Cautious considerations for using multiple covariate distance sampling and seafloor terrain for improved estimates of rockfish density

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Abstract:

Distance sampling is one of the most widely used methods for adjusting fish counts for detectability, which allows the estimation of absolute density. Further, abundance can be estimated spatially beyond the transect width with density surface models. A density surface modelling approach using survey data from line transects and terrain metrics from multibeam acoustic bathymetry data, integrated with a Geographic Information System, was used to estimate the population density of Pacific ocean perch (POP), *Sebastes alutus,* within six sampling areas in the Gulf of Alaska (GOA) at two sampling scales: local and landscape. For adult POP in our GOA sampling sites, the final density model included depth as a significant predictor for density estimation at both the local and landscape scale. Additional factors included sponge coverage (local scale), aspect eastness and seafloor slope (landscape scale). Predicted densities of adult POP are highest on low (<5°) eastern facing slopes with high sponge coverage (>75%), at depths of 100 to 200 m. The methodology used in this paper presents an alternative for estimating rockfish abundance. By using habitat-based density models with data collected from line transect distance sampling and multibeam acoustic seafloor mapping surveys, we provide an alternative method for estimating rockfish abundance in untrawlable areas, which may help improve rockfish stock assessments and essential fish habitat descriptions and maps.

Key words: distance sampling, density surface modeling, rockfish, Sebastes, Gulf of Alaska, seafloor terrain, multibeam, line transects

1. INTRODUCTION

Rockfish (family Scorpaenidae) are economically important commercial species in the northeast Pacific Ocean. Rockfish comprised nearly 10% of the retained commercial catch in the Gulf of Alaska (GOA) and had an ex-vessel value of $14.5 million in 2019 (Fissel et al. 2021). Federally managed rockfish in the GOA have generally been assessed using a biennial multispecies bottom trawl survey, however, survey indices of abundance are often associated with high variances in any given year as well as high variability in abundance across years, resulting in considerable uncertainty when setting harvest levels (Fenske et al. 2020, Williams et al. 2020). This is generally due to the inadequacy of bottom trawl gear to accurately catch rockfish that are associated with untrawlable habitat (Zimmermann 2003, Jones et al. 2021). Line transect sampling has long been used as a method to estimate the density and/or abundance of biological populations, particularly for avian and marine mammal species (Burnham et al. 1980). Submersible observations with line transect methods have been used to improve estimates of rockfish density and abundance and to understand rockfish habitat associations (O'Connell & Carlile 1993, O'Connell et al. 2002, Yoklavich et al. 2007, Brylinsky et al. 2009). Variables such as depth, substrate type, substrate vertical relief, and invertebrate coverage, to name a few, are useful data collected from submersible line transect sampling that can be used in local scale density estimation. High-resolution multibeam acoustic seafloor bathymetry and backscatter data can generate detailed benthic habitat maps and also be incorporated at the landscape scale as additional explanatory variables in density estimation with line transect sampling methods.

Essential Fish Habitat (EFH) is a US fishery conservation and management principle defined as those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity (50 CFR 600.10). EFH regulations require that the National Marine Fisheries Service (NMFS) and regional Fishery Management Councils describe and identify (map) EFH for each life stage of (targeted) species in a Fishery Management Plan (FMP) (50 CFR 600.815) and should strive to define EFH at the highest level of detail possible (50 CFR 600.815(a)(1)(iii)). EFH is described and mapped for species in Alaska using species distribution models (SDM) that incorporate environmental covariates and species response data from bottom trawl surveys, resulting in maps of 1 km spatial resolution across regional fishery management areas such as the Eastern Bering Sea (Laman et al. 2018) and the Gulf of Alaska (Rooney et al. 2018). EFH for most life history stages of rockfish species is currently defined as EFH Level 1 (distribution), whereas EFH Level 2 requires that habitat-related estimates of density or relative abundance are available, which is challenging for many rockfishes using data from bottom trawl surveys alone.

The purpose of this paper is to present methodology and to review the applicability of data collected from line transect distance sampling and multibeam acoustic seafloor mapping surveys for developing habitat-based density models, which would improve rockfish stock assessment and density-based rockfish EFH descriptions and maps. Habitat-based density models relate rockfish observations to environmental covariates to estimate density. These modeled relationships can then be used to predict rockfish densities at different spatial scales applicable to multiple types of surveyed areas. We explore the various applications that this methodology could be applied for management. Specific objectives are to 1) calculate the density of juvenile and adult Pacific ocean perch (POP), *Sebastes alutus,* and shortspine thornyhead (SST), *Sebastolobus alascanus* with data collected using line of sight submersible transects, 2) account for changing substrates and other environmental variables that may affect the probability of rockfish detection along a line transect, and 3) develop quantitative predictive models to estimate the density of rockfish using habitat covariates at two spatial scales: a) local-scale (10’s to 100’s of meters), and b) landscape-scale (100’s of meters to kilometers).

2. MATERIALS AND METHODS

2.1. Submersible Line Transect Sampling

Line transect sampling data that were used in the distance analysis came from submersible dives that were originally part of two surveys to characterize benthic habitat for rockfish, groundtruth multibeam acoustic derived habitat types, and gain information on bottom trawl survey catchability (D. Hanselman unpubl. data). Dive locations were selected on two criteria: 1) high concentrations of rockfish as determined by the biennial NMFS Alaska Fisheries Science Center (AFSC) bottom trawl surveys, and 2) presumed preferred juvenile rockfish habitats as determined by previously collected high-resolution multibeam acoustic seafloor bathymetry and backscatter data, and proximity to oceanographic fronts (e.g. shelf-break fronts). Thirty-three dives were completed in 2005 using the *Delta* submersible on the support vessel *Velero IV* (Table 1). A total of 24 dives were completed in the Eastern Gulf of Alaska (EGOA): twelve dives on the Hazy Islands mapped site, nine dives on the Cape Ommaney mapped site, and three dives in the Gulf of Esquibel (Fig. 1). A total of nine dives were completed in the Western Gulf of Alaska (WGOA) on the Albatross Bank mapped site (Fig. 2).

Data collected from the line transect sampling that was subsequently used in the distance analysis (objectives 1 and 2 of our analysis) include distance from transect line of observed fish (by species and life stage), primary substrate type, vertical relief of substrate, and depth (recorded in the navigation logs; Table 2). Fish that were not readable within the lasers (i.e., they were too small and moved around too much to measure) were labeled as juveniles. All others were called adults. Structural invertebrates such as anemones, corals, and sponges, provide biogenic habitat for rockfishes (Tissot et al. 2006, Rooper et al. 2007, Henderson et al. 2020) and may be used as habitat covariates in models to help distinguish local scale habitat differences between different species that the physical substrates alone cannot. Structural invertebrate data collected from the line transect sampling and used in the distance analysis included total coverage of invertebrates, corals, sponges, and anemones, and the vertical relief of each of these variables (Table 2).

Our focal species were Pacific ocean perch (*Sebastes alutus*, POP) and shortspine thornyhead (*Sebastolobus alascanus,* SST), which are two ecologically and commercially important rockfish species with known differences in habitat associations (Rooper et al. 2007, Rooper & Martin 2009).

2.2. Seafloor Terrain

Our study areas in the GOA were previously surveyed using high-resolution multibeam acoustic seafloor mapping to generate detailed benthic habitat maps. Bathymetry data were collected by these surveys in the areas of Albatross Bank[1] (AB) in the Western GOA, and Cape Ommaney[1] (CO), Hazy Islands[1] (HZ), and Esquibel Bay[2] (EQB) in the Eastern GOA. Bathymetry data was processed by the surveys and then gridded for our analysis as rasters to a recommended spatial resolution of 10 m, using natural neighbor interpolation (Sibson et al. 1981) with ESRI ArcGIS software.

We included the following seafloor terrain metrics in the landscape-scale predictive density modeling analysis to describe attributes of rockfish habitat: depth, bathymetric position index (BPI) (Guisan et al. 1999, Weiss 2000), vector ruggedness measure of seafloor ruggedness (VRM) (Sappington et al. 2007), aspect northness (cosine of aspect), aspect eastness (sine of aspect), and seafloor slope (Horn 1981) (e.g., Wilson et al. 2007, Pirtle et al. 2015, Pirtle et al. 2019). BPI - bathymetric position index - describes the elevation of one location relative to the mean of neighboring locations (Guisan et al. 1999). BPI will emphasize features that are shallower or deeper than the surrounding area, such as ridges and valleys and places with abrupt changes in slope (Pirtle et al. 2019). Vector ruggedness measure (VRM) is a measurement that

[1] Thales GeoSolutions (Pacific), Inc.
[2] National Ocean Service surveys H11577, H11688, and H11690.

incorporates the heterogeneity of both slope and aspect (Sappington et al. 2007). Values of VRM can range between 0 (flat) to 1 (most rugged). Aspect identifies the compass orientation of the maximum gradient of slope. Aspect (east or north) is the compass orientation of the steepest slope, which influences current flow around seafloor features (Mienis et al. 2007, Dolan et al. 2008, Pirtle et al. 2019). Aspect decomposed into sine (east-west; eastness) and cosine (north-south; northness) components of the compass angles can be expressed as continuous surfaces from 1 to −1 and used as predictor variables. Seafloor slope is the rate of change in bathymetry over a defined area. Slope was derived as degrees slope, using Horn's method (Horn 1981). The measure may be useful in determining colonization as flat areas can support different substrate types and benthic communities than steeply sloping regions (Pirtle et al. 2019). Terrain metrics were derived from the bathymetry rasters using neighborhood-based analytical methods in ArcGIS with the Benthic Terrain Modeler (Wright et al. 2012). All terrain metrics were first derived from an analysis window of 3-raster cells (30 m) to characterize seafloor terrain attributes of rockfish habitat at local spatial scales. BPI and VRM were also derived at 150 m and 450 m (BPI only) to represent seafloor terrain features at broader spatial scales. Terrain analysis at multiple spatial scales can help reduce the influence of artifacts and improve the application of seafloor terrain metrics in spatial analysis and habitat characterization (Dolan & Lucieer 2014, Lecours et al. 2015). To reduce the influence of artifacts, slope, aspect northness, and aspect eastness were further processed using multiscale analysis (Dolan & Lucieer 2014, Table 2 Method 5) in ArcGIS at increasing spatial scales and analysis windows from 30-450 m, where an average raster among spatial scales was re-gridded at 10 m resolution using bilinear interpolation. Terrain metric values were extracted for analysis in the density models at each dive segment midpoint (Table 1).

