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Gender-Mediated Habitat Associations of Kelp Greenling (Hexagrammos Decagrammus) Along the Central Coast of California

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GENDER-MEDIATED HABITAT ASSOCIATIONS OF KELP GREENLING (*HEXAGRAMMOS DECAGRAMMUS*) ALONG THE CENTRAL COAST OF CALIFORNIA

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by
Jessica Flower Moye
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GENDER-MEDIATED HABITAT ASSOCIATIONS OF

KELP GREENLING (*HEXAGRAMMOS DECAGRAMMUS*)

ALONG THE CENTRAL COAST OF CALIFORNIA

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ABSTRACT

Gender-mediated habitat associations of
kelp greenling (*Hexagrammos decagrammus*)
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by
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Coastal And Watershed Science And Policy
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Marine fish assemblages are broadly associated with physical habitat attributes such as water temperature and depth. At smaller spatial scales fishes are known to associate with specific substrate types such as rocky reef or unconsolidated sediments. Understanding these fine-scale habitat associations for economically and ecologically important species allows for more refined resource management and spatial planning efforts against a framework of increasing use of the marine environment. This study quantified the distribution and habitat associations of kelp greenling (*Hexagrammos decagrammus*) at four locations across north-central California, ranging from Point Arena to Pillar Point. Data on the distribution of kelp greenling were extracted from continuous video and still photographic imagery collected by a remotely operated vehicle between 2010 and 2011 as part of the baseline characterization of the newly implemented network of California marine protected areas (MPAs). Results indicate kelp greenling associate with low-relief, continuous rock substrates at each of the four sites. Distribution of fish within sites varied significantly based on gender, with females occurring more frequently in sand habitat than males, particularly in areas immediately adjacent to hard substrate. The geo-referenced kelp greenling observations were coupled with bathymetry-derived environmental parameters using generalized linear models to predict areas of fish occurrence beyond the sampled areas. These results advance our understanding of how kelp greenling utilize the habitats in which they occur, while the resulting predictive maps provide information on their distribution at spatial scales appropriate for MPA management and marine spatial planning.

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INTRODUCTION

ECOLOGICAL CONTEXT

Distribution of marine life is broadly correlated with physical habitat attributes, including water temperature and depth (Ekman 1953; Bergen et al. 2001; MacPherson 2003). Within these regional patterns, association to benthic habitats further influences the abundance and distribution of species assemblages (Watling et al. 1988; Langton and Uzmann 1989). It is known that available substrate material (i.e. mud, gravel, or sand), or habitat features (i.e. boulders and cobbles or continental slopes), are largely influential in distributing demersal fish species throughout the seafloor (Auster et al. 2001; Hinz et al. 2006; Anderson and Yoklavich 2007; Anderson et al. 2009; Wedding and Yoklavich 2015). The same habitat feature may be used differently among species to satisfy ecological habitat requirements (Grober-Dunsmore et al. 2008), support specific life history characteristics (Shaw and Hassler 1989; Petrie and Ryer 2006), and provide structure and therefore shelter from predators (Lindholm et al. 1999).

Scale is an important factor when considering fishes' use of benthic habitats (Turner 1989; Syms 1995). Habitat associations can be biotic, such as algae or macro-invertebrates (Heifetz 2002; Diaz et al. 2003), or abiotic such as depth or rock piles that provide relief (Stein et al. 1992; Tissot et al. 2007). For example, Greenstripe rockfish were consistently observed sitting in mud near small, isolated rock patches (Tissot et al. 2007). High abundances of Plaice occur in relatively shallow areas with nearshore conditions, likely due to the area's sand content that enables easier digging for burial or foraging and results in less expended energy (Howell and Canario 1987; Amezcua and Nash 2001; Hinz et al. 2006). These examples indicate how specific habitat features, multiple features, and even the spatial arrangement of these features fulfill particular biological requirements and describe a species' distribution.

The kelp greenling (*Hexagrammos decagrammus*) is a recreationally and commercially exploited demersal fish, endemic to the northeastern Pacific Ocean. It inhabits subtidal waters to approximately 50 meters (m) deep from the Aleutian Islands, Alaska to central California, with occasional southern observations in La Jolla, California (CDFW 2001; Hoobler 2006).

A review of current literature provided little information regarding habitat use by the sexually dimorphic kelp greenling. Association to rock can be assumed, at least seasonally by males, since males defend nests laid on encrusting epifauna or directly onto rock (DeMartini 1986; Crow et al. 1997). Using visual observations from submersibles, Stein et al. (1992) found the kelp greenling of Heceta Bank, OR more significantly correlated to hard-bottom if it were a secondary substrate rather than as a primary substrate and Anderson et al. (2009) concluded the fish in Cordell Bank, CA have a moderate correlation with rock, a weak correlation with cobble, and a negative correlation with mud. Gender differences in habitat use were not examined in these prior studies. Additionally, results from an acoustic tagging study found that adults have established home ranges of 500 - 1500 m^2, female kelp greenling have larger home ranges than males, and juveniles were generally free-roaming and not established (Freiwald 2009).

The ecological rationale for gender-specific habitat use is based on sexual asymmetry in reproductive strategies and mating success due to sexual dimorphism (Croft et al. 2003; Blanckenhorn 2005). Since adult female kelp greenling are larger in size (CDFW 2001) with broader home ranges that aid genetic dispersal, it is possible that habitat use differs from territorial males.

Understanding potential gender differences in habitat associations promotes more informed management of the kelp greenling. Known habitat associations can broadly predict amounts of suitable habitat within an area, effectively aiding in creation or assessment of marine protected areas (MPAs). It is now understood that MPAs are more successful as a network of protected areas, especially when implemented with sufficient protection of redundant habitats on a suitable scale (Bohnsack 1992; Lubchenco et al. 2003; Osmond et al. 2010).

