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Lingcod (*Ophiodon elongatus*) habitat associations in California: implications for conservation and management

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Abstract Understanding the spatial distribution of marine species and the temporal and spatial scales of the processes that drive those distributions continues to be limited, but is increasingly more critical with the implementation of marine spatial planning. Lingcod (*Ophiodon elongatus*) are a common demersal fish on the west coast of North America and are exploited both commercially and recreationally across the entirety of their range. Due to stock declines, Lingcod are managed using a variety of fisheries management tools, including spatial management. This study represents a unique in situ investigation of demersal habitat utilization by Lingcod at the southern portion of their range (Point Arena to Morro Bay, California). ROV and towed camera sled derived underwater video imagery were coupled with high-resolution bathymetry data and evaluated using Generalized Linear Models to investigate: a) how Lingcod are distributed relative to seafloor habitats along California's central coast, b) the extent to which any ontogenetic patterns varied across habitats, and c) how associations based on visual observations compare to those from landscape modeling analysis. The results of this study clearly depicted an ontogenetic shift in Lingcod habitat utilization. Lingcod shifted from primarily low relief, soft sediments as young to mixed substrates at intermediate ages and ultimately to primarily harder substrates as adults. These results are important in the context of on-going marine spatial planning wherein further information on the habitat associations of targeted species can allow for more refined management.

Keywords Lincod · Habitat associations · Ontogenetic shift · GIS · Spatial management

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Introduction

Understanding the spatial distribution of marine species and the temporal and spatial scales of the processes that drive those distributions continues to be limited (Pittman et al. 2007). The subtidal landscape is composed of diverse habitat patches, occurring across multiple different substrate types, and resulting in patchiness of associated organisms (Greenfield and Johnson 1990; Auster et al. 1995; Anderson and Yoklavich 2007; Anderson et al. 2009; Chang et al. 2010). Landscape ecology is now increasingly being used to investigate and understand the distribution of marine organisms (Turner 1989; Irlandi et al. 1995; Bell et al. 1997; Grober-Dunsmore et al. 2008; Hinchey et al. 2008; Pittman et al. 2007). As in terrestrial systems, the level of heterogeneity of a particular landscape is strongly dependent on the scale at which the environment is studied (Turner 1989; Syms 1995). Similarly, the way in which organisms associate with habitat attributes also differs with scale (Syms 1995; Chittaro 2004; Anderson

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and Yoklavich 2007). At fine scales, fishes may associate with specific features, such as a boulder or depression (Risk 1972; Auster et al. 2003; Auster and Lindholm 2005; Lindholm et al. 2007), while at larger scales the same species may be correlated with a latitude (Witman et al. 2004) and/or a depth range (Bergen et al. 2001; MacPherson 2003).

Lingcod (*Ophiodon elongatus*), a common demersal fish along the west coast of North America, exemplifies this diverse association with the landscape. At a fine scale (meters) Lingcod inhabit low relief soft sediment as juveniles and moderate relief rocky reefs as adults (Shaw and Hassler 1989; Petrie and Ryer 2006). At a large scale Lingcod are distributed by depth, located nearshore as pelagic larvae, and to a depth of approximately 400 m as large adults (Miller and Lea 1972; Eschmeyer and Herald 1983; King and Withler 2005). The process underlying this ontogenetic shift in habitat associations has not been investigated in detail to determine where these shifts in habitat occur and if they are consistent with our current understanding.

Lingcod are known to be cannibalistic, possibly resulting in young individuals settling in soft sediment to avoid predation by adult Lingcod (Shaw and Hassler 1989). Many studies have been conducted on the movement and home ranges of Lingcod (Martell et al. 2000; Matthews 1992; O'Connell 1993; Yamanka and Richards 1993) however, these have focused on their northern range (Alaska to Oregon) and have not examined the specific habitats Lingcod use.

Determining Lingcod habitat associations has been improved by advances in geospatial technology, such as geographic information systems (GIS) and benthic seafloor mapping techniques (Hirzel et al. 2002; Rotenberry et al. 2006; Hinchey et al. 2008). Coupling these new landscape modeling technologies with video imagery of the seafloor allows us to explore the patterns of species distributions as well as the ecological and physical processes driving the distributions. We can then extrapolate patterns beyond physical observations to larger geographic areas. The versatility of this technique in marine systems has been highlighted by studies assessing habitat associations of various rockfish species (*Sebastes rosaceus, S. flavidus* and *S. elongatus)* (Young et al. 2010) and extrapolating those models beyond the initial study area (Iampietro et al. 2008).