2.3. Video Processing: Distance of Observed Fish

Two cameras mounted outside the submersible, forward and lateral facing, recorded video and audio feed throughout each dive. Cameras were angled to record horizontally perpendicular to the submersible. Two lasers were mounted on the camera outside the submersible that were used to help determine distances of observed fish from the submersible. Processing underwater video to determine fish presence and distance from line transects can provide valuable data. However, underwater image quality is highly variable and interpreting the video can be difficult. The following methods were practiced while processing dive videos to minimize the observer subjectivity of distance estimation. The distance between two lasers mounted on the camera outside the submersible was 20 cm apart and used as a reference to estimate distance of observations from the submersible. On average, the lasers contacted the seafloor 2 - 2.5 m abeam of the submersible when it was cruising along a level bottom. Under these conditions the video does not contain the first 0.3 - 0.6 m which the video processor must rely on the observer in the submersible to account through recorded audio during the dive transect. Occasionally it is possible to see the observations closer than 0.6 m when looking at the bottom right or left corners of the video. On some dives, the observer used a sonar gun to help with distance estimates.

2.3.2. Seafloor Substrate

The classification scheme used for seafloor substrate and substrate vertical relief was adapted from Pirtle (2005) and Stein et al. (1992). We identified the primary substrate with a specific percent coverage and a vertical relief value for that substrate. In addition, we assigned a specific percent coverage for the second most abundant type of substrate and assigned the secondary substrate a vertical relief value. The classifications using the Wentworth (1922) scale included: mud (M, noticeable organic particles), sand (S, grains distinguishable), gravel (G, ≥ 4 mm and <

2 cm), pebble (P, ≥ 2 cm and < 6.5 cm), cobble (C, ≥ 6.5 cm and < 25.5 cm), boulder (B, diameter ≥ 25.5 cm), and exposed bedrock (R). The vertical relief scale was defined as: 0 – no vertical relief, 1 – low (vertical relief < 0.5 m), 2 - moderate (vertical relief 0.5 m > and < 2 m), and 3 – high (vertical relief > 2 m). In this study the video from the submersible provided a continuous display of substrate. Using Pirtle's (2005) method of distinguishing habitat changes, the substrate code was only changed if the substratum encompassed more than 10 consecutive seconds of video (~4 - 5 m). In addition to the substrate codes, we identified unique substrate features that were less than 10 consecutive seconds in viewing time, but were noticeably different from the substrate patch surrounding it and at least 0.5 m in diameter. For example, a boulder 0.5 m or larger in a sand patch. This separate feature would be assigned a vertical relief value and an estimated distance from the submersible.

2.3.3. Invertebrates

The classification scheme used for invertebrates was also adapted from Pirtle (2005). The percent invertebrate coverage within habitat patches were assigned a code of increasing cover: none (0), light (1, 20 - 50% cover), moderate (2, > 50 - 75% cover), and heavy (3, > 75% cover). Additionally, total percent coverage of coral, sponge, and anemones, and their respective vertical heights (0 = no vertical relief, 1 = vertical relief < 0.5 m, 2 = vertical relief ≥ 0.5 m and < 2 m, and 3 = vertical relief ≥ 2 m), were determined for each habitat patch. For example, if an invertebrate's patch of 10 consecutive seconds or more consists of a total invertebrate coverage of 75 percent and that 75 percent consisted of half sponge and half coral then it would be recorded as total % coverage=75%, coral % coverage=50%, sponge % coverage=50%.

Invertebrates (for example, bryozoans, hydroids, encrusting sponges and corals, and tubiculous polychaetes) that were too small to be counted, or did not occur as solitary individuals, in addition to algae, were grouped into the category of encrusting sessile organisms with a percent coverage. The non-sessile organisms, including stars, sea cucumbers, crabs and shrimp, were assigned a percent coverage as well. Megafaunal invertebrates were operationally defined as epibenthic species larger than 5 cm. Representative taxa include crinoids, upright sponges, anemones, deep cold-water corals, and sea pens. These species may function as a living component of habitat in deep marine ecosystems due to their morphological ability to add structure and complex associated as habitat forming in addition to the substrate. Only larger scale epifaunal invertebrates were identified due to quality of video. This includes mostly structure forming invertebrates and encrusting organisms such as sponges, encrusting sponges, bryozoans, anemones, sea stars, hydroids, small hydrocorals (e.g. stylaster) and gorgonians (e.g. Primnoa). Separate megafaunal invertebrates including primnoa spp., large sponges, sea whips, and metritiums that were noticeably different from their surrounding area were identified as separate features and given a time code, identification code and a vertical relief code, as well as an estimated perpendicular distance from the submersible.

2.4. Distance Sampling Analysis

Distance sampling is one of the most widely used methods for adjusting counts for detectability, which allows the estimation of absolute density. To develop our density surface models (DSM), we followed the two-step modeling process used for spatial modeling of distance sampling data (Hedley & Buckland 2004). First, we fit a detection function with covariates from the line transect sampling data to estimate density (Buckland et al. 2001). Second, given the detection function, we fit a generalized additive model (GAM; Wood 2006) to these densities with explanatory variables provided by spatially referenced environmental covariates at the local- and landscape-scale (Table 2).

2.4.1. Modeling the Detection Function

Detection functions were estimated using the Distance package in *R* version 3.6.1 (Miller et al. 2019). A single observer from the submersible recorded the distance of observed fish from the center transect line, and these observed distances were then used to estimate the detection function, $g(y)$, the probability of detecting a fish at distance y, by modelling the decrease in detectability with increasing distance from the transect line (Miller et al. 2013). Using multiple-covariate distance sampling (MCDS), the detection function was modeled as a function of both distance, y, and one or more additional covariates, represented by the vector $\mathbf{z}$ (Marques et al. 2007, Miller et al. 2019). Both hazard-rate and half-normal models were fit. These are both key functions that determine the basic model shape. Models that did not include covariates were fit with a maximum number of four cosine adjustment terms. The following covariates were included in the determination of the detection function: primary substrate type (factor covariate with seven levels: boulder, gravel, cobble, pebble, sand, mud, and rock) and depth (factor covariate with six variables: 1 – 99 m, 100 - 149 m, 150 – 199 m, 200 – 249 m, 250 – 299 m, and 300 – 349 m). Only sub dives in good visibility were included in the analysis. Data truncation and binning were investigated to reduce the effects of error associated with observers' distance estimates and to improve model fit (Buckland et al. 2001). The detection function was then used to estimate the average probability of detecting a fish given that it is within the width of transect, w, denoted P_a. Fish density can then be estimated as $\widehat{D} = \frac{n}{a\hat{P}_a}$ where n is the number of fish detected and a is the size of the covered region. Because our final objective was to create a density surface model, transect lines were divided into T unequal segments, based on a change in the primary substrate type (as defined in the video processing methods above (Hedley & Buckland 2004, Buckland et al. 2015), and density was estimated per segment T.

Akaike Information Criterion (AIC) was used for model selection among the set of candidate models. The model with the smallest AIC value, for each species and life stage pairing, was selected as the ‘best’ among the models tested. When comparing models, models within two AIC units of the top model were assumed equivalent (Burnham & Anderson 2002). Only the best models were subsequently used for density surface modelling.

2.4.2. Density Surface Modeling (DSM)

Data were then fit, for each species/life stage, to generalized additive models (GAM) where the expected density of rockfish (per segment *i*), D_i, was modelled as the sum of *k* smooth functions of the spatially indexed terrain metrics (z_{ik}) using the DSM analysis engine as part of the Distance package in *R* 3.6.1 (Miller et al. 2013). The following is the general formulation:

$$E\left(\widehat{D_i}\right) = \widehat{p_i} exp[\beta_o + \textstyle\sum_k f_k(z_{ik})],\ i = 1, \dots, T, \tag{1}$$

where f_k are smooth functions of the covariates, β_o is an intercept term, and *T* is the number of segments. Estimated detection probability, *p*, within segment *i* was allowed to vary for each animal, *j*, using the Horvitz-Thompson-like estimator (Hedley & Buckland 2004):

$$\widehat{D_i} = \textstyle\sum_{j=1}^{n_j} \frac{1}{\widehat{p_{ij}}}\ ,\ i = 1, \dots, T\ . \tag{2}$$

Selection for the smooth terms was performed via restricted maximum likelihood (REML), with a logarithmic link and a quasipoisson error distribution (Wood 2011, Winiarski et al. 2013).

