustic bathymetry.

The selected GAM to predict *S. rosaceus* density included depth and hard rock substrata with high and medium complexity ($w_i = 0.99$; Table 3). This selected model accounted for 42% of the variability in *S. rosaceus* density and had a mean $R^2 = 0.40$ for 500 runs of 10-fold cross-validation. From response curves, *S. rosaceus* density increased with depth from 35 to ~70 m and then declined relatively steeply in deeper waters (Fig. 4a). The response curves for transect length-weighted habitat values indicated a steady increase in predicted *S. rosaceus* density with increasing complexity for both large (pinnacle top and rock habitat, Fig. 4b) and medium-to-small substrata (boulder, cobble, pebble, gravel habitat, Fig. 4c).

The selected GAM to predict *S. rosaceus* biomass included depth, hard rock substrata with high and medium complexity, habitat heterogeneity (e.g. number of patches per transect), and BPI ($w_i = 0.81$; Table 3), and accounted for 46% of the biomass variability (mean $R^2 = 0.42$). The response curves for depth and both transect length-weighted habitat values (Lhard and Mhard) revealed the same patterns as in the density response curves (Fig. 4d–f). From the BPI response curve (Fig. 4g), biomass was lowest in canyons and depressions (negative values of BPI) and demonstrated an overall increase to high BPI

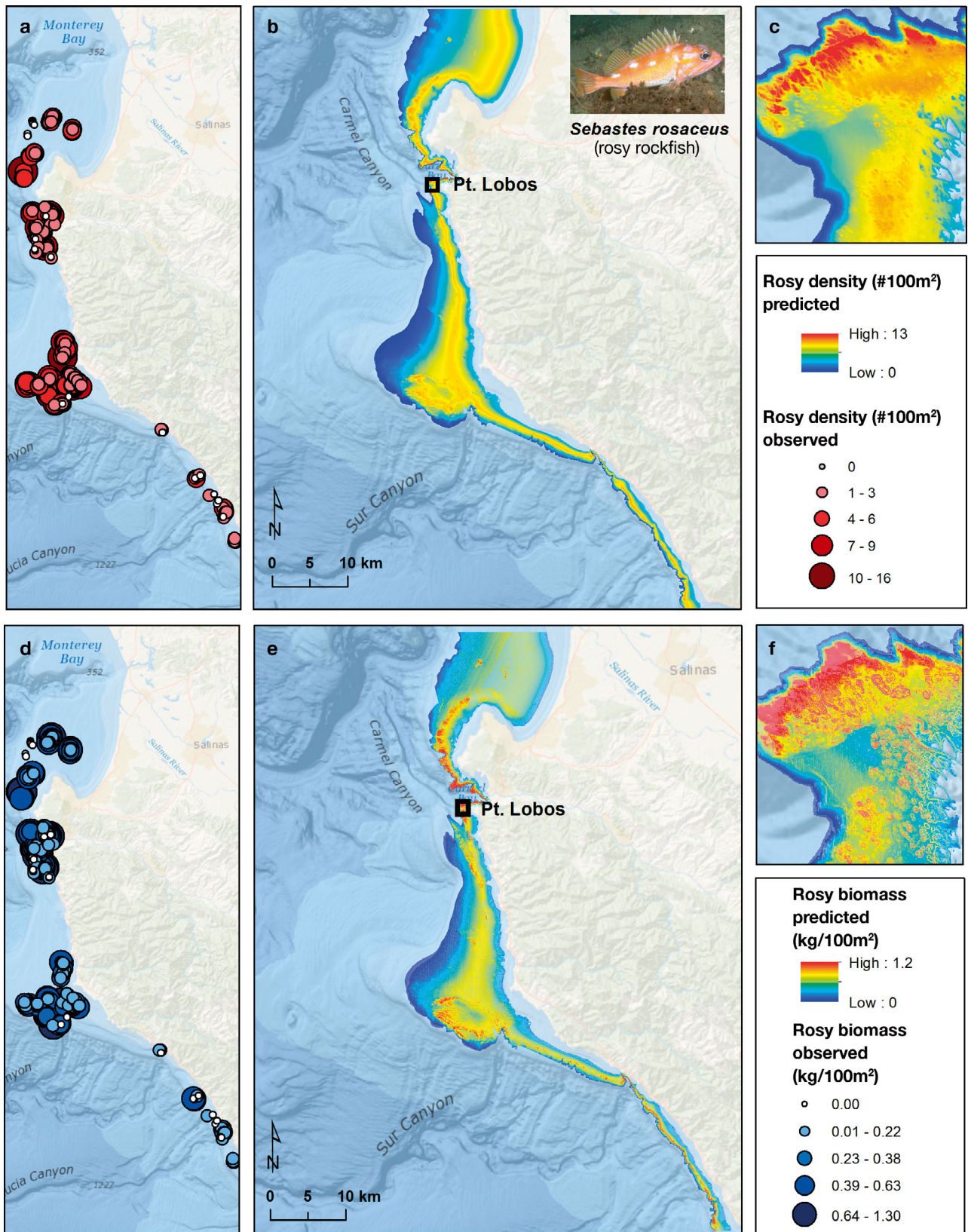


Fig. 2. *Sebastes rosaceus*. Density and biomass off central California, USA: (a) graduated dots of observed density; (b) predicted density throughout study area; (c) predicted density in enlarged map of area off Pt. Lobos; (d) graduated dots of observed biomass; (e) predicted biomass throughout study area; and (f) predicted biomass in enlarged map of area off Pt. Lobos