Precise knowledge on the distribution and habitat associations of Lingcod are vital to successful management of the species. Lingcod were declared overfished in 1997 from Washington to California (Jagielo and Hastie 2001). Through successful use of more restrictive fishing regulations including large area closures and size restrictions, coupled with favorable oceanographic conditions for recruitment, Lingcod stocks were declared rebuilt in 2005 (Jagielo and Wallace 2005). This population rebound has provided a unique opportunity to study the habitat associations of Lingcod at a healthy population to further inform, and potentially improve, the management strategies for this species.

This study represents a unique in situ investigation of the habitat utilization and ontogenetic movement of Lingcod across approximately 600 linear kilometers of coastline. We used sub-surface imagery derived from three separate field projects coupled to high-resolution bathymetry data to investigate a) the spatial scales at which Lingcod of different size classes associated with specific seafloor habitat attributes, and b) the extent to which any ontogenetic patterns varied significantly.

Methods

Study area

Sampling across three separate field projects was conducted along the central coast of California, ranging from Point Arena in the north to Morro Bay in the south (Fig. 1). Specific study sites varied in substrate composition from unconsolidated soft sediments (e.g. north Monterey Bay and Morro Bay) to high relief rocky reefs (e.g., Farallon Islands and Point Sur) depending on the objective of the individual project.

Field collection of video imagery

Lingcod observations were extracted from an imagery archive dating from 2007 to 2013 (June through October) collected with both a towed camera sled and a remotely operated vehicle (ROV) at depths ranging from 15 to 500 m. The sled (Deep Ocean Engineering and Research) consisted of a steel frame (190 × 44 × 52 cm) protecting a single, forward-facing high-resolution color camera with paired 500 mW lasers spaced at 10 cm, two 250 W tungsten/halogen lights, an altimeter, and an electronics cylinder. The cylinder contained circuitry and served as a junction to supply power and to communicate imagery and data (depth, heading, altitude)