This study aims to understand 1) kelp greenling distribution along the coast of northern California relative to specific, fine-scale habitat attributes of the seafloor, 2) how gender mediates this habitat-specific distribution, and 3) the predicted distribution of kelp greenling beyond the relatively limited sample areas using predictive habitat modelling.

METHODS

STUDY AREA

The study sites included state waters of and around Point Arena (PA), Bodega Head (BH), Southeast Farallon Islands (FI), and Pillar Point / Montara (PP) (Figure 1A-D). MPAs surveyed included State Marine Reserves (SMRs), State Marine Parks (SMPs), State Marine Conservation Areas (SMCAs), and State Marine Recreational Management Areas (SMRMAs). Across these regions, the seafloor is generally comprised of soft sediment beyond the 30 m isobath, however available hard substrate creates near-shore patch reefs containing rocky outcrops, pinnacles, and steeply sloping walls (CMLPAI 2007).

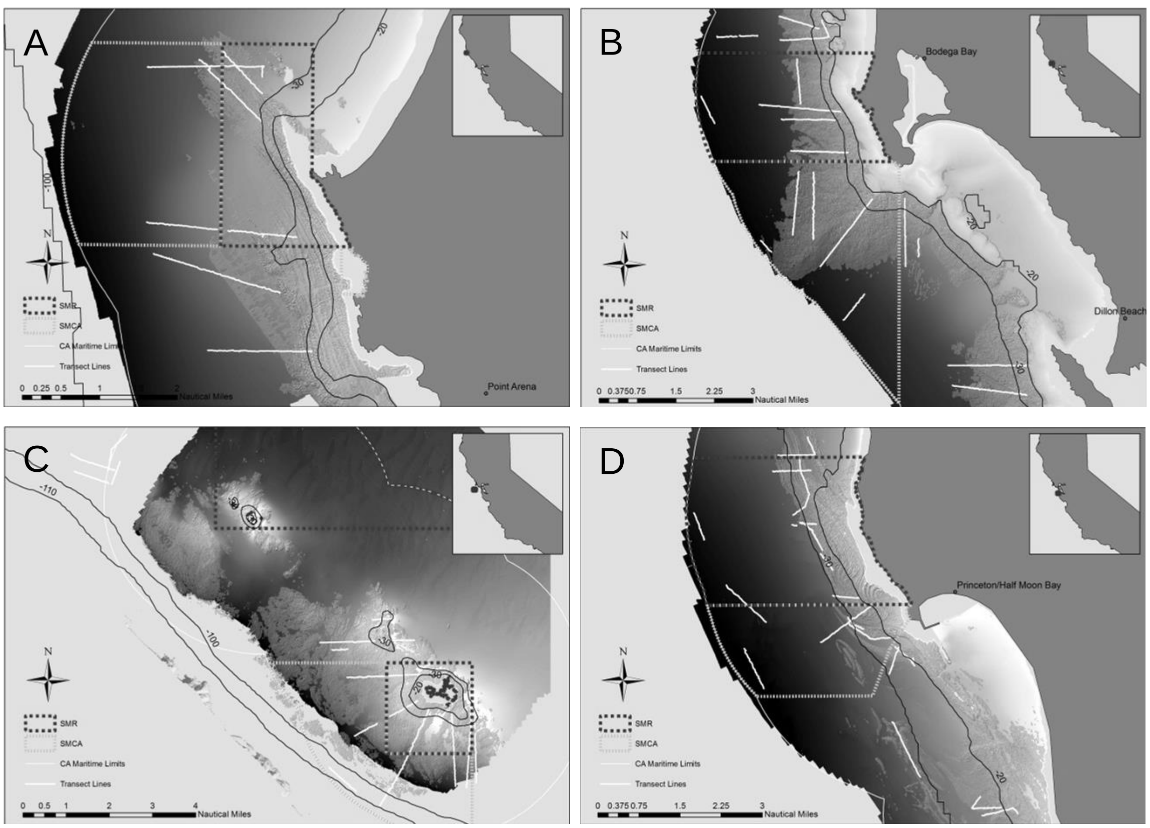


Figure 1. Study site maps of ROV transect placement conducted at (A) Point Arena, (B) Bodega Head, (C) Southeast Farallon Islands, and (D) Pillar Point / Montara. Includes MPA boundaries, 20 and 30 m isobaths, and sun-illuminated topographic maps of the seafloor.

SAMPLING DESIGN

Study sites were surveyed June – August 2010 and 2011. Within each site, underwater visual surveys were conducted using a remotely operated vehicle (ROV) inside the MPAs as well as in unprotected areas adjacent to the MPAs. The ROV Beagle, a Vector M4 ROV (owned by The Nature Conservancy and operated by Marine Applied Research and Exploration), was equipped with forward-facing multibeam sonar, an altimeter, a CTD, two halogen lights, and two high powered HMI lights. A Trackpoint III ® acoustic positioning system tracked the ROV's position on the seafloor and coordinates were logged into Hypack ® navigational software. Four brushless motor thrusters were mounted on the ROV to allow directed movement rather than drift. Three video cameras recorded high-resolution forward-, down-, and rear-facing video and one down-facing camera collected still photographs. Live video feed was transmitted from the ROV to the boat through an armored coaxial cable and recorded digitally. Forward and down paired sizing lasers were spaced 10 cm apart and were captured in the video and still photographs. The ROV was 'flown' at a mean altitude of 0.2 m with an approximate speed of 0.6 knots. The forward-facing video camera captured an area of approximately 2 m by 5 m in each frame along the transect.