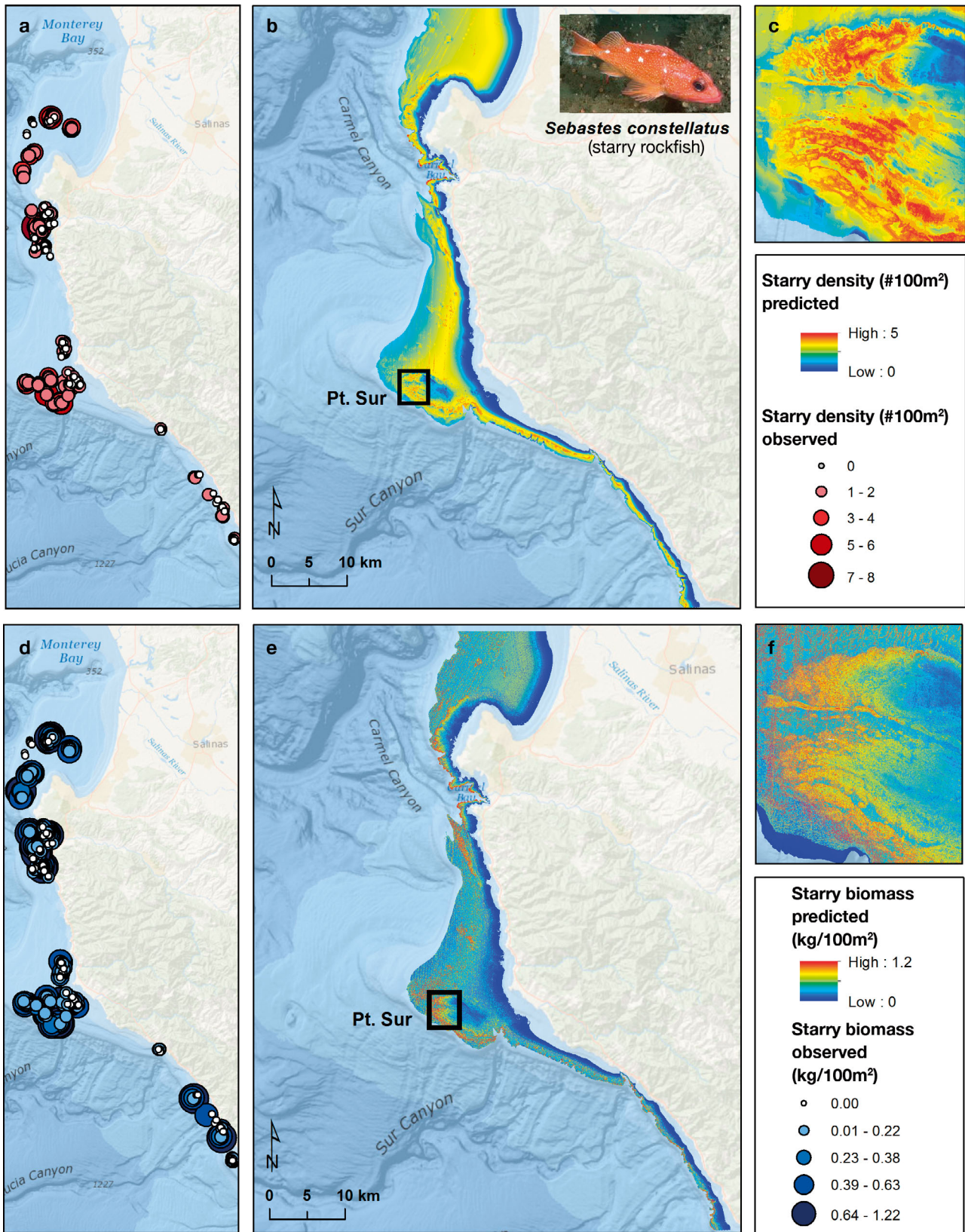


Fig. 3. *Sebastes constellatus*. Density and biomass off central California, USA: (a) graduated dots of observed density; (b) predicted density throughout the study area; (c) predicted density in enlarged map of area off Pt. Sur; (d) graduated dots of observed biomass; (e) predicted biomass throughout the study area; and (f) predicted biomass in enlarged map off Pt. Sur

Table 3. Results of model selection to predict *Sebastes rosaceus* density and biomass off central California for 2 sets of models: (1) visual and bathymetry models and (2) bathymetry alone to support GIS-based predictive mapping. Models were ranked by Akaike's information criterion (ΔAIC) and Akaike weights (w_i). Models having $\Delta\text{AIC} < 2$ were combined using a weighted (w_i) model average and are in **bold**. Lhard = high complexity or large structured hard substratum (pinnacle top, rock, and flat rock); Mhard = medium complexity hard substratum (boulders, cobble, pebble, and gravel); Soft = low complexity substratum (sand and mud)

Model type	Model selection results	ΔAIC	w_i
Models based on co-variables from both visual surveys and multibeam bathymetry			
Density	<i>S. rosaceus</i> ~ Depth + Lhard + Mhard	0	0.99
Density	<i>S. rosaceus</i> ~ BPI + Lhard + Mhard	28.65	0.01
Biomass	<i>S. rosaceus</i> ~ Depth + Lhard + Mhard + Habitat Heterogeneity + BPI	0	0.81
Biomass	<i>S. rosaceus</i> ~ Depth + Lhard + Mhard + BPI	3.71	0.13
Biomass	<i>S. rosaceus</i> ~ Depth + Lhard + Mhard + BPI + factor(Rough)	5.39	0.01
Models based on co-variables derived from multibeam bathymetry			
Density	<i>S. rosaceus</i> ~ Depth + BPI	0	0.45
Density	<i>S. rosaceus</i> ~ Depth + BPI + factor(Rough)	0.96	0.28
Density	<i>S. rosaceus</i> ~ Depth	2.12	0.15
Density	<i>S. rosaceus</i> ~ Depth + factor(Rough)	2.49	0.13
Biomass	<i>S. rosaceus</i> ~ Depth + BPI + Habitat Complexity	0	0.62
Biomass	<i>S. rosaceus</i> ~ Depth + BPI + Habitat Complexity + factor(Rough)	1.69	0.27
Biomass	<i>S. rosaceus</i> ~ Depth + BPI + factor(Rough)	4.41	0.07

features (e.g. pinnacle tops). Biomass of *S. rosaceus* was highest in areas of ~4 to 6 habitat patches per 100 m² (Fig. 4h), with declining biomass in areas of very low and high habitat heterogeneity (e.g. patchiness).