Data collected during the line transect sampling were used as the predictor variables in the local-scale modeling: depth, total invertebrate coverage, total coral coverage, total anemone coverage, and total sponge coverage (Table 2). Terrain metrics derived from the multibeam mapping data and extracted at each dive segment midpoint were included as the predictor variables in the landscape-scale modeling: depth, bathymetric position index, vector ruggedness measure of seafloor ruggedness, northness, eastness, and slope (Table 2).

Exploratory analysis was conducted to test correlation among explanatory variables. GAMs were fit with all possible combinations of covariates, after eliminating the pairs of covariates that were highly correlated, by removing and adding covariates in a stepwise fashion based on significance. The best GAMs were selected based on explained deviance. Covariates included in the final set of models are reported (Table 2).

2.5. Density Predictions and Mapping Products

Densities for juvenile and adult SST and POP, were predicted across the study areas using the "best" DSM for each species and rasters of the significant terrain metrics.

3. RESULTS

A total of 2,863 Pacific ocean perch (POP), *Sebastes alutus,* and shortspine thornyhead (SST), *Sebastolobus alascanus* observations were made across 33 transects: 40 juvenile POP, 99 juvenile SST, 463 adult SST, and 2,261 adult POP. Group abundance ranged from 1 to 27 fish, but the majority of rockfish were observed alone (1,974 observations). Juveniles of both species showed an affinity for sand: 88% of observed juvenile rockfish were found in sandy habitat, and were easily detected up to an approximate distance of 4 m (Fig. 3). Habitat preference for adults varied by species. The majority (74%) of adult SST were found in sandy habitat, while the largest percentage (40%) of adult POP were found on gravel (Fig. 3). As expected, adult rockfish were easily detected at a farther distance, up to approximately 8 m (Fig. 4). A large difference in the preferred depth range was evident between the two species of rockfish (Fig. 5). Shortspine thornyhead were observed at deeper depths: 79% of combined juvenile and adult SST were observed between depths of 250 and 300 m. In contrast, POP were observed in shallower depths: 80% of juvenile POP were detected above 150 m, and 89% of adult POP were observed between depths of 150 and 200 m (Fig. 5). It is important to note that transects were not chosen randomly, and that sampling was disproportioned among the depth bins and various substrate types. The majority of the sampling effort in the Eastern GOA occurred at depths between 150 and 200 m, with relatively equal sampling among boulder, cobble, and rock habitats. In the Western GOA, most of the sampling effort occurred at depths between 0 and 100 m, with equal sampling occurring between boulder and sand habitats (Table 3).

Unfortunately, model convergence was not achieved and/or confidence was low for model results for juvenile SST and POP, and adult SST. Therefore detection function results are shared below for each species/life stage, but modeling results are only included for adult POP.

3.1. Model Results

3.1.1. Juvenile Shortspine Thornyhead

Results from local and landscape-scale DSMs are unavailable due to low confidence in model results and convergence warnings. Only results of the fish detection function are reported. Juvenile SST observations from the Eastern GOA (Cape Ommaney; $n = 4$) and Western GOA (Albatross Bank; $n = 95$) were combined for the detection function analysis. Our results recommend using a hazardrate detection function with no covariates or binning, left truncated at 0.25 m and right truncated at 4 m, to best detect juvenile SST when performing line transect sampling in our study areas (Fig. 4a). Detection probability was high ($p > 1$) until approximately 2.5 m, where it dropped dramatically ($p < 0.2$; Fig. 4a). The majority of juvenile SST were observed on sandy habitat (Fig. 3a) at depths of 250 m (Fig. 5a), containing a higher percentage (> 60 %) of invertebrate coverage (Fig. 6a) and little to no (< 10 %) coral coverage (Fig. 7a).

3.1.2: Juvenile Pacific Ocean Perch

Density surface models were unable to be fit due to insufficient number of observations. Only results of the fish detection function are reported. Juvenile POP observations from the Eastern GOA (Hazy Islands and Cape Ommaney; n = 8) and Western GOA (Albatross Bank; n = 26) were combined for the detection function analysis. It is recommended to use a hazard-rate detection function with no explanatory covariates or data binning, left truncated at 1 m and right truncated at 5 m, to best detect juvenile POP when performing line transect sampling in our study areas (Fig. 4b). Detection probability was high between 1.5 and 3.5 m ($p > 1$), where it dropped dramatically ($p < 0.2$; Fig. 4b). The majority of juvenile POP were observed on sandy habitat (Fig. 3b) at depths <150 m (Fig. 5b), with invertebrate coverage between 45 and 85% (Fig. 6, top right), and with less than 60% coral coverage (Fig. 7b).

3.1.3. Adult Shortspine Thornyhead

Results from local and landscape-scale DSMs are unavailable due to low confidence in model results and convergence warnings. Adult SST observations from the Eastern GOA (Cape Ommaney and Hazy Islands, n = 125) and Western GOA (Albatross Bank, n = 337) were combined for the detection function analysis. Our results recommend using a hazard-rate detection function with depth included as a covariate, data binned into 1 m intervals, left truncated at 0.25 m and right truncated at 6 m, to best detect adult SST when performing line transect sampling in our study areas (Fig. 4c). Detection probability was high until approximately 4 m ($p > 0.6$; Fig. 4c). The majority of adult SST were observed on sandy habitat (Fig. 3c) at depths between 250 – 300 m (Fig. 5c), with a higher percentage (> 50%) of invertebrate coverage (Fig. 6c) and little to no (<10 %) coral coverage (Fig. 7c).

3.1.4. Adult Pacific Ocean Perch

Adult POP observations from the Eastern GOA (Cape Ommaney and Hazy Islands; n = 1,399) and the Western GOA (Albatross Bank; n = 267) were combined due to an inadequate number of samples to make regional comparisons. Our results recommend using a hazard-rate detection function with no covariates, data binned into 2 m intervals, left truncated at 0.25 m and right truncated at 8 m, to best detect adult POP when performing line transect sampling in our study areas (Fig. 4d). Detection probability was high until approximately 6 m ($p > 0.6$; Fig. 4d). Adult POP were primarily observed on gravel (Fig. 3d), at depths of 150 – 199 m (Fig. 5d), and with approximately 30 – 50% invertebrate (Fig. 6d) and little to no coral (<10 %) coverage (Fig. 7d).

The final local-scale spatial model to predict adult POP density in our GOA study sites included smooth terms of sponge coverage (Fig. 8, top left panel) and depth (Fig. 8, bottom left panel), had an adjusted-R^2 score of 0.691, and explained 83.9% of the deviance (Table 4). At the local-scale, predicted densities of adult POP are highest in areas containing increasing sponge coverage (>75%; Fig. 8, top right panel) and at depths between 100 and 200 m (Fig. 8, bottom right panel). Note that error surrounding areas of highest density increases greatly for both sponge coverage (Fig. 8, top right panel) and depth (Fig. 8, bottom right panel). Also, results of the sponge smooth function (Fig. 8, top left panel) appear to be inconclusive, as the smoother appears to bounce between zero and 60% sponge coverage before the uncertainty becomes too high to determine a trend. The final landscape-scale spatial model to predict adult POP density in our GOA study sites included a smooth term of aspect eastness (Fig. 9, top left panel), seafloor slope (Fig. 9, middle left panel), and depth (Fig. 9, bottom left panel), had an adjusted-R^2 score of 0.7, and explained 85% of the deviance (Table 4). At the landscape-scale, predicted densities of adult POP are highest on low (<5°, Fig. 9 middle right panel) eastern facing slopes (Fig. 9, top right panel) at depths of 100 to 200 m (Fig. 9, bottom right panel). Note the large amount of error surrounding density estimates that include eastness and depth (Fig. 9). Model results from the landscape-scale DSM for adult POP indicated low density in all sampled study areas (Fig. 10), with slight increases in areas close to shore (Fig. 10). This is most evident in the Gulf of Esquibel location (Fig. 10).

4. DISCUSSION

Traditional abundance estimation methods (e.g., area-swept trawl surveys, mark recapture) are not often useful for rockfishes given their distribution, life history, and physiology. In addition, species habitat characterization at multiple spatial scales is needed to gain better understanding of species-habitat relationships and ecosystem processes. We present an example of an alternative abundance estimation method, using submersible line transect sampling of fish species and habitat coupled with seafloor terrain metrics to create predictive density models based on habitat covariates for adult Pacific ocean perch at local and landscape spatial scales. Our results indicate that depth is the most influential terrain metric for predicting the density of POP in the adult life history stage at both the local scale of 10s to 100s of meters and landscape scale of 100s to 1000s of meters. Pacific ocean perch show ontogenetic differences in density with depth: adults are associated with deeper depths and juveniles with shallower depths. Additionally, densities of POP are influenced at varying degrees by the amount of sponge coverage, and the degree and orientation of the seafloor slope. Aspect (east) is the compass orientation of the steepest slope, which influences current flow around features. Model results show that densities of POP are low in our study sites, however, confidence in these results is low for reasons further discussed.