ROV transects averaged 3.2 km and were conducted between 20-116 m depths. Transect lengths were not standardized and therefore captured between 0.5 to 4 hours of imagery, depending upon at sea conditions. Transect were placed using high-resolution (2 m) data from multibeam and sidescan sonar systems as part of the California Seafloor Mapping Project courtesy of CSU Monterey Bay's Seafloor Mapping Laboratory (CSUMB SFML). Transect placement was stratified by habitat type (hard substrate, soft sediments, and transitional habitats). Transects were not re-sampled between 2010 and 2011, but rather distributed to collect as much seafloor imagery as possible, then pooled as one dataset within each study site.

VIDEO ANALYSIS

Data was collected from the forward-facing video, since it captured fish presence, response to ROV, and habitat availability. Since lights and sound are shown to cause altered responses of fishes through attraction or avoidance to underwater vehicles

(Stoner et al. 2008; Ryer et al. 2009; Rountree and Juanes 2010) the reaction of individual kelp greenling was recorded at the initial moment of ROV detection to determine if ROV presence altered activity.

To standardize the inconsistent visibility between and within study sites, only fish viewed below the paired lasers were counted. For each kelp greenling observation time code, depth, total length, gender, reaction at first site, and habitat immediately used by the fish were quantified. The time code (GMT rounded to the nearest second, i.e. 20:15:45), which is linked to the ROV's geo-referenced location, altimeter, and CTD information was used to estimate each individual's location. Habitat immediately used was considered the predominant substrate in the video frame when the fish was centered as close to the pairing lasers as possible.

Species identification, gender, and size measurements of the kelp greenling were verified by using the down-facing video and still photographs. Fish total length was binned by 5 cm increments. Only fish greater than 10 cm were considered since species detection, identification, and sizing accuracy beyond this was not completely reliable with the ROV imagery and varying visibility.

Habitat associations were classified using fine-scale seafloor substrate and relief metrics (Table 1). With the fish as close to the sizing lasers as possible, dominant substrate was quantified using a modified substratum classification established by Greene et al. (1999). Relief was the dominant, vertical height of the physical substrata off the seafloor and estimated using the paired lasers.

Table 1. Substratum and relief categories used to define fine-scale habitat.

Substrate Type	**Criteria**
Continuous rock	Outcropping or bed of solid rock
Large rock (Boulder)	≥ 20 cm loose, individually distinguishable rocks
Small rock (Cobble)	< 20 cm loose, individually distinguishable rocks
Sand	Unconsolidated, small particle size
Substrate Relief	**Criteria**
Flat	Featureless sand or flat rock (most commonly used for sand habitats)
Low	0 - 1 m vertical relief (for rock or sand habitats)
Moderate	1 - 2 m vertical relief (for rock habitats)
High	> 2 m vertical relief (for in rock habitats)

To understand if male and female kelp greenling use different attributes of the fine-scale habitats, data were split into three categories based on gender (all kelp greenling, identified males, and identified females). All statistical analyses were conducted using the R statistical package (R Development Core Team 2011). Data were tested for normality using a Shapiro-Wilk normality test. Univaritate comparisons were conducted to compare habitat characteristics used by males and females (i.e. substrate and relief) using the non-parametric Mann-Whitney-Wilcoxon test (wilcox.test) and post-hoc test in R (pairwise.wilcox.test).

Geospatial Analysis

The Marine Geospatial Ecology Toolbox (MGET; Roberts et al. 2010), was used to predict the probability of occurrence in the non-surveyed areas of each study site by combining the kelp greenling geo-referenced points (presence points) and true absence points. Absence points were randomly selected using ArcGIS 10.1 (ESRI 2011) for each transect with a 1:1 ratio. A 5 m buffer was placed around each presence point to ensure all absence points were at least 5 m away from other absence points and presence points. Five meters was chosen as a realistic distance between each kelp greenling observation after reviewing all video imagery. In three observations, two fish were recorded sitting on substrate within 1 m of each other. These observations were separated by one second to keep the total count of presence points. The spatial separation was negligible and left as is since it provided insight into the nature of kelp greenling distribution within the region.

All study sites were analyzed individually to control the confounding factors acting upon the populations because of differences in the amount of data collected, oceanographic conditions affecting the area, and the amount of soft, hard, and transitional habitat surveyed. Following the approaches of Iampietro et al. (2008) and Young et al. (2010), separate habitat raster layers for each site were derived from 2 m resolution bathymetric digital elevation models created by the CSUMB SFML. These environmental parameters included depth, vector ruggedness measure (VRM), topographic positioning index (TPI), northness, eastness, curvature, slope, and distance to rock (see Young et al. 2010 for raster creation method), all of which successfully described the occurrence in reef fishes in the Monterey Bay (Iampietro et al. 2008;

Young et al. 2010; Krigsman et al. 2012; Wedding and Yoklavich 2015). After all rasters were created, the values were extracted to each presence and absence point.

MGET's generalized linear model (GLM) tool was used for analysis with the stepwise backward comparison. Instead of dividing the dataset into 'training' and 'testing' data, the three datasets (all, males, females) were fitted using the entire Bodega Head dataset because it had the most observations. The overall accuracy and area under the receiver operating characteristic (ROC) curve were used as evaluation criterion to establish best fit. Once the best fit model for each Bodega Head dataset was established, it was applied to the other three study site datasets to test each model's accuracy. This method was chosen because assessing models for accuracy using independent data can increases precision in suitability maps (Verbyla and Litaitis 1989).