Predictive maps of *Sebastes rosaceus* density and biomass

The predictive maps for density and biomass were based solely on co-variables derived from acoustic multibeam bathymetry.

The selected GAM to create a predictive map of *S. rosaceus* density accounted for 33% of its density variability ($R^2 = 0.32$). The model was based on a weighted average of M1: *S. rosaceus* ~ Depth + BPI, $w_i = 0.45$ and M2: *S. rosaceus* ~ Depth + BPI + factor(Rough), $w_i = 0.28$ (Table 3). Model-averaged response curves for depth (Fig. 5a) and BPI (Fig. 5b) had greater density values for the rough substratum factor than for the smooth factor. In the response curve for BPI, density was lowest in canyons and depressions (similar to Fig. 4g), but also demonstrated distinct peaks in density associated with medium-relief habitat features (e.g. boulder fields) and high BPI features (e.g. pinnacle tops) (Fig. 5b).

The selected GAM for *S. rosaceus* biomass predictive map was a weighted model average M1: *S. rosaceus* ~ Depth + BPI + Habitat Complexity, $w_i = 0.62$ and M2: *S. rosaceus* ~ Depth + BPI + Habitat

Complexity + factor (Rough), $w_i = 0.27$ (Table 3). This model accounted for 38% of the biomass variability ($R^2 = 0.35$). Response curves for depth (Fig. 5c), BPI (Fig. 5d), and habitat complexity (Fig. 5e) had greater biomass values for the rough substratum factor than for the smooth substratum factor. The response curve for predicted biomass versus depth was similar to that of the density curve, and demonstrated an increase in *S. rosaceus* biomass from 35 to ~70 m and a decrease in biomass at greater depth ranges (Fig. 5c). In the response curve for BPI, *S. rosaceus* biomass followed the same pattern as the density curve and was lowest in canyons and depressions and was characterized by distinct peaks in biomass associated with low-relief habitat features (e.g. boulder fields) and high BPI features (e.g. pinnacle tops) (Fig. 5d). Habitat complexity was not important for modeling density, but for biomass this response curve indicated a sustained increase in *S. rosaceus* biomass with increasing complexity (Fig. 5e).

Predictive maps of *S. rosaceus* density (Fig. 2b) and biomass (Fig. 2e) were produced based on the average of the top 2 models by weight. Spatial patterns of biomass predicted across the study region were similar to that of density, with higher biomass coincident with areas of greater habitat structural complexity off the Monterey Peninsula, Point Lobos (Fig. 2c,f), and Point Sur. The highest predicted density and biomass of *S. rosaceus* rockfish were mapped on the continental shelf at 50 to 90 m water depth off Point Pinos and Point Sur. The predictive maps of *S. rosaceus* density