When designing a line transect survey, there are many considerations that must be included to ensure reliable abundance and density estimates. This study used existing footage collected from submersible video transects in areas thought to be prime juvenile rockfish habitat, as determined by geological characterizations from previous multibeam acoustic seafloor mapping surveys (Greene et al. 1999). While the approach of spatial modeling used in this analysis is generally well suited for the type of data that can be obtained from multi-purpose research cruises (such as surveys in which collecting sightings data is subordinate to other research priorities), the *post hoc* effort accounting for the coverage probability can be difficult depending on the shape of the study area (Buckland et al. 2004). If one can assume that: 1) the coverage probability is constant within the covariates of interest (such as our terrain metrics), 2) the line transects provide a good spatial coverage of the study area, 3) the extrapolation area is reasonable, 4) the sample size is not too small, 5) there is confidence in the detection function, and 6) the resulting spatial model is a good approximation of reality, then it can be assumed that the spatial model can provide a reliable estimation of abundance and density (e.g., Katsanevakis 2007). We were not able to meet these assumptions. However, we contend that demonstrating this alternative method to estimate habitat-related abundance and density for rockfish species that are challenging to sample with traditional abundance estimation methods will be useful in future applications with sampling scenarios where these assumptions can be met. Justification for use of these methods for future application are provided in the remaining discussion.

Transects were not chosen randomly, and the line transect data do not provide constant or representative coverage of all covariates of interest, nor do they provide good coverage of the study areas (multibeam mapped areas; Fig. 1 and 2). Sampling was disproportioned among the depth bins and various substrate types (Table 3). The majority of the sampling effort in the Eastern GOA occurred at depths between 150 and 200 m, with relatively equal sampling among boulder, cobble, and rock habitats. In the Western GOA, most of the sampling effort occurred at depths between 0 and 100 m, with equal sampling occurring between boulder and sand habitats. As a result, our model results changed drastically with different data pooling strategies, highlighting the disproportionate sampling among the various habitat types and between various sampling sites (Eastern GOA vs. Western GOA, etc.), the disproportionate number of fish observations among the sampled sites, and the evident spatial differences in terrain and species distributions within the GOA that must be considered. The result of this violation is that many terrain metrics that *a priori* knowledge led us to believe would be significant factors (Pirtle et al. 2015, 2019) were excluded from the results, likely because the majority of samples were taken from the same habitat type. For example, features from G. Greene maps that were rugged, local bathymetric highs, were targeted in the initial study for sampling juvenile rockfish habitat, and spatial models created from non-random transect sampling cannot correct for bias arising when transects systematically follow geographic features (Buckland et al. 2004). The result is that there is no variability for the model to distinguish with presence/absence and BPI or VRM.

Following considerations of survey design, one must be cognizant of the spatial coverage included in the study. By including the multibeam mapping data, we were able to detect how the variation in terrain affects density at the broader, landscape spatial scale, which would not have been possible at the local spatial scale of the transect. While spatial modelling can be incredibly useful, estimating density or abundance for too large of an area or within areas that are geographically unrealistic can be strongly misleading and filled with error. Density estimates may be derived for unsurveyed areas by fitting habitat models in extensively surveyed areas and carefully extrapolating them, but extrapolation is risky because of the lack of observations for evaluating model predictions, and the potential bias in predicted densities (Conn et al. 2015). The multibeam mapped areas within this study in which we extrapolate our density predictions may be considered "extensively surveyed" at the landscape scale, but rockfish are known to have patchy distributions, often only occurring in large numbers in just a handful of hauls on the AFSC groundfish trawl survey (e.g., Northern rockfish; Hulson et al. 2020). The result is high variance associated with the biomass estimate. Extrapolating density estimates to too large of an area for a rockfish species could result in unreliable density estimates, especially if spatial modeling has shown there to be an affinity towards certain habitats. The same can be said for management purposes: assuming that the spatial distribution of a rockfish species is consistent throughout the spatial extent of a management area (Western GOA, Central GOA, and Eastern GOA), could lead to localized depletion if not cautious. This study is a great example of how vastly different the habitat and oceanography are in the various regions of the GOA. Choosing the appropriate spatial scale for density estimation must first be addressed when developing the survey design, while never underestimating the importance of assessing predictions against ecological knowledge. Oftentimes, the spatial scale chosen for density estimation is driven by predetermined management areas, which have not always been determined for biological reasons. While this may be appropriate for some species and areas, this could lead to erroneous results in others.

In addition to survey design and appropriate spatial coverage, sample size is an extremely influential factor that can potentially lead to unreliable results, as was likely a contributor with this study and the inability to achieve model convergence for juvenile SST and POP and adult POP (Buckland et al. 2015). There are several ways in which sample size may affect results, the first being the number of transects in the survey. A general rule of thumb is that it is better to have more short transects scattered throughout the area of interest (our landscape scale multibeam mapped area) to ensure that the variability through the study area is adequately represented and to provide a reliable and more precise estimate of density. This is particularly true when studying a population that has a patchy distribution, such as rockfish species. The recommended minimum is 10-20 replicate lines (Buckland et al. 2015). These older surveys were generally pilot surveys conducted to explore multiple objectives and replicate lines were not possible. The second influence of sample size is the number of detections made. Results can be influenced by the distribution of observations among transects if the number of sightings per meter of transect is roughly equal across transects, or if there are transects with many sightings and transects with none, such as the case with patchily distributed rockfish. The number of rockfish observations was highly disproportionate among transects in our study. Buckland et al. (2001) recommends a minimum of 60-80 animal detections for reliable estimation of the detection function for line transect sampling, which again was not possible in an exploratory study such as this. Recent developments with multiple-covariate distance sampling have relaxed these requirements of minimal number of transects and observations, which were explored in this study. We were able to pool data and apply a single detection function model across strata with stratum as a factor-type covariate, which allowed for fewer detections (Marques et al. 2007, Buckland et al. 2015). However, confidence in model output for both juvenile species in this study was low, and much of this can likely be attributed to the low sample sizes used in the respective analyses.

Lastly, uncertainty in estimates of density across a study area may stem from uncertainty in the estimates of the detection function parameters. Uncertainty in a detection function may be caused by variability in the encounter rate between transects, and variability in encounters between transects tells a great deal about how variable animal density is across the study area (Buckland et al. 2015). Spatial models have been known to be less reliable than conventional distance sampling when there are many zeros in the data collected, such as with our dataset. Model selection in this study was extremely difficult, as several GAMs had similar results. This is concerning, as a poor model could introduce substantial bias in density estimation. If these data were to be revisited in the future, it would be recommended to fit more than one plausible model and carry out model averaging or ensembles (Buckland et al. 1997).

In spite of all the concerns noted above, the GOA demersal shelf rockfish (DSR) stock complex is currently assessed using density estimates (Wood et al. 2021) from direct observation line transect sampling methods, highlighting the potential and success of these methods (Burnham et al. 1980, Buckland et al. 1993, Wood et al. 2019). The methods used for estimating DSR abundance differ in that the transect locations are randomly selected within areas that are believed to be rocky habitat (known habitat preference for DSR). Therefore, density is estimated without any covariates or spatial components (Brylinsky et al. 2009), similar to this study's first objective: calculate the density of adult POP via data collected using line of sight submersible transects. This approach to density estimation is appropriate if one is confident in the habitat use of the species and the area being sampled. The surveys used in our study were exploratory, with one purpose being to groundtruth suspected rockfish habitat as determined from multibeam mapping surveys. We chose our focal species due to data availability. If a follow up study were to occur, survey locations would be chosen based on the most recent GOA EFH determinations of both these species, which are based on species distribution models of habitat-related density or abundance (Rooney et al. 2018).

We suggest that the method presented here could be used in combination with other sampling techniques such as acoustic-optic surveys (Rooper et al. 2010, Jones et al. 2012, Jones et al. 2021) to help with abundance estimation of species such as rockfish that inhabit untrawlable areas. The results presented here should be considered exploratory and not be used within current stock assessment models due the concerns mentioned previously on the non-random nature of sampling design, limited spatial coverage, low sample size, and issues with model selection. However, if designed appropriately, observations of habitat associations and relative densities along line transects by habitat type, similar to this study, could be combined with acoustic-optic surveys or other sampling methods to determine density in trawlable versus untrawlable habitats. This could be applied as a prior on the catchability estimate for the larger-scale bottom trawl survey that does not sample untrawlable habitat, and could improve stock assessments and fishery management decisions (Hulson et al. 2020).

The sampling and habitat-related density estimate methods that we present will also be useful to improve understanding of species habitat relationships to advance EFH descriptions and maps, which meets an another ecosystem-based fisheries management information need. EFH descriptions and maps for species in untrawlable habitats would be improved with better sampling of these areas through alternative methods. Again, the results of this study should be considered exploratory, but given an appropriate sampling design and strategy, the density surface model could be used to fill sampling gaps for untrawlable areas in the current EFH species distribution models (Laman et al. 2018). This may be particularly helpful for species life history stages that are often undersampled by bottom trawl surveys due to their prevalence in untrawlable habitats, including the juvenile life stage of several rockfish species in Alaska. Another application of this alternative habitat-informed density estimation technique is understanding species-habitat relationships at multiple spatial scales. The species distribution modeling approach used to describe and map EFH (Laman et al. 2018) across the regional fishery management areas at landscape scales (1 km resolution) can be extended to model and map species habitat at local scales (10s to 100s of meters) for areas of interest such as juvenile rockfish nurseries in offshore untrawlable areas, where local scale EFH maps can be nested within the broad management area EFH maps (e.g., Grüss et al. 2021 as proposed for nearshore areas). Understanding the relationships between habitats and the species they support is a critical need for implementing ecosystem-based fisheries management (EBFM) (Peters et al. 2018). An approach to describe and identify species habitat relationships using alternative methods and at multiple spatial scales will improve understanding of ecosystem processes and advance the success of EBFM.