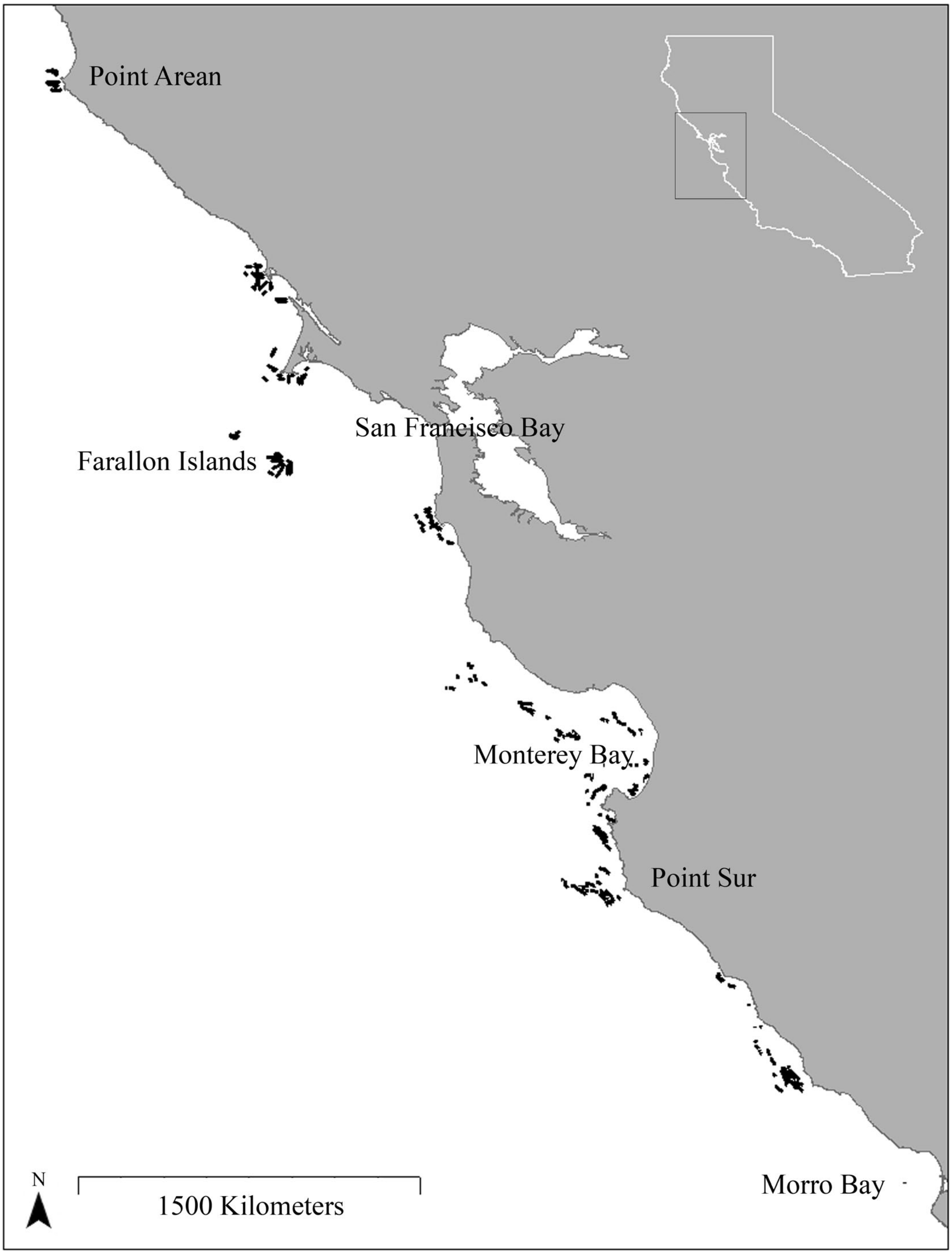

Fig. 1 Map of study area from Point Arena in the north to Morro Bay in the south. Dark lines represent individual transects conducted from 2007 to 2013

with the surface system via the 16-pin 250 m armored coaxial cable tether.

The Vector M4 ROV (Deep Ocean Engineering and Research) was equipped with forward-looking standard and HD video, down-looking video and a digital still camera and strobe. Two Quartz halogen and HMI lights, provided illumination for the video. Paired forward- and down-looking lasers (10 cm apart) provided reference points within the area imaged by each camera. The ROV was also equipped with an altimeter, forward-facing multibeam sonar, and conductivity, temperature, depth (CTD) sensor.

The objectives of the three separate projects (including baseline characterization and monitoring of new marine protected areas, on-going site characterization of a national marine sanctuary, and a study of the impacts of bottom trawls on unconsolidated seafloor habitats) were similar enough to allow us to extract comparable imagery from each project to answer questions about Lingcod habitat associations. All three projects focused on the seafloor and associated demersal fish communities. Each project involved the "flight" of the vehicles at a mean altitude of 0.2 m above the substrate at a speed of 0.5 to 0.75 knots and collected continuous video imagery across multiple substrate types. The position of the ROV relative to the vessels used for two of the projects was monitored using a Trackpoint III system with an angular accuracy of 0.1 degrees. Vessel position was used as a proxy for the position of the towed sled, which was actually deployed as a drift camera directly below the vessel.

Data extraction from video imagery

The associated substrate, relief, water depth, and the total length (TL) were recorded from the video imagery for each individual Lingcod. The geographic coordinates of each individual were later gathered using the unique date-time code in the navigation files.

Substrate was classified according to modified version of Greene et al.'s (1999) habitat classification scheme. Sand and mud substrates were classified as soft sediment (S), while hard substrates were classified as small rock (SR) (gravel to cobble), large rock (LR) (boulders) or continuous rock (CR) (exposed bedrock or reef). Both primary and secondary substrates were characterized for each Lingcod observation. Primary substrate was classified as greater than 50% of the frame and secondary substrate is classified as 20% or greater of the remaining frame (Yoklavich et al. 1999), where a frame was considered the area within view when the video was paused for data collection.

Relief was classified into one of four categories: low (L), wave (W), moderate (M) and high (H). Low relief was classified as one meter or less, wave was classified as distinct peak and trough patterns present in soft sediment, moderate was one to three meters and high was over three meters high off the seafloor. Height off the seafloor was estimated using the altimeter on both vehicles, as well as the ten centimeter sizing lasers. Similar to the substrate classification, primary and secondary relief were characterized for each Lingcod observation. Fish size was estimated using 10 cm paired sizing lasers attached to both the ROV and camera sled. In select cases where the size could not be determined, the fish was recorded, but not included in the size specific analyses.

Latitude and longitude coordinates for each observation were extracted from the Trackpoint III ® acoustic tracking system on the ROV through the Hypack ® navigational software. These coordinates were incorporated into the creation of the habitat suitability maps as they provide precise points where Lingcod were observed. Lingcod location was recorded as ROV position. The camera sled was not equipped with an on-board tracking system. Since there was no reliable way to tracking the precise location the camera sled, it was not incorporated into the GIS habitat suitability modeling.