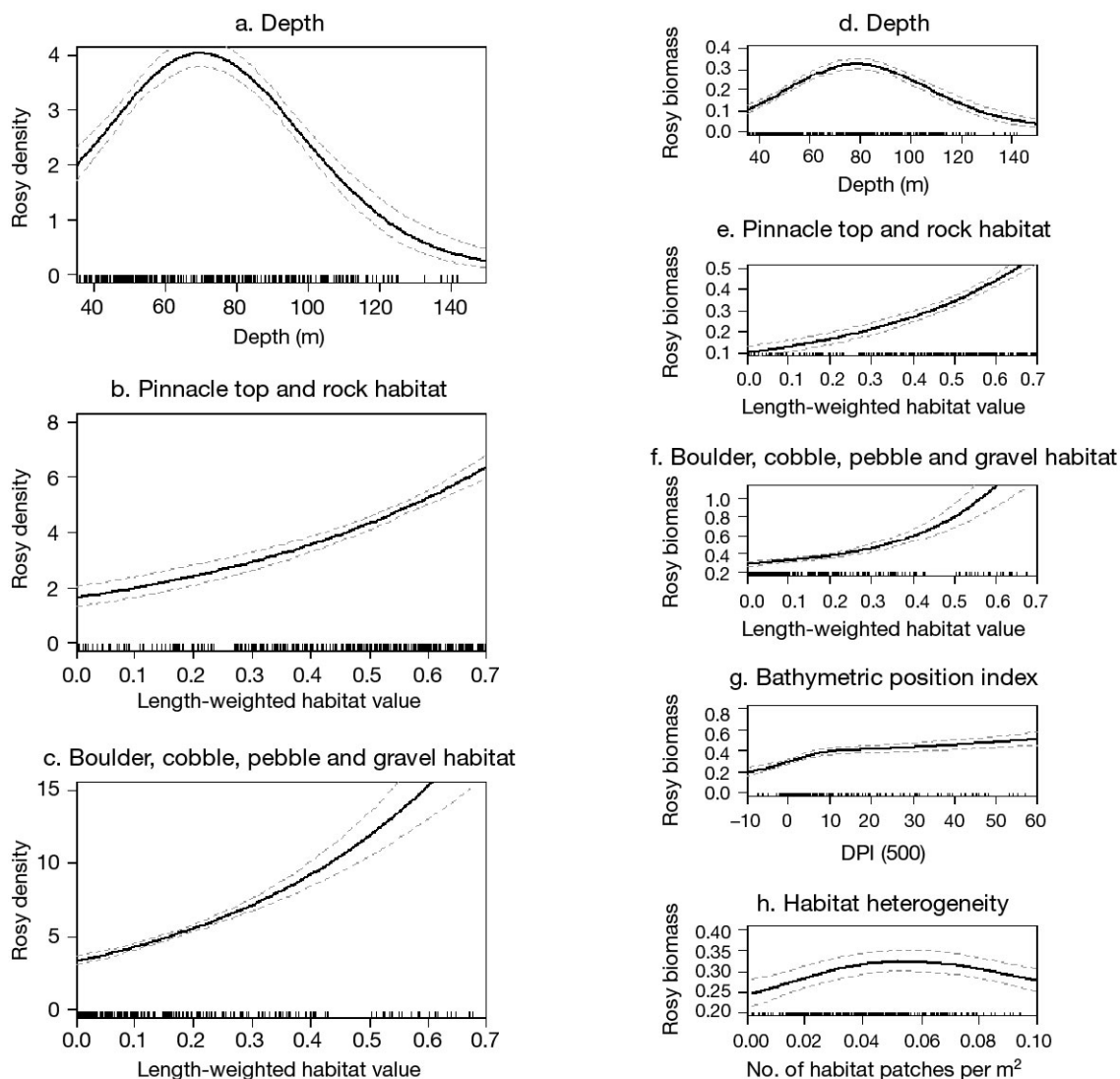


Fig. 4. *Sebastes rosaceus*. Response curves, based on habitat co-variables from visual surveys and acoustic multibeam bathymetry, for generalized additive model (GAM) predicted density versus (a) depth, (b) length-weighted habitat values in high-relief rock (Lhard) and (c) length-weighted habitat values in low-relief rock (Mhard); and GAM-predicted biomass versus (d) depth, (e) length-weighted habitat values in Lhard, (f) length-weighted habitat values in Mhard, (g) bathymetric position index (BPI), and (h) habitat heterogeneity. Solid lines = mean (± 1 SE, dashed lines). Rug plots along the x-axis = calibration data points

and biomass had an accuracy of Spearman's $\rho = 0.63$ and 0.66 and Kendall's $\tau = 0.46$ and 0.49 , respectively.

Modeling of *Sebastes constellatus* density and biomass

The selected GAM to predict *S. constellatus* density included depth and hard rock substrata with high and medium complexity ($w_i = 0.99$, Table 4), and concluded in similar results to the *S. rosaceus* model. The model accounted for 43% of the variability in *S.*

constellatus density ($R^2 = 0.41$). From response curves, *S. constellatus* occurred deeper than *S. rosaceus*, with relatively high densities in water depths >80 m (Fig. 6a). Similar to *S. rosaceus*, the response curves for transect length-weighted habitat values indicated a steady increase in predicted *S. constellatus* density with increasing complexity for both large (pinnacle top and rock habitat, Fig. 6b) and medium-to-small rocky substrata (boulder, cobble, pebble, gravel habitat, Fig. 6c).

The model for *S. constellatus* biomass was a weighted average of depth, hard rock substrata

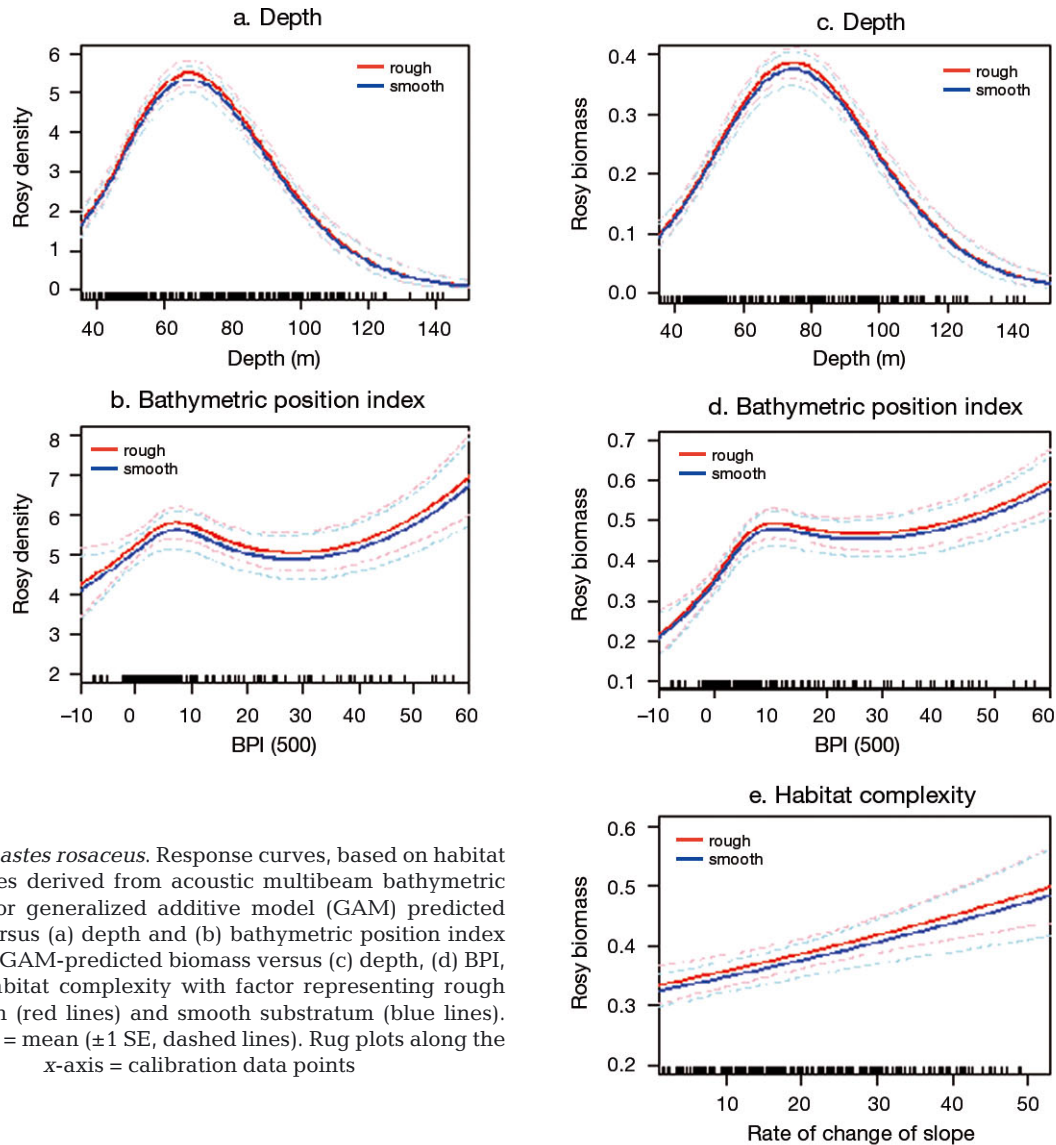


Fig. 5. *Sebastes rosaceus*. Response curves, based on habitat co-variables derived from acoustic multibeam bathymetric surveys, for generalized additive model (GAM) predicted density versus (a) depth and (b) bathymetric position index (BPI); and GAM-predicted biomass versus (c) depth, (d) BPI, and (e) habitat complexity with factor representing rough substratum (red lines) and smooth substratum (blue lines). Solid lines = mean (± 1 SE, dashed lines). Rug plots along the x-axis = calibration data points