Once applied to the other study sites, models were evaluated with MGET's deviance values, accuracy values, and ROC values. Higher deviance values of a parameter are considered to provide greater predictive power. Model accuracy values were calculated by considering the error rate of positive and negative predictions. ROC values were interpreted using Hosmer and Lemeshow's (2000) scale where 0.5 is the predictive ability achieved by chance, 0.7 – 0.8 is an acceptable discrimination prediction, 0.8 – 0.9 is excellent, and > 0.9 is outstanding.

Habitat suitability maps of all sites were created using the Predict from Rasters tool in MGET to visualize the spatial arrangement of the statistically significant habitat in areas that lacked data collection. The ROC cut off value was used to discriminate suitable and unsuitable habitat. For each study site, MPA boundaries were overlaid onto the predicted map enabling the total area of kelp greenling habitat to be compared inside and immediately outside the protected areas. Immediate area outside the MPAs was considered the strip of state waters 1500 m north and south of the MPA. This area was chosen based on Freiwald's (2009) findings of kelp greenling home ranges.

RESULTS

IMAGERY OBSERVATIONS – FINE-SCALE HABITAT USE AND DISTRIBUTION

A total of 775 kelp greenling (371 identified males, 286 identified females) were observed in over 129 hours of forward-facing video imagery. Across sites, depth observations of kelp greenling ranged from 15.3 m – 95.4 m and paralleled the survey effort. Sizes ranged from 10 – 50 cm with over 56% of fishes observed between 25 – 35 cm. No observations were smaller than 10 cm or larger than 50 cm. Size distributions were similar across sites with most fish in the 25-30 cm size class, except for the Farallones that had more observations in the 30-35 cm class (Figure 2A). Within each study site, more males were observed than females but females were observed at deeper depths (> 55 m) (Figure 2B). The majority of occurrences were at Bodega Head, but larger fish (> 35 cm) were observed in the Farallones.

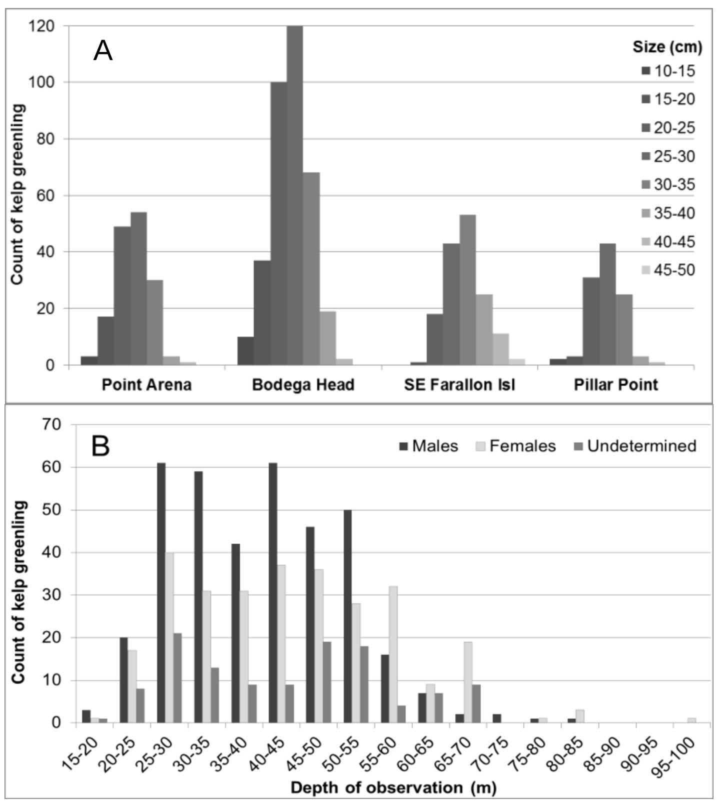


Figure 2. (A) Distribution of size classes for kelp greenlings by study site (North to South / left to right) (*n* = 775). (B) Gender by depth bins for kelp greenling observations across all sites.

The kelp greenling reactional observation survey indicated that observed fish had a neutral response to the ROV (Table 2). The survey included 636 out of 775 fish (82%); of these observations, 39% were identified females and 47% were identified males. More than 50% of the surveyed fish were recorded in direct contact or adjacent to structure and/or substrate when the ROV approached and over 36% of fish were recorded swimming slowly through the water column in a single direction with no visible response to the ROV's presence. Therefore, over 85% of surveyed fish had no observable response to the ROV. Less than 8% of fish appeared disturbed by the ROV through a fleeing response after it was initially observed in direct contact with structure or slowly swimming in a single direction.

Table 2. Kelp greenling reactional observation survey categories and results across all study sites.

Behavior	Code	Description	Observed
Station-keeping on Bottom Position	SB	Direct contact with or adjacent to structure using little or no fin movements to maintain position.	51.10%
Station-keeping Swimming	SS	Maintaining position over a seafloor feature using active fin movements.	0.16%
Continuous Swimming	CS	Directed, slow swimming in single bearing; no movements directed at obvious prey, no attempts at predation.	36.64%
Hesitated sprint	HS	Visible shift in alertness - began CS or SB then changed to S in frame	7.86%
Sprint	S	Directed, urgent swimming either away from or towards the remotely operated vehicle	4.09%

Kelp greenling were commonly observed over continuous rock with low relief (Figure 3A-B), however male and female kelp greenling use of substrate and relief categories were non-identical populations ($p < 0.003$ in both cases). There was a significant difference between the use of sand and rock substrate for males and females, with females having a higher occurrence in sand ($p < 0.005$). The relief category flat was commonly combined with sand substrate and used significantly more by females than males ($p < 0.021$).