5. CONCLUSION

We modeled density of POP in the adult life stage using available submersible transect data and habitat-based covariates, and extrapolated predictions to multibeam surveyed areas to demonstrate an alternative method for sampling rockfish species at two ecologically meaningful spatial scales. Unfortunately, results were inconclusive for SST and juvenile POP. We conclude that this approach is generally an applicable method for most geographic areas, marine taxa and management requirements in areas of sparse survey effort. The extent to which habitat-based models of rockfish density are useful for the management and conservation of these species depends on their accuracy. This was the case for our model results for SST and juvenile POP. While models for both juvenile and adult SST achieved convergence, results were improbable and would have reported abundance estimates with a large amount of error. Unvalidated models that overestimate or underestimate regional densities or do not match known patterns of species distribution can be more misleading than helpful. However, the complete absence of spatial information on species distribution and density also hampers conservation and management efforts because it is not possible to focus on the areas of greatest importance to each species.

When creating predictive density surfaces, one needs to account for the broader landscape, including the influence of processes occurring on geologic time-scales when considering the spatial extent of habitat for marine species. Habitat-specific density, biomass estimates, and EFH most likely need to be predicted at spatial scales nested within our large management areas in the Gulf of Alaska (Western GOA, Central GOA, and EGOA) to adequately account for habitat and ecosystem processes influencing rockfish species presence and community structure. Density surface modelling and the inferred relationships to habitat covariates may provide insights and act as the starting point for further ecological investigations, process studies, and manipulative experiments seeking causal relationships between abundance and habitat covariates. The availability of spatial line transect models will encourage researchers to identify and measure variables more directly relevant to the species of interest.

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7. FIGURES

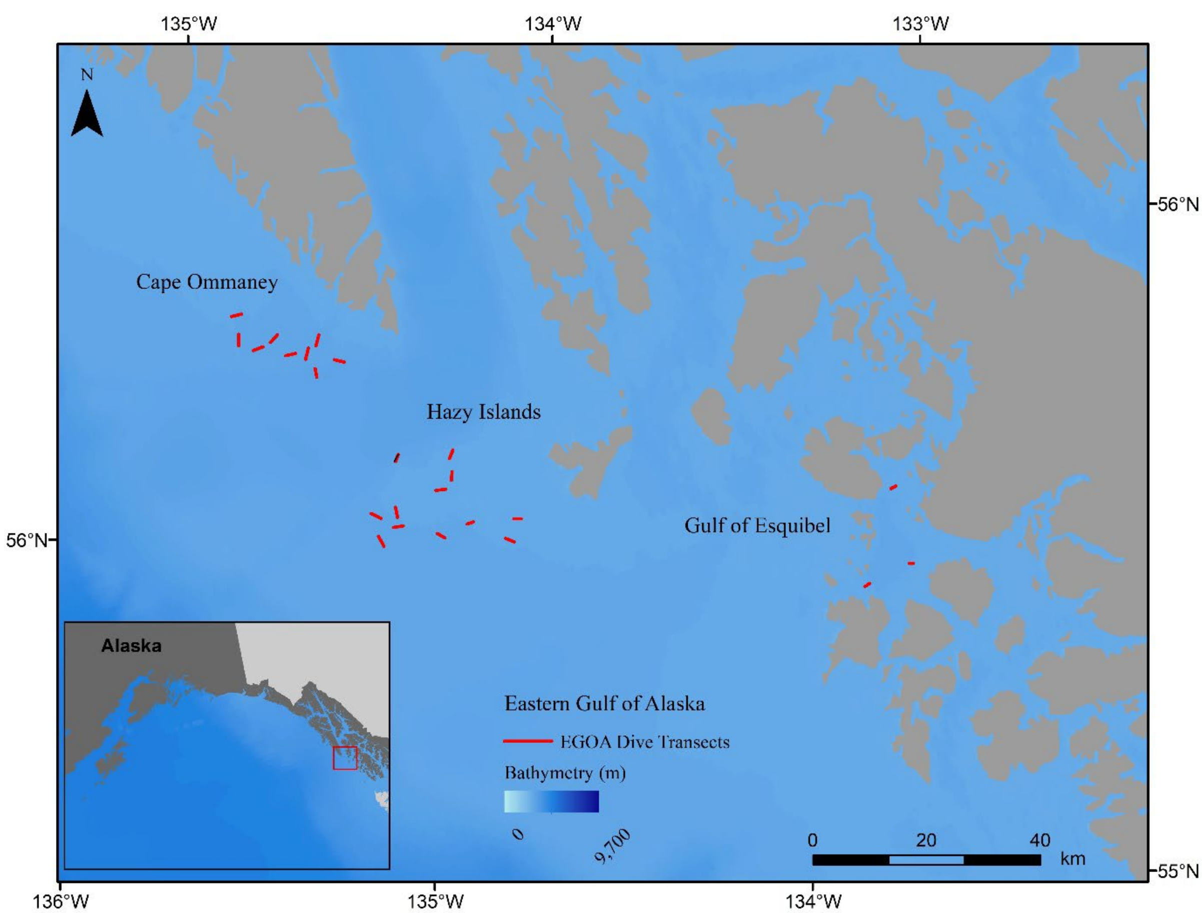


Figure 1. Location of dive transects in the Eastern Gulf of Alaska sampling sites: Cape Ommaney, Hazy Islands, and Gulf of Esquibel. Map inset is for location reference. Each red line represents a dive transect.

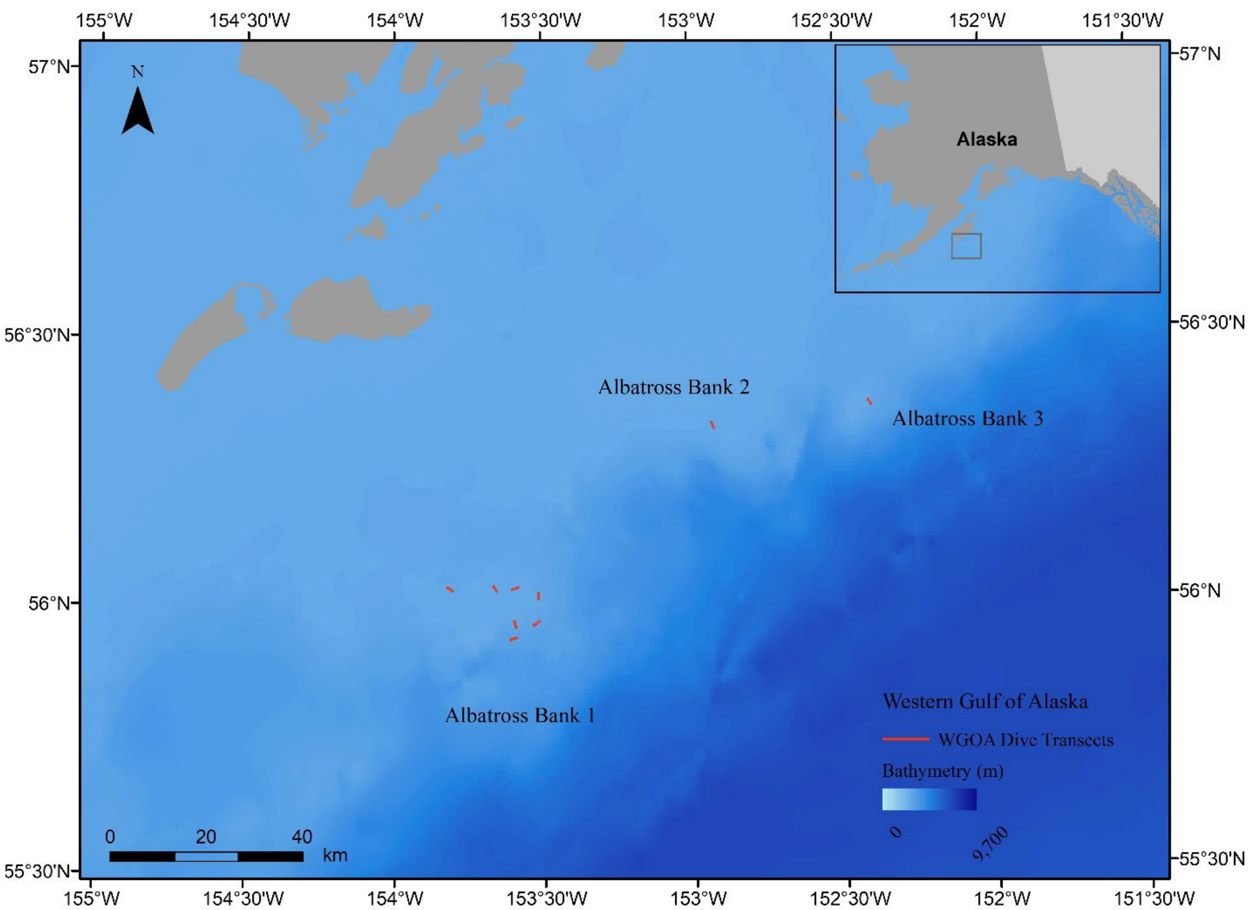


Figure 2. Location of dive transects in the Western Gulf of Alaska, Albatross Bank sampling locations: Albatross Bank 1, Albatross Bank 2and Albatross Bank 3Map inset is for location reference. Each red line represents a dive transect.