with high and medium complexity, habitat heterogeneity, and BPI (Table 4), which accounted for 54% of its variability ($R^2 = 0.40$). The response curves for depth (Fig. 6d) and one transect length-weighted habitat co-variable (i.e. Mhard; Fig. 6f) revealed the same patterns as in density response curves for this species. However, the response curve for the transect length-weighted habitat co-variable Lhard (Fig. 6e), which characterizes highly complex pinnacle top and rock, demonstrated an increase in biomass to an intermediate level followed by a steady increase at the highest complexity. As with *S. rosaceus*, BPI was not an important co-variate in the model that predicted density but was included in the selected GAM to predict biomass for *S. constellatus*; predicted biomass was lowest in submarine canyons and depressions (negative values of

BPI) and peaked at low-relief habitat features (e.g. boulder fields, Fig. 6g). The response curve for habitat heterogeneity (Fig. 6h) demonstrated a different pattern than that of *S. rosaceus* biomass; predicted biomass of *S. constellatus* was greater in areas of more homogenous habitat (i.e. low numbers of habitat patches per m^2).

Predictive maps of *Sebastes constellatus* density and biomass

The selected GAM to predict *S. constellatus* density was a weighted average of depth, BPI and rough substratum as a factor (Table 4). This model accounted for 29% of the variability in predicted *S. constellatus* density ($R^2 = 0.27$). Density of *S. constellatus*

Table 4. Results of model selection to predict *Sebastes constellatus* density and biomass off central California for 2 sets of models: (1) visual and bathymetry models and (2) bathymetry alone to support GIS-based predictive mapping. Models are ranked by Akaike's information criterion (ΔAIC) and Akaike weights (w_i). Models having $\Delta\text{AIC} < 2$ were combined using a weighted (w_i) model average and are in **bold**. Lhard = high complexity or large structured hard substratum (pinnacle top, rock, and flat); Mhard = medium complexity hard substratum (boulders, cobble, pebble, and gravel); Soft = low complexity substratum (sand and mud)

Model type	Model selection results	ΔAIC	w_i
Models based on co-variables from both visual surveys and multibeam bathymetry			
Density	<i>S. constellatus</i> ~ Depth +Lhard +Mhard	0	0.99
Density	<i>S. constellatus</i> ~ BPI +Lhard + Depth	33.01	0.01
Biomass	<i>S. constellatus</i> ~ Depth + Lhard +Mhard+ Habitat Heterogeneity + BPI	0	0.60
Biomass	<i>S. constellatus</i> ~ Depth +Lhard +Mhard + BPI	1.48	0.29
Biomass	<i>S. constellatus</i> ~ Depth +Lhard +Mhard + BPI + factor(Rough)	3.45	0.10
Models based on co-variables derived from multibeam bathymetry			
Density	<i>S. constellatus</i> ~ Depth + BPI	0	0.72
Density	<i>S. constellatus</i> ~ Depth + BPI + factor(Rough)	1.94	0.27
Density	<i>S. constellatus</i> ~ Depth	23.14	0.01
Biomass	<i>S. constellatus</i> ~ Depth + BPI + Habitat Complexity	0	0.54
Biomass	<i>S. constellatus</i> ~ Depth + BPI + Habitat Complexity + factor(Rough)	0.36	0.45
Biomass	<i>S. constellatus</i> ~ Depth + Habitat Complexity	7.71	0.01

peaked at 70 to 90 m in the response curves for depth of both substratum types (Fig. 7a). The response curve for BPI indicated that *S. constellatus* density was lowest in canyons and depressions followed by a steep increase to relatively low positive BPI values that are associated with fine-scale habitat features such as boulder or rocky substrata at higher elevation relative to surrounding seascape (Fig. 7b). Density increased even more at the highest BPI values, indicating an association of *S. constellatus* with pinnacle tops.

The selected GAM for *S. constellatus* biomass was a weighted average of depth, BPI, habitat complexity, and rough substratum as a factor (Table 4). This model accounted for 32% of the variability in *S. constellatus* density ($R^2 = 0.23$). From response curves of co-variables depth (Fig. 7c), BPI (Fig. 7d), and habitat complexity (Fig. 7e), *S. constellatus* biomass was greater for the rough substratum factor than for the smooth factor. Peak biomass of *S. constellatus* was predicted at deeper depth (i.e. ~100 m) than that of peak density (~80 m). The response curve for BPI indicated that *S. constellatus* biomass was lowest in canyons and depressions followed by a sharp peak associated with fine-scale habitat features that rise slightly above the surrounding seascape (Fig. 7d). The habitat complexity response curve indicated an increase in *S. constellatus* biomass with increasing habitat complexity.

The accuracies of the predictive maps of *S. constellatus* density and biomass were characterized by

Spearman's $\rho = 0.36$ and 0.63 and Kendall's $\tau = 0.53$ and 0.46 , respectively. Spatial patterns of predicted biomass of *S. constellatus* were highest in areas of complex rock off Point Lobos (Fig. 3e) and Point Sur (Fig. 3e,f); these areas were also associated with high predicted biomass of *S. rosaceus*.