Data extraction from digital elevation models

Bathymetry digital elevation models (DEM) were collected and compiled for the entire study area at a 5 m resolution (Point Arena to Morro Bay, CA) from the Seafloor Mapping Lab at California State University, Monterey Bay. Several rasters were created from the bathymetry DEM, including: slope, vector ruggedness measure (VRM), topographic position index (TPI) TPI_{20}, TPI_{40} (also referred to as bathometric position index), aspect, and distance from rock .

VRM was derived using the Terrain Tools extension for ArcGIS 9.3.1. TPI was calculated using the annulus algorithm (Weiss 2001), resulting in a raster that distinguishes hilltops (TPI > 1), valley bottoms (TPI < 1), and flat plains (TPI = 0) from the surrounding seafloor features. TPI neighborhood sizes of 20 m and 40 m were used to represent the seafloor features relative to the surrounding seafloor within a 20 m and 40 m radius respectively. Finally, distance from rock was generated using Euclidean distance and the VRM raster as a proxy for hard substrate. These variables are widely used in habitat modeling because they portray various aspects of the seafloor (Iampietro et al. 2005; Iampietro et al. 2008; Young et al. 2010).

Data analysis- fine scale modeling from visual analysis

Generalized linear models (GLM) were created in the statistical package R (R Development Core Team 2010) to test which of the predictor variables best described Lingcod distribution. Akaike's Information Criterion (AIC) was used to rank each model to determine the extent to which each model, or combination of models, best explains Lingcod habitat associations. Models within 2 ΔAIC of the top model were considered to have substantial evidence for the model, and therefore were included further analysis and interpretation (Burnham and Anderson 2002).

Non-detection points were randomly generated from the navigation data. The points were constrained to the transects because they represent true non-detection points of places where we looked and did not find a Lingcod. The number of non-detection points was equal to detection points in order to achieve standardization.

Lingcod were binned by size to determine if a significant difference in habitat associations, or an ontogenetic shift, could be detected. Total length was used to determine what habitats specific age classes were associating with (Shaw and Hassler 1989). Individuals were measured to the nearest 5 cm to determine age class: Young-of-the-year (year-1) Lingcod ≤25 cm TL, year-2 Lingcod 25–45 cm TL, and year-3+ Lingcod ≥50 cm. After three years, male and female growth rates diverge (Shaw and Hassler 1989); therefore Lingcod larger than 50 cm were binned into one category of 3+ years.

Data analysis- landscape modeling & habitat suitability mapping

Habitat suitability maps were created using the Marine Geospatial Ecology Toolbox (MGET). This method has proven useful in mapping areas that are optimal for specific species by extrapolating beyond surveyed areas using known important habitat features (Iampietro et al. 2008; Young et al. 2010). MGET is unique in that it links the geographic information system ArcGIS to the statistical package R (Roberts et al. 2010).

Lingcod detection points were imported into ArcGIS 10.1 using the associated latitude and longitude coordinates collected during video surveys. The Lingcod observations collected with towed camera sled were omitted from this spatial analysis because the sled did not have tracking equipment. Non-detection points were then randomly generated along the transect lines using a 5 m buffer around the detection points to ensure that detection and non-detection points did not overlap with one another. GLM models were then run and compared using AIC to determine which variables best explain Lingcod distribution.

Results

The imagery included in this study covered approximately 587 km of seafloor from Point Arena to Morro Bay, California. A total of 1476 Lingcod were observed, ranging from 5 cm to 90 cm TL. The shallowest depth at which a Lingcod was observed was 17 m water depth, while the deepest was observed at 350 m water depth. Of the 1476 total Lingcod observed, 390 individuals were unable to be measured due to poor visibility or body position with respect to the vehicles.

Fine-scale modeling from visual analysis

A total of 83 models were compared for all Lingcod observations to look at general habitat associations. All 1476 Lingcod observations were used in this analysis, including measured and unmeasured individuals. When models were compared using AIC, the best model was more than two ΔAIC from the next model. This model included the predictor variables: primary relief, secondary relief, combined substrate, and Lingcod size.