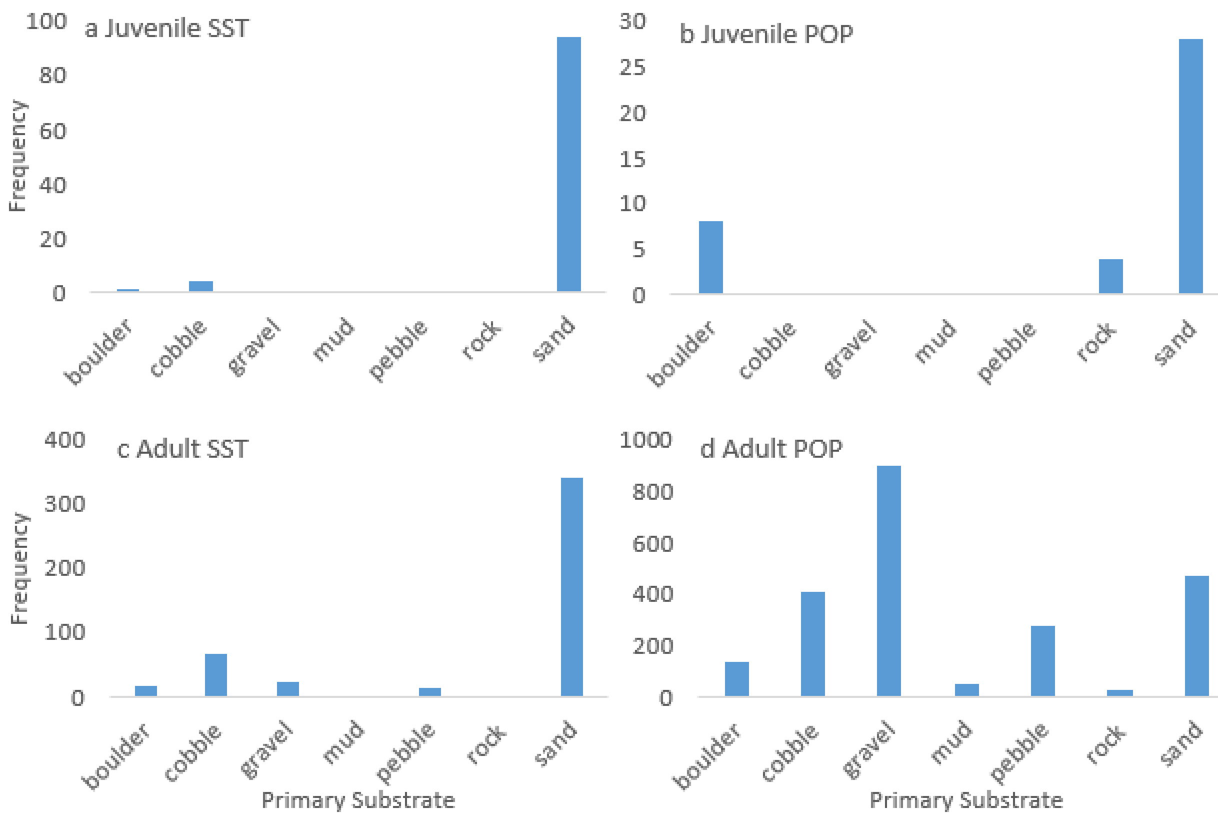


Figure 3. Frequencies of observed juvenile (top panels) and adult (bottom panels) shortspine thornyhead (SST; left panels) and pacific ocean perch (POP; right panels) by substrate type. Primary substrate types: boulder, cobble, gravel, mud, pebble, rock, and sand. Note different frequency scales between the panels.

a b

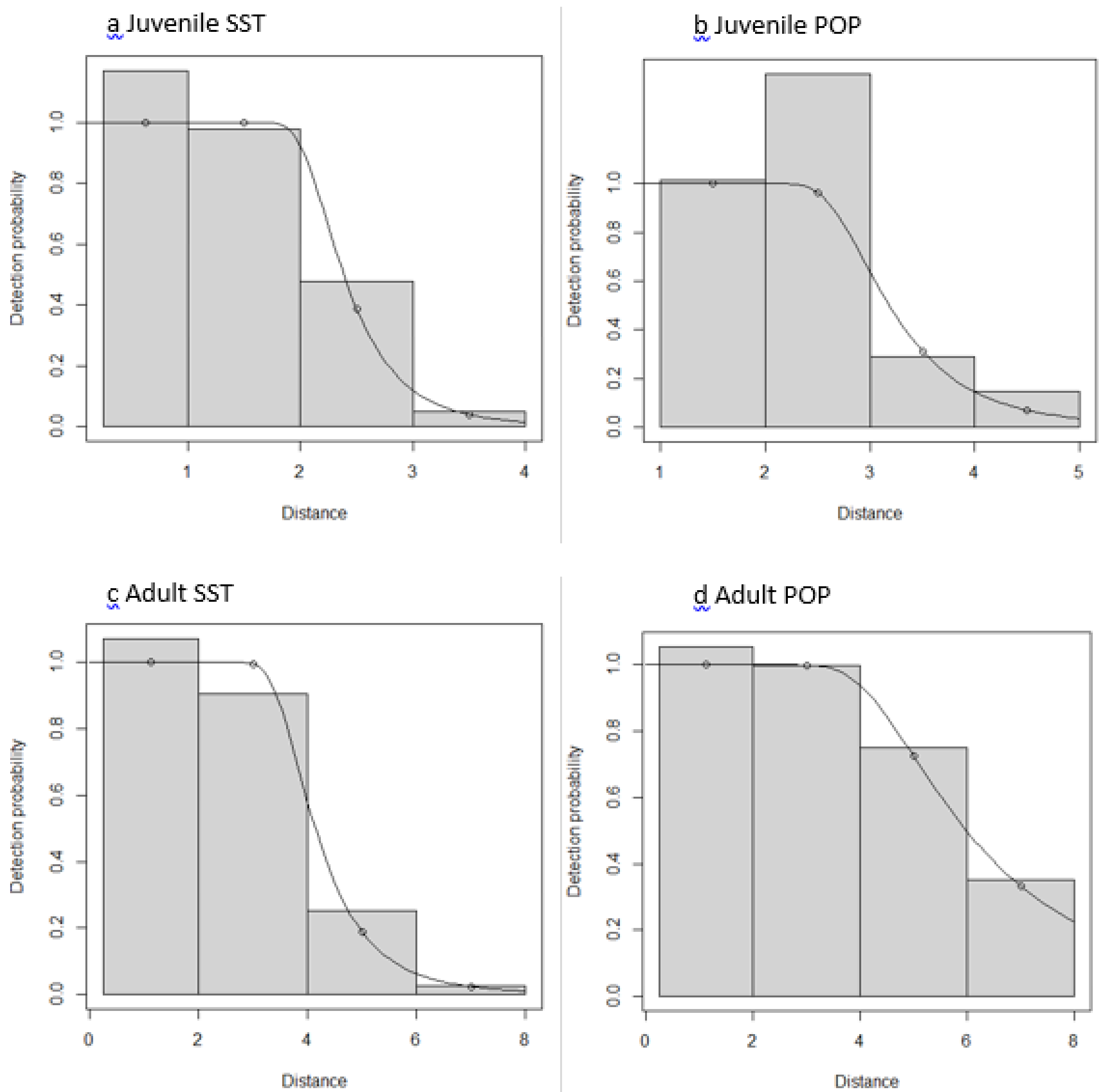


Figure 4. Distribution of perpendicular detection distances (m) from submersible of all a) juvenile shortspine thornyhead (SST), b) juvenile Pacific ocean perch (POP), c) adult SST, and d) adult POP in sampled sites observed during submersible transect surveys with the fitted (hazard-rate) detection function (line) overlaid onto the scaled perpendicular distance distribution. Boxes: observation bins

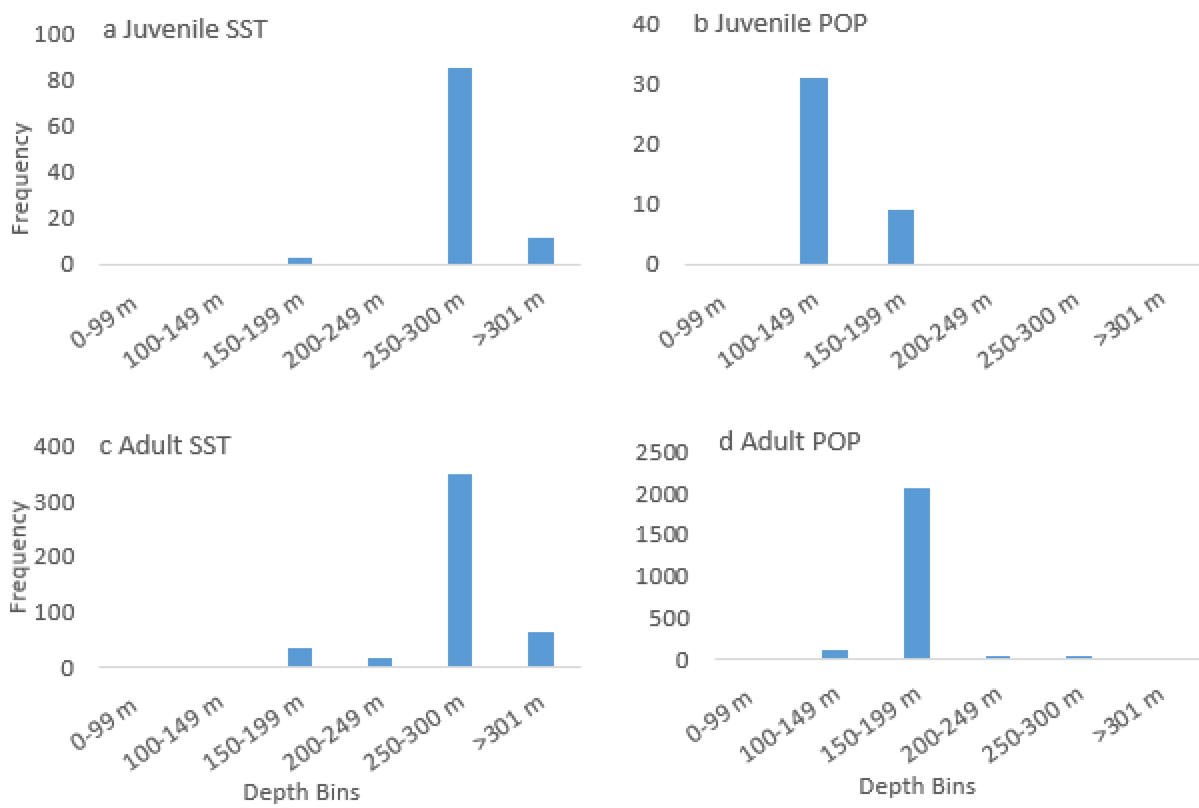


Figure 5. Frequencies of observed juvenile (top panels) and adult (bottom panels) shortspine thornyhead (SST; left panels) and pacific ocean perch (POP; right panels) by depth: 0 – 99 m, 100 – 149 m, 150-199 m, 200-249 m, 250-300 m, and>301 m. Note different frequency scales between the panels.