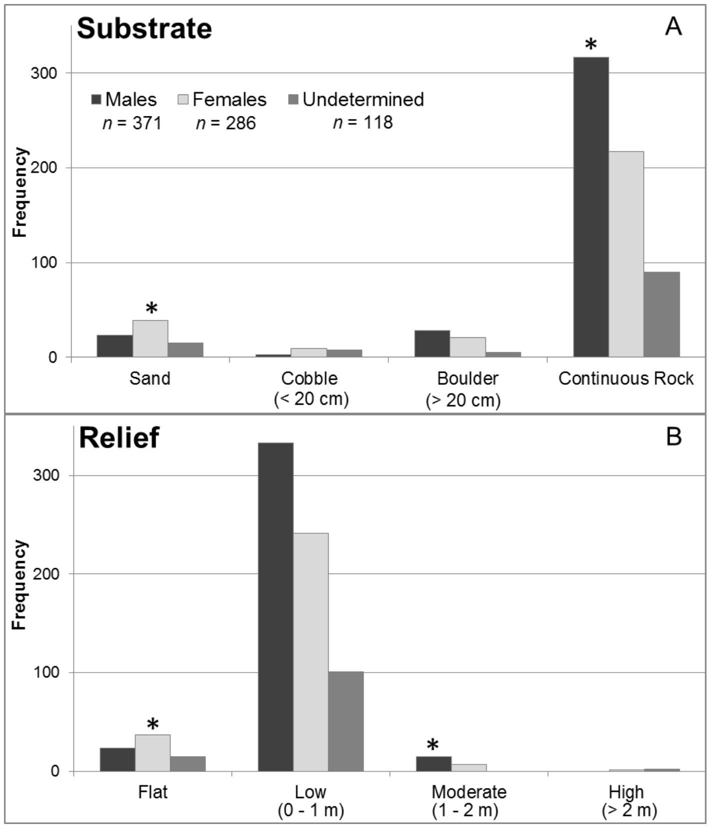


Figure 3. Frequency of substrate (A) and relief (B) categories observed for identified male, identified female, and undetermined kelp greenling across all sites. (*) indicates significant differences in the use of the habitat between genders and the category in which each gender associates.

GEOSPATIAL ANALYSIS – PREDICTED REGIONAL DISTRIBUTION

Results from the GLM backward stepwise comparison in MGET concluded there were different significant environmental parameters for the all, male, and female kelp greenling models (Table 3). For the all kelp greenling model, there was a significant inverse relationship for the distance to rock and depth parameters and a significant positive relationship with VRM; meaning, kelp greenling are not likely to be observed far from hard, rugose substrate or in deeper depths. For males, the highest deviance explained was the significant inverse relationship with depth and the significant positive relationship with slope. For females, the highest deviance explained was the significant inverse relationship with distance to rock and a significant positive relationship with

VRM. Topographic position index was included across all winning models but not significant.

Table 3. Results of generalized linear model backward stepwise comparisons of kelp greenling distribution relative to environmental predictor variables, including the explained deviance, direction, and significance level of any relationship.

	Model Parameter	Deviance Explained	Significance
All Fish	Depth	13.659	(-)***
	Northness		
	Curvature	3.964	(+)*
	Distance to Rock	24.860	(-)***
	TPI	0.301	(-)
	Slope		
	VRM	13.329	(+)***
Males	Depth	16.084	(-)***
	Northness		
	Curvature		
	Distance to Rock	5.743	(-)*
	TPI	2.862	(-) .
	Slope	11.970	(+)***
	VRM		
Females	Depth		
	Northness	1.816	(+)
	Curvature	4.053	(+)*
	Distance to Rock	18.974	(-)***
	TPI	0.086	(-)
	Slope		
	VRM	6.750	(+)**

Significance = '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1
TPI = Topographic position index
VRM = Vector ruggedness measure

Habitat suitability maps for the all, male, and female kelp greenling models in Bodega Head indicate kelp greenling are more likely found in nearshore, hard substrate environment than in soft substrate areas offshore (Figure 4). No kelp greenling are predicted to occur in the soft substrate (blue/cool colors), except for a small strip of area surrounding the hard substrate; this area (subsequently referred to as halo) around the hard substrate is indicated in light green and most evident in the map predicting female occurrence. The male kelp greenling map has a larger amount of highly suitable habitat indicated by red/warm colors found mostly along the shallower, nearshore hard substrate.

Bodega Head		
All kelp greenling *n* = 356	Male kelp greenling *n* = 143	Female kelp greenling *n* = 142