Lingcod had a significant negative association with the combination of soft sediment substrate ($p < 0.001$) and areas with primary and secondary low relief ($p < 0.001$). All Lingcod had a significant positive association with mixed ($p < 0.001$) and most hard substrate types ($p \leq 0.003$), as well as moderate ($p \leq 0.011$) and high ($p < 0.001$) relief areas. Size was not significant in this model ($p = 0.96$); however is present in the top five best performing models. Furthermore, when size was removed from the top model, its performance dropped from first to 56 out of 83, indicating that, although not significant, size does play some role in the distribution. Lingcod were then binned into different age classes (1, 2, and 3+) and 63 models were compared. Of the 1476 observations, 1086 Lingcod were measured, resulting in 703 year-1, 234 year-2, and 149 year-3+ observations. These 1086 observations were used in subsequent size specific model comparisons to investigate if there is a change in habitat associations with a change in Lingcod size.

Whenyear-1 models were compared using AIC, four models were within two ΔAIC of the top model. However, when the number of parameters was taken into account, there were substantially more parameters in the subsequent models (up to seven) than in the top model (three) indicating that the number of parameters may influence the model ranking. Also, when compared using a Chi-Square, the additional parameters were correlated with one another ($p < 0.001$) (e.g., secondary substrate and combined substrate), therefore only the top model was considered.

In the best model, year-1 Lingcod had a significant negative association with continuous rock substrate ($p < 0.001$), the combination of low-wave relief ($p = 0.029$), and depth ($p < 0.001$). There was also a significant positive relationship with homogeneous sand ($p < 0.001$) and small rock substrates ($p \leq 0.011$), combinations of sand with small rock ($p \leq 0.006$), large rock ($p < 0.028$), and homogeneous low and wave reliefs ($p < 0.001$). This indicates that lower relief areas and the substrates generally associated with low relief, as well as shallower depths are best for small Lingcod. Other variables that were not significant in this model included high and moderate reliefs and most hard substrate types.

Year-2 Lingcod had two models within two ΔAIC of each other. Both models included the variables primary and secondary substrate and combined relief. One model also included depth, but it was not significant.

Both models indicated year-2 Lingcod had a significant negative association with soft substrate ($p \leq 0.001$) and low relief ($p \leq 0.001$) areas. Year-2 Lingcod had significant positive associations with the primary and secondary substrates small rock ($p \leq 0.029$) and large rock ($p = 0.002$) as well as wave relief ($p = 0.002$), indicating they are associating with areas of increased complexity.

A total of five models were within two ΔAIC for year-3+ Lingcod. All models contained primary relief, four contained secondary substrate, three included primary and combined substrate, and one included depth. Two models were removed from consideration after a Chi-square analysis showed correlation between primary and/or secondary substrate with combined substrate ($p < 0.001$).

The remaining three models showed significant negative associations with soft sediment ($p < 0.001$) and low relief ($p < 0.001$) areas. Year-3+ Lingcod had a significant positive association with hard ($p \leq 0.02$) and mixed ($p \leq 0.002$) substrates, as well as primary moderate relief ($p < 0.001$). Relief did not have any other significant associations indicating that substrate type may play a more important role in year-3+ Lingcod distribution.

Landscape modeling & habitat suitability mapping

A total of 1035 individual Lingcod observations were used in the habitat suitability analysis. The smallest Lingcod in this analysis was 5 cm and the largest was 80 cm TL. Depth ranged from 19 m to 358 m. A total of 427 year-1, 154 year-2, and 107 year-3+ Lingcod were used to determine if the ontogenetic shift in habitat utilization could be detected in a GIS based analysis. Some individuals observed with the ROV were not sized and therefore were left out of subsequent age class models ($n = 347$). No observations made with the towed camera sled were used for the habitat suitability modeling because accurate GPS tracking data are necessary to ensure accurate model results. A total of 83 models were run for all size classes of Lingcod.

Three models were within two ΔAIC for all Lingcod (Table 1). All models included the variables distance from rock and depth. Two models included VRM and one model included slope but none were significant ($p > 0.05$). The variables slope and VRM were correlated and not considered in further analyses because their interaction was unknown. The remaining two models showed a significant negative association with distance from rock ($p < 0.001$) and significant positive association with depth ($p < 0.001$).

Two models for year-1 Lingcod were within two ΔAIC (Table 1). Both showed a significant negative association with slope ($p < 0.001$) and TPI_{40} ($p < 0.001$), indicating an affinity for low relief or flat areas (Fig. 2a). One model also included north as a predictor variable, but it was not significant ($p = 0.25$).