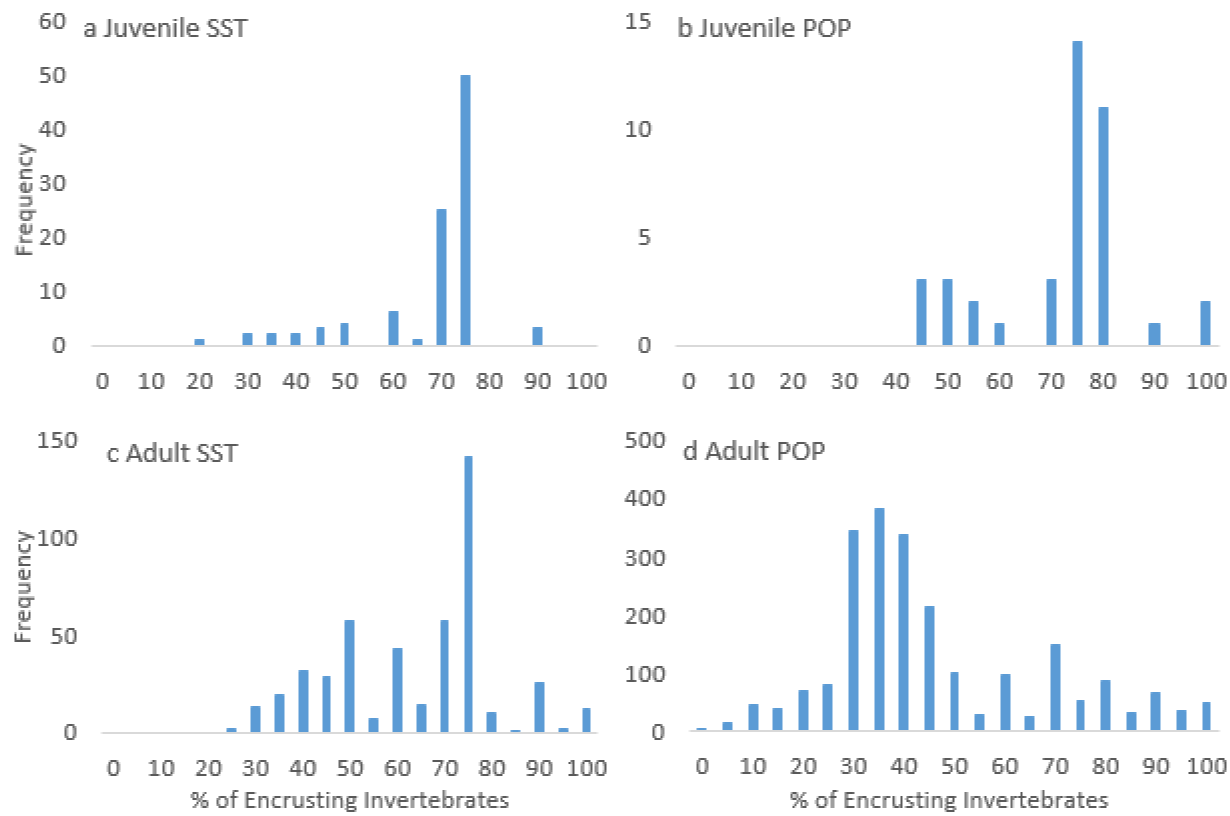


Figure 6. Frequencies of observed juvenile (top panels) and adult (bottom panels) shortspine thornyhead (SST; left panels) and pacific ocean perch (POP; right panels) by percentage of encrusting invertebrate coverage. Note different frequency scales between the panels.

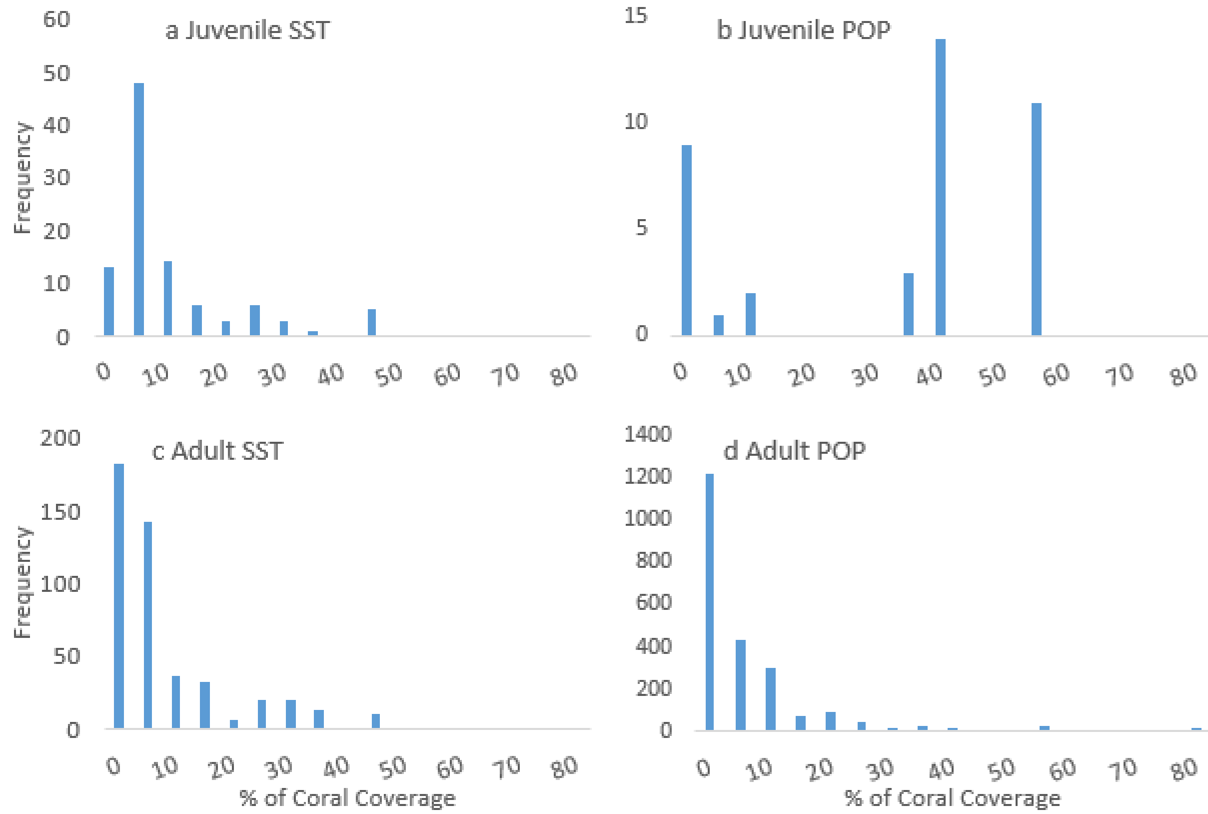


Figure 7. Frequencies of observed juvenile (top panels) and adult (bottom panels) shortspine thornyhead (SST; left panels) and pacific ocean perch (POP; right panels) by percentage of coral coverage. Note different frequency scales between the panels.