DISCUSSION

Until recently, predictive habitat-based models and maps of demersal marine fish distribution had been largely developed from presence/absence or presence-only fish data (Iampietro et al. 2008, Young et al. 2010). In this paper, we attempt to advance beyond presence/absence and presence only models to develop predictive regional maps of rockfish density and biomass at the individual species level in a temperate ecosystem. There have been a number of spatially predictive mapping and modeling studies in tropical ecosystems. Costa et al. (2014) integrated habitat data from acoustic sensors (i.e. splitbeam and multibeam echosounders) in the US Virgin Islands to predict fish density, and found the model performed best at larger body sizes (≥ 29 cm) to identify fish aggregations and help coastal managers prioritize areas of higher conservation value. Pittman & Brown (2011) similarly developed predictive maps for several key fish species associated with Caribbean coral reef seascapes and found that habitat complexity derived from Light Detection and Ranging Data

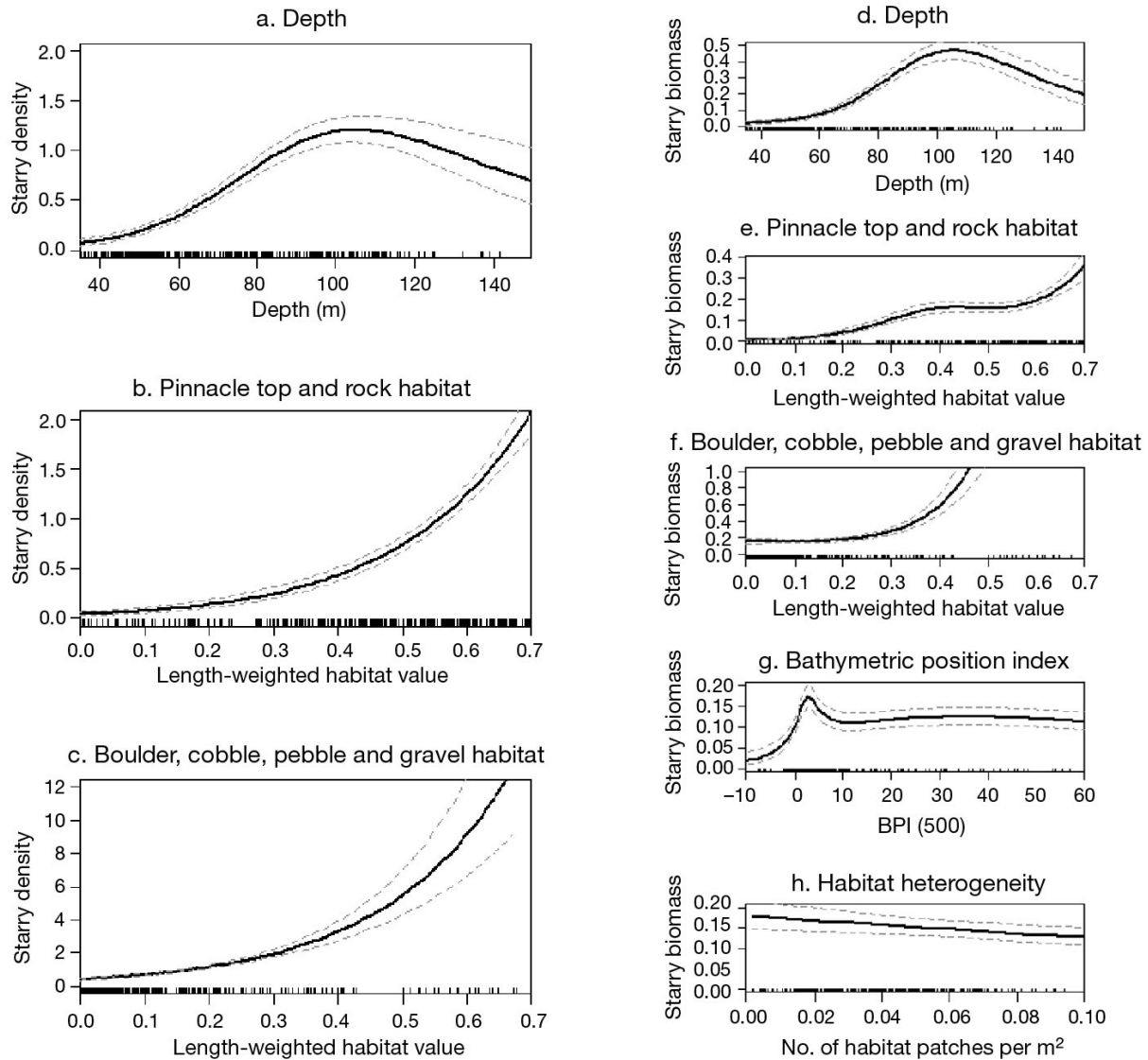


Fig. 6. *Sebastes constellatus*. Response curves, based on habitat co-variables from visual surveys and acoustic multibeam bathymetry, for generalized additive model (GAM) predicted density versus (a) depth, (b) length-weighted habitat values in high-relief rock (Lhard) and (c) length-weighted habitat values in low-relief rock (Mhard); and GAM-predicted biomass versus (d) depth, (e) length-weighted habitat values in Lhard, (f) length-weighted habitat values in Mhard, (g) bathymetric position index (BPI), and (h) habitat heterogeneity. Solid lines = mean (± 1 SE, dashed lines). Rug plots along the x-axis = calibration data points

(LiDAR) contributed most to the spatial model of habitat suitability for *Stegastes planifrons* (threespot damselfish). Habitat complexity, particularly the slope of the slope (a measure of the maximum rate of slope change) was found to be the most useful predictor of diversity and abundance of fishes and corals in the Caribbean (Pittman et al. 2009).