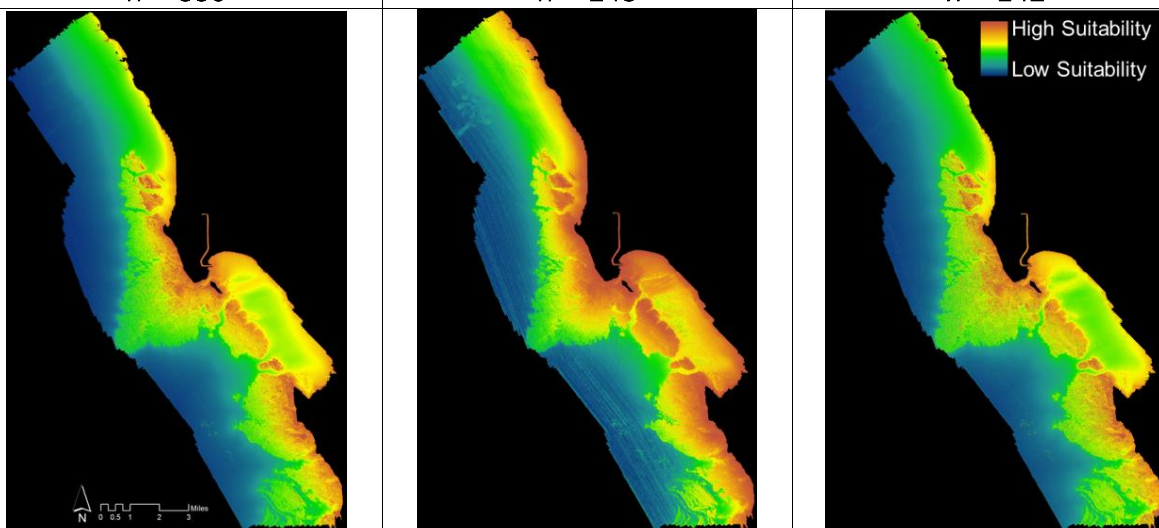
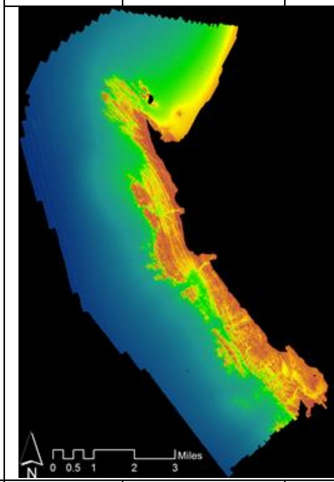
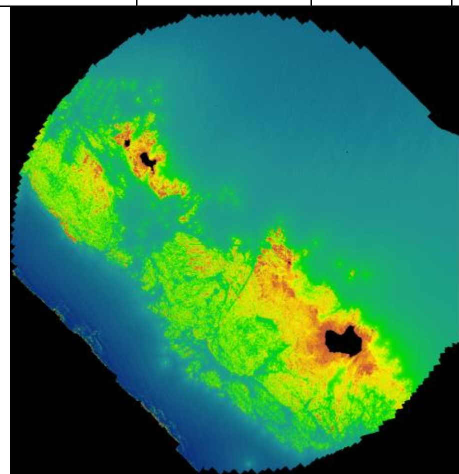
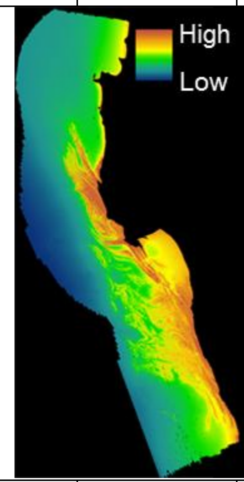
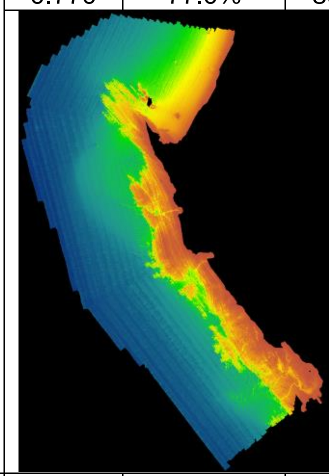
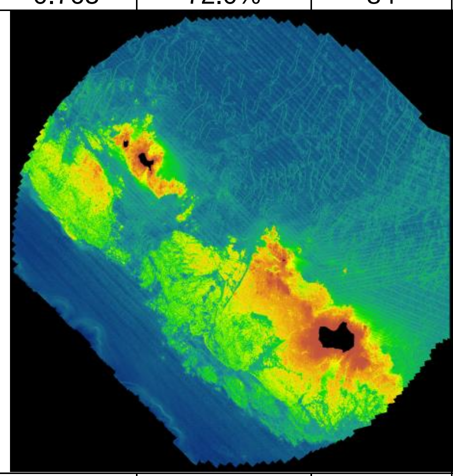
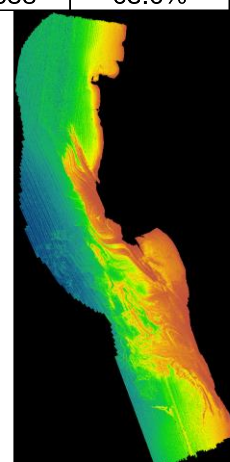
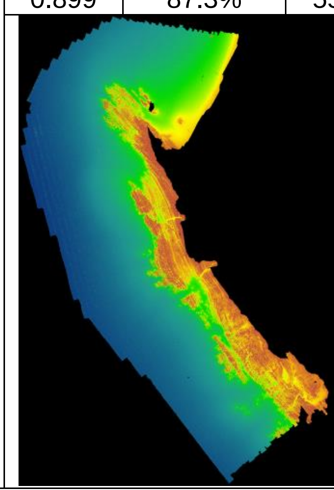
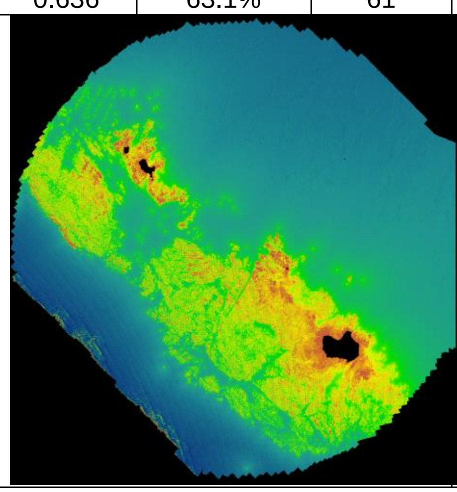
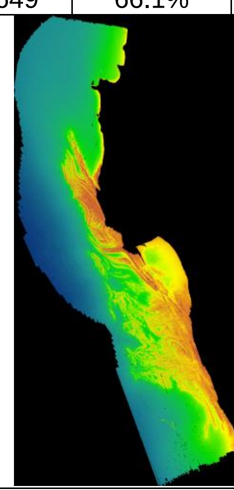


Figure 4. Habitat suitability maps for Bodega Head constructed with all observations from the study site. Warm colors indicate areas of more suitable habitat and higher likeliness of kelp greenling occurrence.