Nine models were within the two ΔAIC for year-2 Lingcod (Table 1). All models showed significant negative associations with distance from rock, indicating that year-2 Lingcod had a positive association with areas close to hard substrate ($p \leq 0.001$) (Fig. 2b). Other models included the predictor variables VRM,

Table 1 AIC table for the top GLM models of each age class, including *p*-values, variable coefficients, and AIC parameters

Model	Variable	Coefficient	*p*-value	Df	AIC	AICc	ΔAIC	AICw
AllM41				4	2724.76	2724.78	0	0.346
	VRM	−0.117	0.09					
	Distance from rock	−0.385	< 0.001					
	Depth	0.002	< 0.001					
AllM21				3	2725.86	2725.87	1.08	0.212
	Distance from rock	-3.00×10^{-4}	< 0.001					
	Depth		< 0.001					
AllM60				5	2726.65	2726.68	1.89	0.141
	VRM	−0.145	0.119					
	Distance from rock	-3.13×10^{-4}	< 0.001					
	Depth	0.002	< 0.001					
	Slope	0.003	0.739					
Y1M25				3	1129.43	1129.44	0.00	0.255
	Slope	−0.088	< 0.001					
	TPI_{40}	−0.731	< 0.001					
Y1M49				4	1130.11	1130.13	0.69	0.118
	Slope	−0.084	< 0.001					
	North	0.127	0.25					
	TPI_{40}	−0.737	< 0.001					
Y2M2				2	389.30	389.30	0.00	0.107
	Distance from rock	−0.002	< 0.001					
Y2M18				3	389.81	389.82	0.52	0.082
	Distance from rock	−0.002	< 0.001					
	East	0.211	0.223					
Y2M20				3	390.01	390.02	0.72	0.074
	Distance from rock	−0.002	< 0.001					
	TPI_{40}	0.274	0.267					
Y3M46				4	259.49	259.51	0.00	0.288
	Distance from rock	−0.001	0.027					
	Slope	0.173	< 0.001					
	Depth	0.008	0.025					
Y3M60				5	260.72	260.75	1.24	0.155
	Distance from rock	−0.001	0.027					
	Slope	0.159	0.001					
	Depth	0.007	0.029					
	VRM	62.246	0.436					

The top three models for all Lingcod contained distance from rock and depth. Both of these variables were also significant in the models. Year-1 Lingcod models contained slope and TPI_{40} as significant variables. Model 49 also contained the variable north, but it was not significant. There were nine models for year-2 Lingcod, but only the top three are shown in the table as the consistent and only significant variable in all models was distance from rock. The top two year-3+ Lingcod models contained the variables: distance from rock, slope and depth. Model 60 also contained VRM, but it was not significant

north, east, TPI_{20}, TPI_{40}, and slope, but none were significant ($p > 0.05$).

Year-3+ Lingcod had two models within two ΔAIC of one another (Table 1). Both models included