Many rockfish species demonstrate habitat preferences for complex rocky substrata (Love & Yoklavich 2006, Love et al. 2009). Young et al. (2010) applied generalized linear models to predict the highest

probability of occurrence (presence/absence) of *Sebastes rosaceus* in high relief rocky areas of Cordell Bank on California's northern coast, with habitat complexity included as a strong predictor in these models. We found densities of *S. rosaceus* and *S. constellatus* to have similar patterns of habitat affinity in relation to fine-scale remotely sensed measures of habitat complexity. We also found that intermediate levels of habitat heterogeneity were important in explaining *S. rosaceus* variability across the seascape and to demonstrate the importance of composition

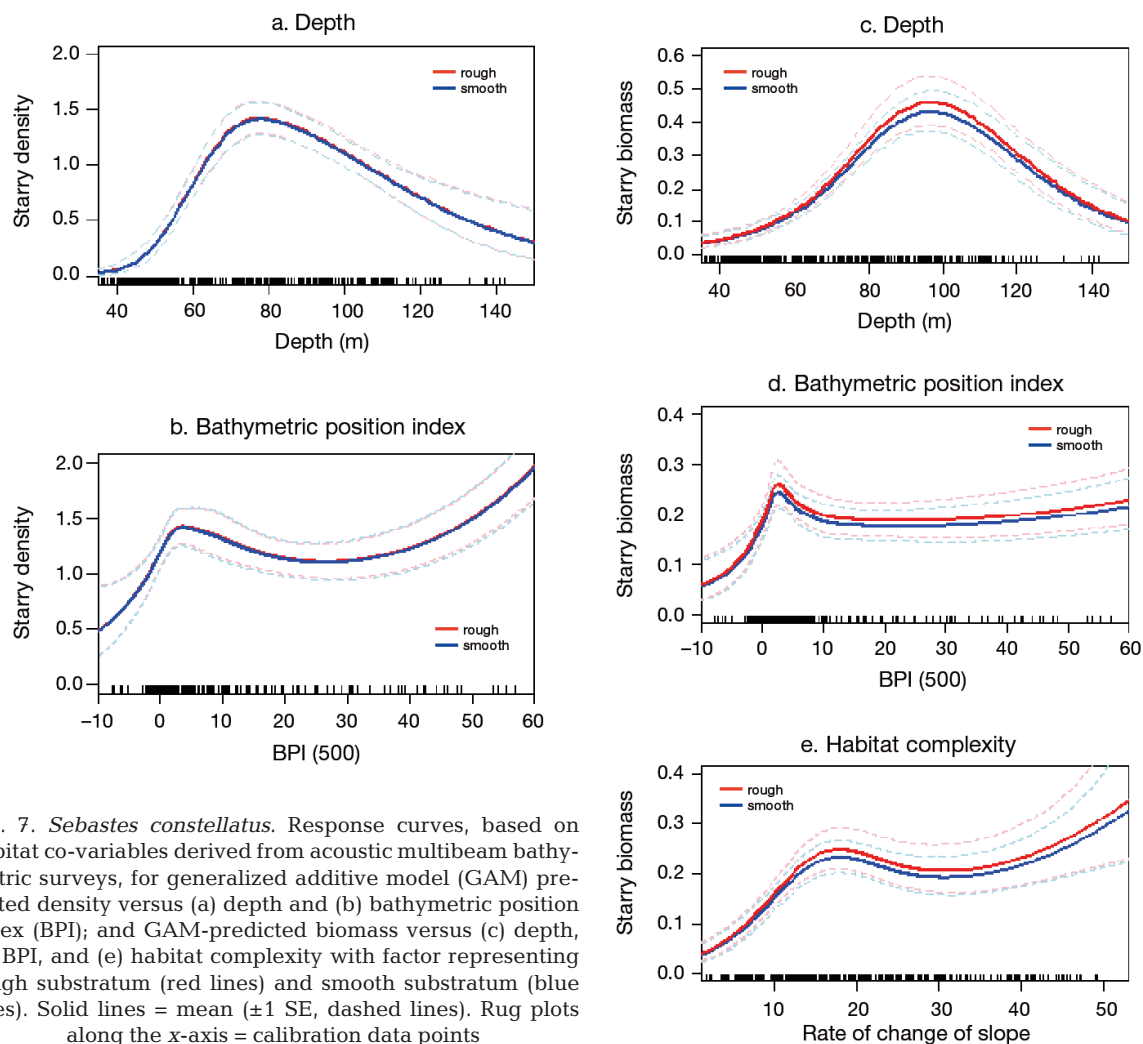


Fig. 7. *Sebastes constellatus*. Response curves, based on habitat co-variables derived from acoustic multibeam bathymetric surveys, for generalized additive model (GAM) predicted density versus (a) depth and (b) bathymetric position index (BPI); and GAM-predicted biomass versus (c) depth, (d) BPI, and (e) habitat complexity with factor representing rough substratum (red lines) and smooth substratum (blue lines). Solid lines = mean (± 1 SE, dashed lines). Rug plots along the x-axis = calibration data points

and configuration of habitat features. Further, the BPI co-variable highlights areas in the seascape that are tops of large pinnacles or rocky outcrop features adjacent to canyons (e.g. Point Pinos and Point Sur). Anderson & Yoklavich (2007) reported *S. rosaceus* rockfishes were found in groups of other large-bodied rockfishes (e.g. *S. paucispinis*, *S. flavidus*, *S. rubrivinctus*, and *Sebastes* spp.) with strong associations to high-relief rocky outcrops. In addition to the refuge provided by structurally complex habitat, relatively productive waters associated with rocky pinnacles and outcrops in and adjacent to canyons could support greater fish biomass.

The visual survey methods used in this study can be more effective than extractive trawl surveys in estimating abundance of rockfish species living in high-relief rocky areas. As with all survey methods, there are several assumptions and sources of uncertainty associated with visual surveys. We have criti-

cally evaluated several of these assumptions using similar survey techniques in prior field surveys (Yoklavich et al. 2007, Laidig et al. 2013). The strip transect method used in our study assumes 100% detection of the target species within the strip. To help meet this assumption, we used a relatively narrow strip width (2 m) during our surveys. That said, it is unlikely that 100% of *S. rosaceus* and *S. constellatus* were seen in the transects, particularly the smallest individuals nestled in the rocky substrata. This would result in an underestimation of densities by some unknown amount. Additional studies will be required to estimate true detectability of these species in high-relief habitats.