The Bodega Head models were applied to the datasets of Point Arena, the Farallones, and Pillar Point / Montara to test model fit (Figures 5 - 7). All, male, and female models scored between 63.1% and 87.3% accurate out of 100%, indicating the ability of the fitted models to detect true presence and absence. Models scored highest accuracy in Point Arena (all kelp greenling = 80.1%, males = 77.0%, females = 87.3%) (Figure 5). The all and male models scored lowest accuracy in Pillar Point (63.9% and 63.6%, respectively) (Figure 7). The female model scored lowest accuracy in the Farallones (63.1%) (Figure 6). This parallels the results for the area under the ROC curve values, where models had excellent to nearly outstanding values in Point Arena (all = 0.813, males = 0.770, females = 0.899) to barely acceptable discrimination prediction in other sites (Pillar Point: all = 0.667, males = 0.638; Farallones: females = 0.636).

Figure 5. Habitat suitability maps constructed using Bodega Head model and applied to predict kelp greenling distribution in in Point Arena, Southeast Farallon Islands, and Pillar Point. Area under the ROC curve (AUC), model accuracy, and sample size are reported. Warm colors indicate areas of more suitable habitat.

	Point Arena			**Southeast Farallon Islands**			**Pillar Point / Montara**		
	AUC	Accuracy	*n*	AUC	Accuracy	*n*	AUC	Accuracy	*n*
All Fish	0.813	80.1%	158	0.710	68.0%	153	0.667	63.9%	108
									
Males	0.770	77.0%	89	0.765	72.0%	84	0.638	63.6%	55
									
Females	0.899	87.3%	55	0.636	63.1%	61	0.649	66.1%	28
									

Point Arena model accuracies were higher than all other sites even with a modest amount of observations. Point Arena had 10° steeper slopes than all study sites, which may have strongly influenced the male kelp greenling model. Vector ruggedness measures were also higher in Point Arena and Pillar Point and likely increased the all and female model accuracies of these sites.

From north to south, Point Arena quantified the highest amount of kelp greenling per square kilometer and the highest rate of males at size at 50% maturity (maturity sizes taken from CDFW 2012) (Table 4). Bodega Head summed the most observations and the largest area of rock however this did not translate to the highest amount of kelp greenling per rock area. The number of male and female kelp greenling per square kilometer of rock was comparable in Bodega Head, the Farallones, and Pillar Point. Even with more rock coverage than Point Arena, Pillar Point had the least amount of kelp greenling observations, fewer fish per square kilometer, and in general models scored relatively low accuracies. No noticeable latitudinal trend in area protection is evident.

Table 4. Distribution of kelp greenling (KG) relative to available rocky substrate at each study site; see Figure 1 for area used in model calculations.

	Point Arena	Bodega Head	Southeast Farallon Isl	Pillar Point
Total area of rock (km^2)	14.64	43.66	21.54	17.97
KG per km^2 of rock	24.3	3.5	7.3	6.0
Males per km^2 of rock	6.1	3.3	3.9	3.1
Females per km^2 of rock	3.8	3.3	2.8	1.6
Males - size at 50% maturity per km^2 of rock	5.4	3.0	3.9	2.9
Females - size at 50% maturity per km^2 of rock	2.0	1.9	2.4	1.3

Marine protected area boundaries were overlaid on the predictive maps and the area of suitable kelp greenling habitat was quantified inside and immediately adjacent to the MPAs (Table 5). For the all kelp greenling model, Bodega Head MPAs totaled the highest amount of protected habitat across all sites (59.9%) and extremely high amounts of suitable habitat in the unprotected area immediately surrounding the MPAs (74.0%). The Farallones had the largest discrepancy of protected to unprotected suitable habitat (difference of 15.7%). For the male kelp greenling model, there was 14.9% more suitable habitat immediately outside the Bodega Head MPAs than inside the boundaries. The Farallones had the least amount of suitable habitat inside the boundaries (13.7%) and a nearly untraceable amount immediately outside (3.6%). For female kelp greenling, suitable habitat was comparable inside and outside Bodega Head MPAs. In the Farallones, suitable habitat adjacent to the MPAs was 21.1% less than inside the boundaries. Across all models, Point Arena and Pillar Point had comparable amounts of suitable habitat inside and outside the MPAs (differences ≤ 3.1% or 7.3%, respectively). It is interesting that except for females in Pillar Point and all models in the Farallones, there was more suitable habitat adjacent to the MPAs than protected within the boundaries.

Table 5. Percentage of suitable kelp greenling habitat inside and immediately outside of marine protected area (MPA) boundaries for all, male, and female kelp greenling. Study sites are listed north to south.