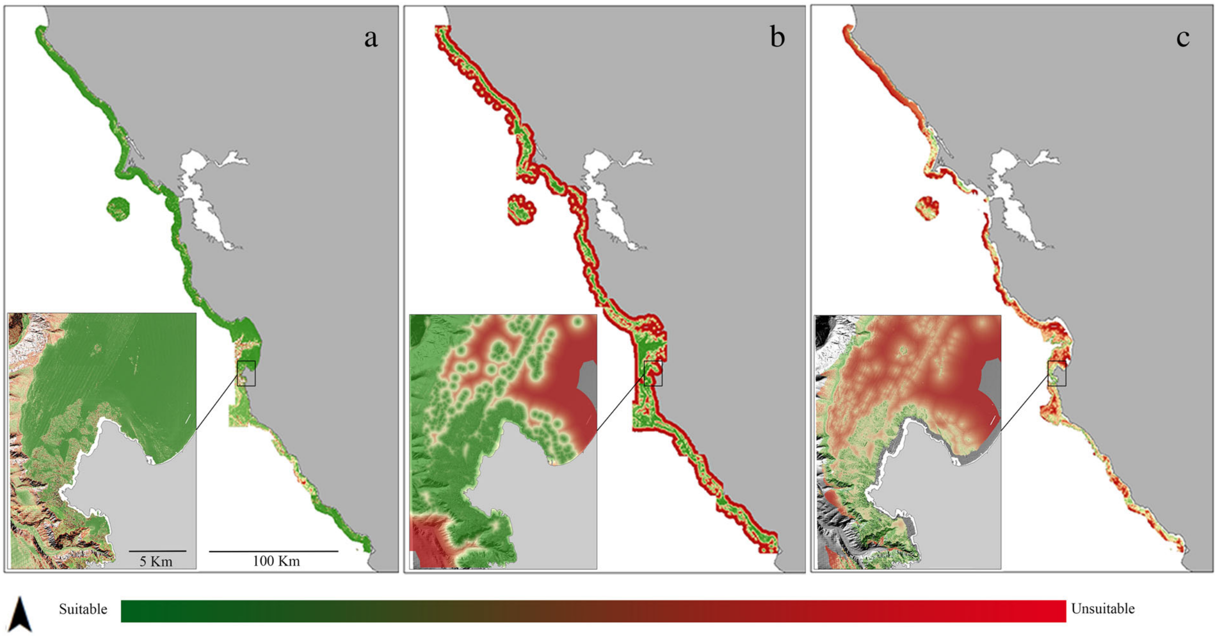

Fig. 2 Habitat suitability models for (**a**) year-1 Lingcod; (**b**) year-2 Lingcod; and (**c**) year-3+ Lingcod. Inset boxes show a zoomed-in view of the Monterey Peninsula, CA. Suitable habitat for year-1 Lingcod is predominately in the soft substrate areas. Rocky reefs are red, indicating highly unsuitable habitat. Year-2 Lingcod suitable habitat is concentrated on and around hard substrate. Year-3+ Lingcod have a similar pattern as year-2, with less of a halo around hard substrate, indicating that soft sediment is unsuitable habitat

distance from rock, slope, and depth; one included VRM. Year-3+ Lingcod had a significant positive association with distance from rock ($p \leq 0.05$), slope ($p < 0.001$), and depth ($p \leq 0.05$), while they had a significant negative association with VRM ($p = 0.43$). These results imply that year-3+ Lingcod have a positive association with steep, deep areas that are close to hard substrate (Fig. 2c).

Discussion

The results of this study clearly depict an ontogenetic shift in Lingcod habitat utilization across the southern portion of its range. Lingcod shifted from primarily low relief, soft sediments as young to mixed substrates at intermediate ages and ultimately to primarily harder substrates as adults. Direct video observations confirmed these patterns while observations coupled with high-resolution topographic maps depict how Lingcod are likely to use the habitats beyond sampled transects. These results are important in the context of on-going marine spatial planning efforts wherein more refined spatial data can allow for more refined management, for example reexamining spatial closures. Furthermore, projects such as this demonstrate the utility of utilizing existing imagery archives to ask new questions.

Small, year-1 Lingcod were positively associated with shallow, homogenous soft sediment and low and wave relief areas. This aligns with the current understanding of small Lingcod, as Petrie and Ryer (2006) found that post-settlement Lingcod were predominately found in sandy areas adjacent to eelgrass beds in Yaquina Bay, Oregon. However, year-1 Lingcod were also positively associated with homogenous small rock and mixed substrate types. Small Lingcod associating with these hard substrate types has not been documented before to our knowledge. Many studies suggest that year-1 Lingcod live in the shallows near vegetation such as kelp or eelgrass beds (Phillips and Barraclough 1977; Cass et al. 1990). However, eelgrass beds are highly susceptible to anthropogenic impacts, resulting in loss of this already sparse ecosystem (Williams and Davis 2006). With the lack of eelgrass beds in California, small Lingcod may select other structurally complex habitats such as the hard and mixed substrate types found in this study. This study did investigate the outer kelp forest habitats, but did not explore any eelgrass beds. Finding small Lingcod associating with habitat types outside of what is discussed in the literature may be a factor of looking in different areas than previous studies, thus expanding our knowledge of Lingcod habitat associations. It is also important to note that the size-age ratios used for this study derived from a study conducted by Shaw and Hassler in Washington and Oregon (1989). This study did not seek to validate the age-length ratios previously published and we suggest a study focused on Lingcod growth rates in California be conducted to validate age-length ratios used in this study.

All but one other study on Lingcod have been conducted from Oregon to Alaska (Mathews and LaRiviere 1987; Cass et al. 1990; Jagielo 1990; Matthews 1992; O'Connell 1993; Yamanka and Richards 1993; Martell et al. 2000; Pacunski and Palsson 2001; Starr et al. 2005; Petrie and Ryer 2006; Beaudreau and Essington 2007; Tolimieri et al. 2009) therefore, it is important to think critically about the assumptions we make about Lingcod populations in California. There are differences in the oceanographic conditions and habitat availability along Lingcod's range that should be considered when extrapolating current knowledge on the habitat associations of Lingcod.