Another important assumption of these underwater surveys is that rockfish behavior is independent of the observer and submersible (i.e. no avoidance or attraction). Laidig et al. (2013) reported that 6 and 10% of *S. rosaceus* near (total $n = 134$) and on ($n = 10$)

the seafloor, respectively, reacted mostly by swimming toward or to the left of the *Delta* submersible during surveys off central California. *Sebastes constellatus* reacted similarly, with 5 and 8% of fish near ($n = 21$) and on ($n = 13$) the seafloor responding to the survey vehicle². Both species moved an average distance of 2 to 3 m per reaction. This type of reaction could bias estimated densities if the fish entered or exited the strip transect; otherwise, these relatively small movements would not influence the resultant densities. In addition, the assumption that the fish are distributed randomly with respect to the transect was met by randomizing survey sites and traversing haphazardly across substratum types and depth gradients within designated rocky habitats.

There also are potential sources of error related to fish measurements. In an earlier study (Yoklavich et al. 2007), we estimated error associated with our underwater estimates of fish size. From the submersible we measured fish replicas of known total length, and size generally was underestimated by a relatively small amount (mean \pm SD deviation: -1.1 ± 1.2 cm). This would result in an underestimate of biomass. Biomass estimates also contain some unknown amount of error related to the conversion of length to weight. However, the regression of weight and length (Love et al. 1990) provided an excellent fit for both of our target species, so the amount of error introduced using length to calculate weight is expected to be small.

Further, our research is limited by the temporal and spatial extent of the study. Our visual surveys were conducted only in Fall (September to November) of 2007–2008, and we did not expect a seasonal effect in abundance because these sedentary rockfish species are not known to be wide-ranging (Love et al. 2002). However, repeating these surveys to establish time series in density and biomass over several years would allow us to evaluate change in rockfish abundance across the region as well as inside and outside marine protected areas (MPA). In particular, this study represents a baseline for monitoring the deep-water portion of 8 MPAs that were established on the central coast coincident with the commencement of our surveys in September 2007. With future monitoring, we will be able to include an MPA term in the models to evaluate the efficacy of these closed areas in protecting deep-water species of rockfishes. The

geographic scale of our study could also be expanded to include data from our visual surveys in rocky areas of southern California where both target species are common.

We developed 2 sets of models in this study: one set based on co-variables from both the visual surveys and region-wide high-resolution bathymetry and the other set of models based only on co-variables derived from the bathymetry. Our motivation was to examine the added value of data collected *in situ* from a submersible compared to that collected solely from acoustic surveys. The models using all of the co-variables (including those from the visual surveys) accounted for more of the overall variance (42 to 54%) in estimated density and biomass for both species than those using only derived variables from multibeam bathymetry (29 to 38%). Clearly data from the visual surveys improved the predictive capabilities of the models. However, in order to apply predictions on a region-wide scale, only the bathymetric co-variables could be used because *in situ* data were not available on a broad scale.

Benthic terrain analysis of multibeam bathymetric acoustic data is a valuable way to identify seafloor habitat that supports individual species and assemblages (Wilson et al. 2007, Guinan et al. 2009). Quantifying and mapping elements of rockfish habitat, such as seafloor substratum type, texture, and complexity, are critical for evaluating the effectiveness of these areas to maintain rockfish stocks (Yoklavich et al. 2000, 2007). Our ability to derive indices of benthic habitats (e.g. habitat complexity, depth, BPI) from multibeam acoustic data^{3,4} that were recently synthesized across California state waters supports the production of spatially predictive maps of demersal fish populations at a regional scale relevant to the assessment of fish stocks in rebuilding status. Further, providing a spatial component to these predictions can be critical in the management of relatively sedentary rockfish species to safeguard against local depletion (Parker et al. 2000).

Currently it is challenging to integrate oceanographic and benthic habitat predictor variables into habitat models and maps, largely because the spatial resolution of available oceanographic data (e.g. temperature, salinity, and bottom currents from regional oceanographic modeling systems [ROMS]) is 10s of km, and the resolution of the benthic habitat data is several orders of magnitude greater (<1 m from

²Pers. comm., T. Laidig, Fisheries Ecology Division, Southwest Fisheries Science Center, NOAA, 110 Shaffer Rd., Santa Cruz, CA 95060, USA

³<http://walrus.wr.usgs.gov/mapping/csmp/>

⁴<http://seafloor.otterlabs.org/csmp/csmp.html>

visual surveys and 2–5 m from multibeam acoustic surveys of bathymetry). Our models were developed only with benthic habitat predictors. However, the inclusion of oceanographic variables could further improve the predictive capability of our models and maps when these data become available at finer spatial scales.

Rockfishes are among the most valuable fisheries in California, have extremely vulnerable life-history characteristics, and cannot sustain levels of fishing mortality; as a result, they are being managed more conservatively than in the past. The predictive maps of density and biomass of *S. rosaceus* and *S. constellatus* will improve our understanding of habitat variables that influence the spatial distribution and abundance of these species across the central coast. The results of our study provide information to support stock assessments of these 2 species of rockfishes, both considered to be data-poor species by the PFMC. For example, using our predictive maps of biomass, stock assessors could estimate total biomass (and associated uncertainty) of these species within our designated study area off central California and consider those estimates in context with assessments based solely on commercial and recreational landings (Dick & MacCall 2010, Ralston et al. 2010). Such estimates of habitat-specific abundance are critical to effectively control the magnitude of fishing mortality and to support the local recovery of depleted populations.

CONCLUSIONS

In this study we developed models of rockfish density and biomass based on *in situ* observations of fish numbers, size, and associated seafloor substratum variables and derived variables from region-wide multibeam bathymetry. Model results were expressed as predictive maps of density and biomass on a regional scale. Such maps allow us to quantify habitat capacity, prioritize habitat conservation, and evaluate potential risk of various human activities to rockfish populations over broad spatial scales. These results have direct application to coastal and marine spatial management, particularly in (1) the design and monitoring of MPAs, (2) improving the identification of essential fish habitats, (3) distinguishing those areas important to the restoration or rebuilding of depleted stocks, and (4) advancing our understanding of the effects of a changing climate on the spatial distribution and abundance of Pacific coast groundfishes.

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