	% suitable habitat inside MPA boundaries	% suitable habitat outside MPA boundaries
All kelp greenling		
Point Arena	26.9	27.6
Bodega Head	59.9	74.0
Farallones	21.6	5.9
Pillar Point	21.4	25.0
Male kelp greenling		
Point Arena	29.2	32.3
Bodega Head	47.4	62.3
Farallones	13.7	3.6
Pillar Point	25.2	32.5
Female kelp greenling		
Point Arena	22.6	23.1
Bodega Head	32.6	38.2
Farallones	28.9	7.8
Pillar Point	20.9	19.0

DISCUSSION

This study is the first to our knowledge to describe gender-mediated habitat utilization by kelp greenling. While kelp greenling associated with low relief, continuous rock features common throughout the study area, females occurred more frequently in sand habitat than males, particularly in areas immediately adjacent to hard substrate. Males tended to occur within continuous rock habitat. Both Stein et al. (1992) and Anderson et al. (2009) found an association of kelp greenling to hard-bottom but the correlation may have been more significant if genders were quantified and analyzed separately. Results also depicted the relative abundance of suitable habitat for kelp greenling inside and out of MPAs from Point Arena to Pillar Point, offering insight into potential future performance of selected MPAs with respect to protection of kelp greenling.

The neutral response of kelp greenling to the ROV in the reactional survey provides true insight of the interaction between kelp greenling and their habitat. This is supported by Ryer et al. (2009) who determined that underwater vehicles are unlikely to bias abundance estimates when observing lingcod, a species similar in biological and reproductive behavior to kelp greenling (CDFW 2001), since lingcod were the least active fish surveyed. Unbiased results are also confirmed by Yoklavich et al. (2007) who surveyed a sedentary, non-schooling fish (*Sebastes levis*) using submersible observations.

Geospatial analyses confirmed observational habitat associations and quantified a larger amount of highly suitable habitat for males than females, especially in rocky nearshore areas. This is interpreted as female kelp greenling do not have as strong of an association to specific habitat as males. Interestingly, all female habitat suitability maps illustrate neon green ‘halos’ around the edges of hard substrate, suggesting the females’ frequent use of the rock/sand interface. This glow around rock edges is absent in the male habitat maps indicating males are not departing from rock reef into soft substrates like females.

The female halo in the suitability maps, likely driven by the distance to rock parameter, may be an explanation for low model accuracies in the Farallones and in

Pillar Point. Previous publications simply suggest kelp greenling associate with rock (Eschmeyer et al. 1983; DeMartini 1986; Stein et al. 1992; Anderson et al. 2009). While the two study sites had sufficient available rock substrate, results suggest it is not only available substrate but perhaps habitat configuration that is a more important driver for distribution.

The females' halo is possibly a response to an indirect biological edge effect that influences the dynamics of species interactions (Murcia 1995). If females are generally associated with rock substrate but are utilizing sand substrate and the rock/sand interface more than males, differences in prey preferences or hunting strategies potentially exist between genders. Conceivably, female kelp greenling are feeding within the sand habitat, which is similar to Ferrell and Bell (1991) who suggested that sand adjacent to seagrass patches is utilized as feeding areas because of the proximity to shelter.

Recent findings from Hurst et al. (2013) describe spatial and temporal variability in edge effects. Data were not collected during spawning season, however results still establish kelp greenling habitat association by gender. It is possible that additional sampling with temporal variability could provide a more evident discrepancy in habitat use as males defend nests and have a smaller home range than females (DeMartini 1986; Freiwald 2009). Smaller home ranges combined with the unresponsive reaction to the ROV may be one reason for the skewed gender ratio of higher male occurrence across all sites, which is not previously reported in literature.

Highly suitable habitat and the percentage protected within MPAs varied across sites for all, male, and female kelp greenling. Variation in survey effort may be responsible for this discrepancy, though it is difficult to compare survey sites because MPAs are created with different goals. It is interesting that Bodega Head totaled the highest amount of protected habitat and the highest effort but did not quantify the most kelp greenling per square kilometer. Concurrently, the Farallones have the lowest amount of protected habitat for male kelp greenling (~13%) but the largest observed fish. This may be due to the Farallones' deeper survey depths and geographic location since limited access can naturally reduce fishing pressure, adding to the MPA effect.

Implementation of the newly created network of MPAs mandated by the Marine Life Protection Act (Marine…1999) was underway during data collection years. Results from this study provide baseline information of kelp greenling distribution along the North Central Coast (NCC) region. This aids the NCC Monitoring Plan that, in part, aims to understand the biomass and distribution of fishes within and around MPAs as a component of evaluating MPA effectiveness. Specifically, the plan calls for kelp greenling density and size structure to aid in understanding trophic structure of omnivorous fishes (MPA Monitoring Enterprise 2010).

Further investigation into the influence of habitat configuration on kelp greenling distribution would be useful especially since this study detects an edge effect for females and the hard substrate characteristics (i.e. ruggedness) do not entirely describe occurrence. Data collection during breeding season may also provide insight into a definitive difference in the use of habitats between males and females. These answers may indicate discrepancies in prey preference and feeding behaviors between genders, providing information on trophic structure.

Along with the biological results from this study, the predictive habitat suitability maps for kelp greenling can be combined with other species' maps to determine 'hot spots' of suitable habitat. Collectively, these maps can be useful in determining MPA placement, as they effectively provide species distribution information. Depending on the goals and performance metrics of MPAs, utilizing model results of known habitat associations to determine if a certain amount of suitable habitat is protected can aid in evaluation of the conservation strategy.

Previous to this study, limited knowledge existed for kelp greenling habitat associations and distribution. Video imagery collected by the ROV confidently collected kelp greenling observations and confirmed a difference in habitat use by gender. Results from this study, as well as a growing pool of evidence (i.e. Yoklavich et al. 2000; Auster et al. 2001; Laidig et al. 2009; Wedding and Yoklavich 2015) confirm that understanding species-specific associations with environmental attributes provide valuable insight of species distributions across the seafloor. Application of this information may be useful in MPA evaluation metrics and in efforts towards the use and conservation of a marine resource.

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