Year-2 Lingcod had negative associations with soft substrate and low relief areas, contrary to year-1 Lingcod. Year-2 Lingcod had a positive association with large and small rock substrates as well as the heterogeneous combinations of moderate and low relief. This is in agreement with Cass et al.'s (1990) findings in the Strait of Georgia, where they documented year-2 Lingcod resided in similar habitats as larger Lingcod, but may stay in shallower depths to avoid predation by larger individuals.

The significant positive association of year-2 Lingcod with homogenous wave relief has not been documented in previous studies. Year-2 Lingcod may not associate with the wave relief as a habitat measure, but rather as a source of prey. Beaudreau and Essington (2007) found rockfish consistently in the stomach contents of Lingcod larger than 30 cm. Hallenbeck et al. (2012) found large numbers of small Canary Rockfish in features called rippled-scour depressions in Monterey Bay, California. The juvenile fishes that reside in these coarse-grain soft sediment areas could be attracting year-2 Lingcod.

Although year-3+ Lingcod had a positive association with hard substrate, they did not demonstrate the same association with depth as Starr et al.'s (2005) paper documented in Alaska. Starr et al. (2005) found large, reproductive Lingcod generally inhabited deeper waters and females mainly came in shallower depths to lay their eggs. Our study did not seek to investigate potential habitat shifts made by different sexes or seasonally. We did not attempt to sex individuals observed on video, as it requires observing the presence (male) or absence (female) of small external papillae. We also did not investigate any potential seasonal changes in habitat use. No video was collected during the Lingcod mating and nest-guarding season (November through March) (King and Withler 2005); therefore we assumed no change in habitat utilization for non-reproducing Lingcod.

The GIS model results paralleled those of the visual analysis. As many of the predictor variables are similar, this result was expected. VRM, slope, and TPI could be considered aspects of relief and distance from rock is a proxy for hard and soft substrate. As with the visual analysis, all Lingcod in the GIS analysis associated with shallow, complex areas close to hard substrate. This finding highlights the necessity to investigate size-specific habitat associations, as it completely neglects the habitat associations of year-1 Lingcod. It is important to understand these more nuanced relationships with various habitat types, especially when protecting a species through spatial management strategies, as in the case of Lingcod.

This study also highlighted the utility of combining multiple methods when investigating habitat associations. The visual analysis resulted in fine-resolution habitat associations (e.g., specific types of hard substrate), while the landscape modeling analysis allowed for extrapolation to areas not surveyed in this study. Although the two techniques resulted in similar findings, it is important to note the video analysis was at a much finer resolution (sub meter), while the GIS analysis was at a 5 m resolution. As such, the video analysis allowed us to put context to the larger resolution GIS analysis. For example, the GIS analysis for year-1 Lingcod showed a significant negative association with slope and TPI, while the video analysis showed a positive association with soft and mixed sediments, as well as low and wave relief types. The finer resolution analysis allows us to get more in-depth information on specific habitat associations and the GIS analysis allows for a visual representation of the models in a map form. We suggest, when possible, for a combination of both techniques to get a complete understanding of habitat associations of a particular species.

Currently, Lingcod are managed spatially through the establishment of rockfish conservation areas (RCAs) and with size limits (currently 22 in. 55.88 cm). RCAs provide refuge for many groundfish species from fishing pressure as mandated by Pacific Fisheries Management Council. However, if these spatial closures are only protecting a portion of the life history of Lingcod, their populations would still be vulnerable without other fisheries management measures (e.g., size limits). When creating spatial management plans for any species, it is critical to understand what drives their distribution as much as possible and how those drivers may differ over a large geographic range. As more information about habitat distribution and the species that associate with those habitats becomes available, it is important to re-evaluate current management boundaries with updated knowledge. Many spatial management strategies incorporate adaptive management, allowing for re-evaluation as more information becomes available.

This study provides insight on the specific habitat associations of Lingcod at various life stages, as well as spatially explicit models of these findings for a geographic area where little work has been conducted. We validated the current understanding of Lingcod habitat associations, but highlighted that these associations may be more nuanced than previously thought. Understanding the differences in habitat associations across a large geographic range is especially important for a spatially managed species. While Lingcod in California had similar habitat associations as individuals further north, this study highlighted that subtle shifts in habitat availability may alter how one life stage associates with the environment.

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