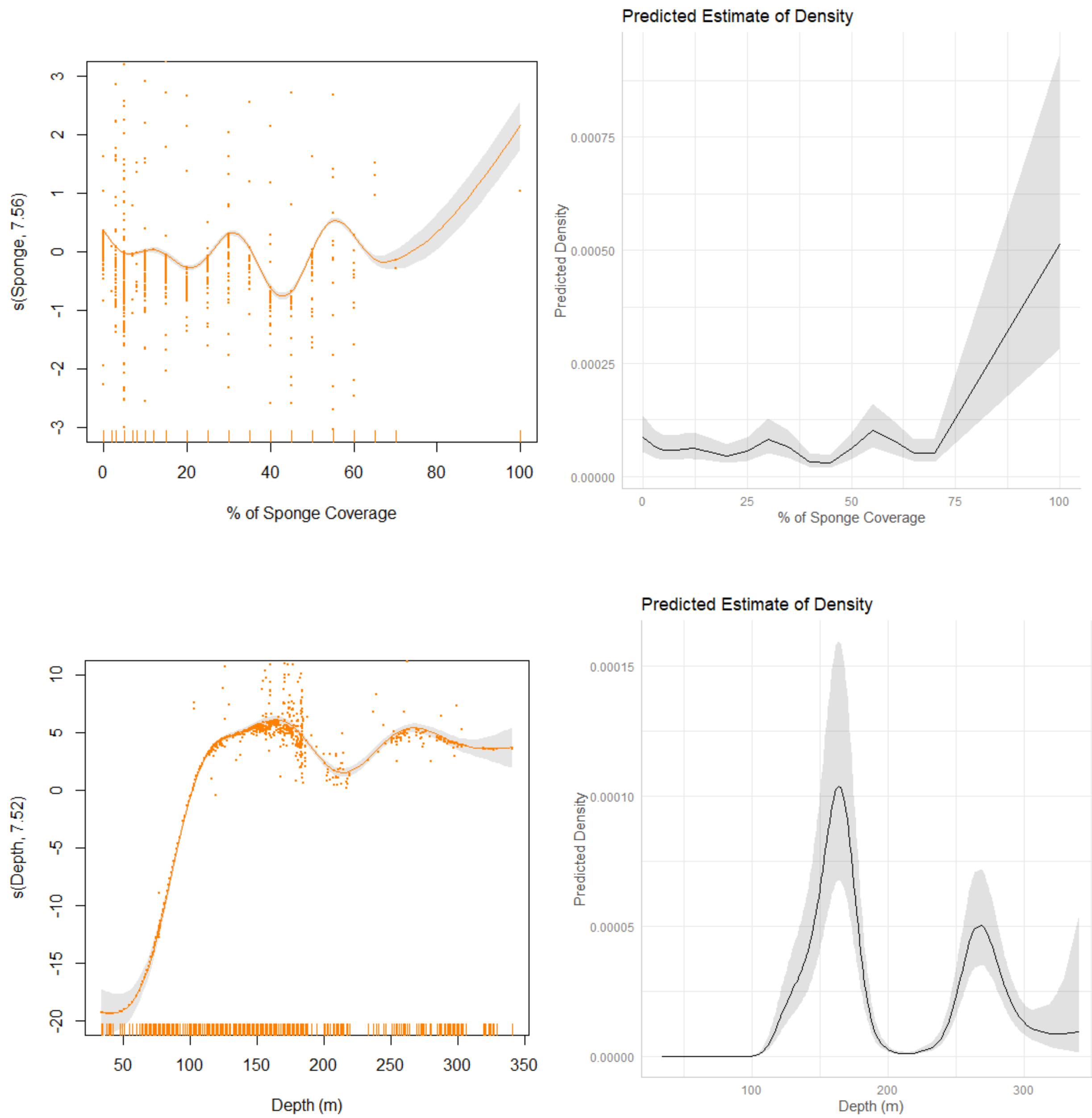
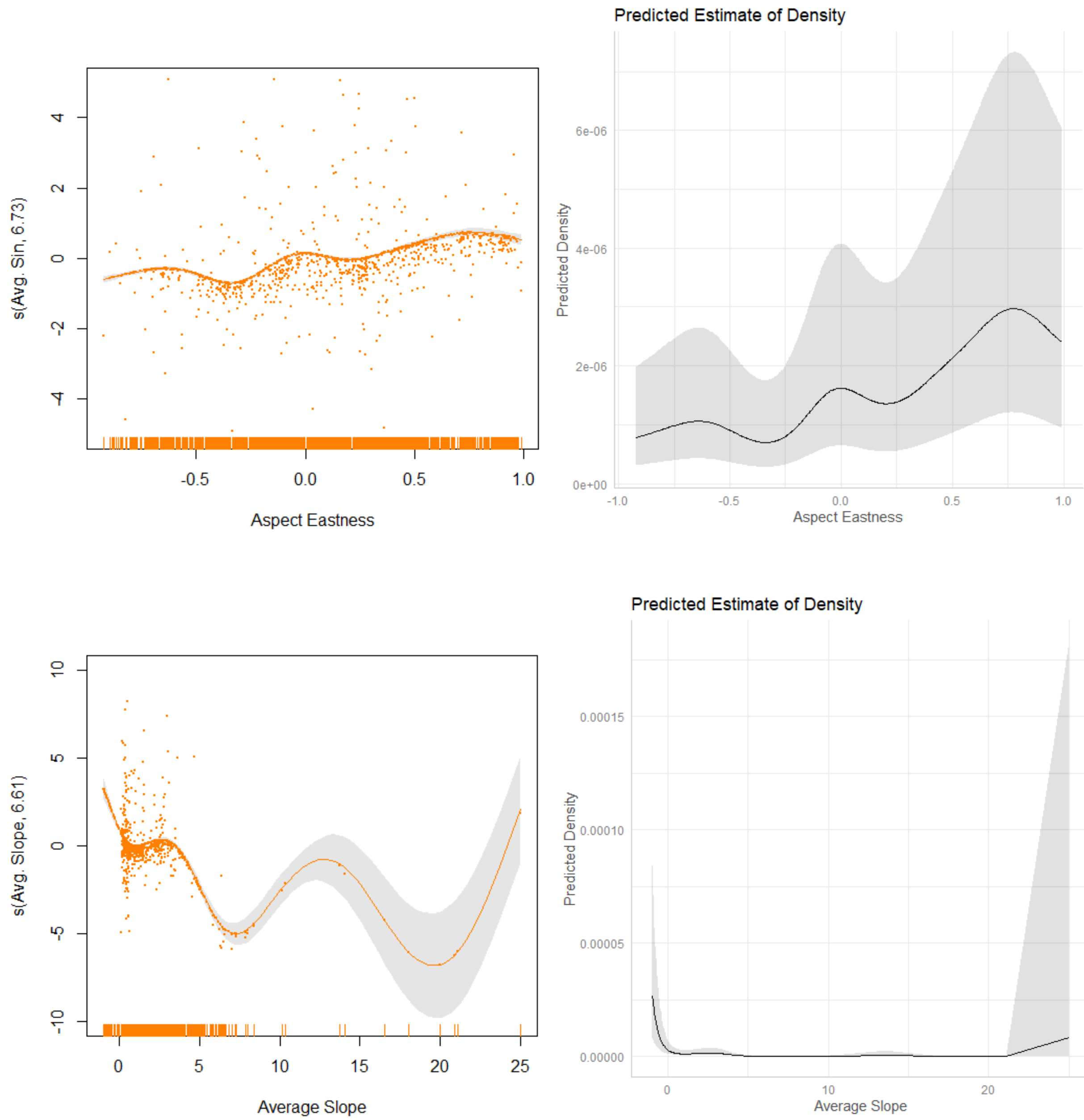


Figure 8. Smooth functions for the factors included in the best model for predicting density of adult Pacific ocean perch (POP) at the local scale in our study sites. Top row: plotted smooth function of the percentage of sponge coverage (left panel) and estimated predicted density (fish/m^2) of adult POP at various sponge coverage (right panel). Bottom row: plotted smooth function of depth (m; left panel) and estimated predicted density of adult POP at various depths (m; right panel).

Gray shading: approximate 95% confidence intervals. Covariate values as a rug plot are along the bottom of each left panel plot. Smooth function plots are of the relationship between the covariate value and the linear predictor, with effective degrees of freedom.



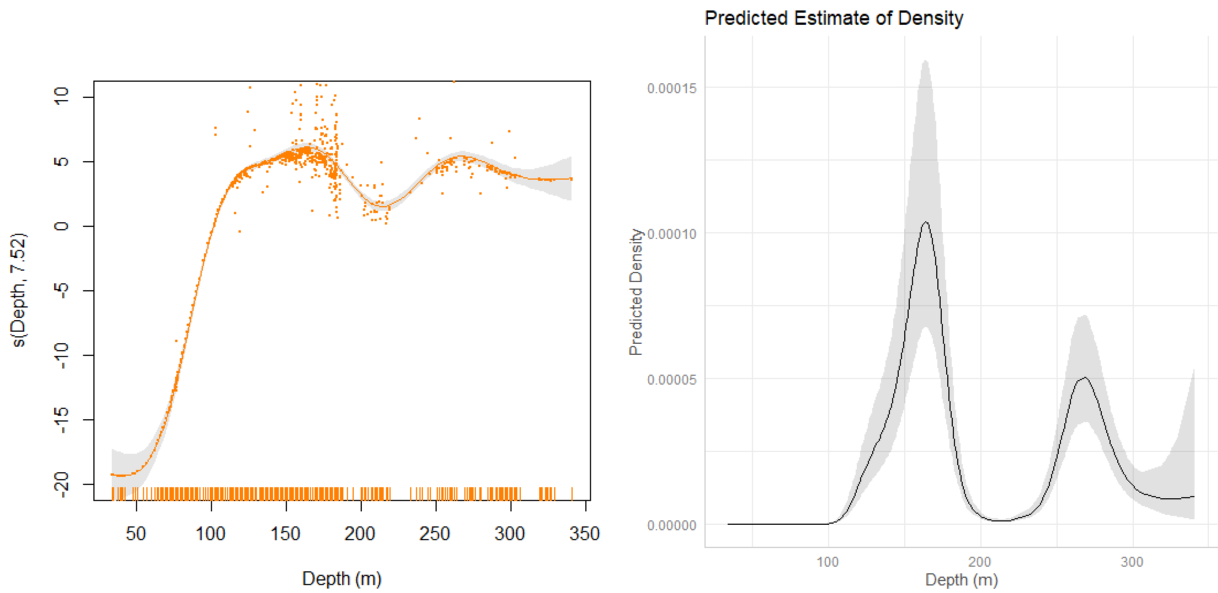
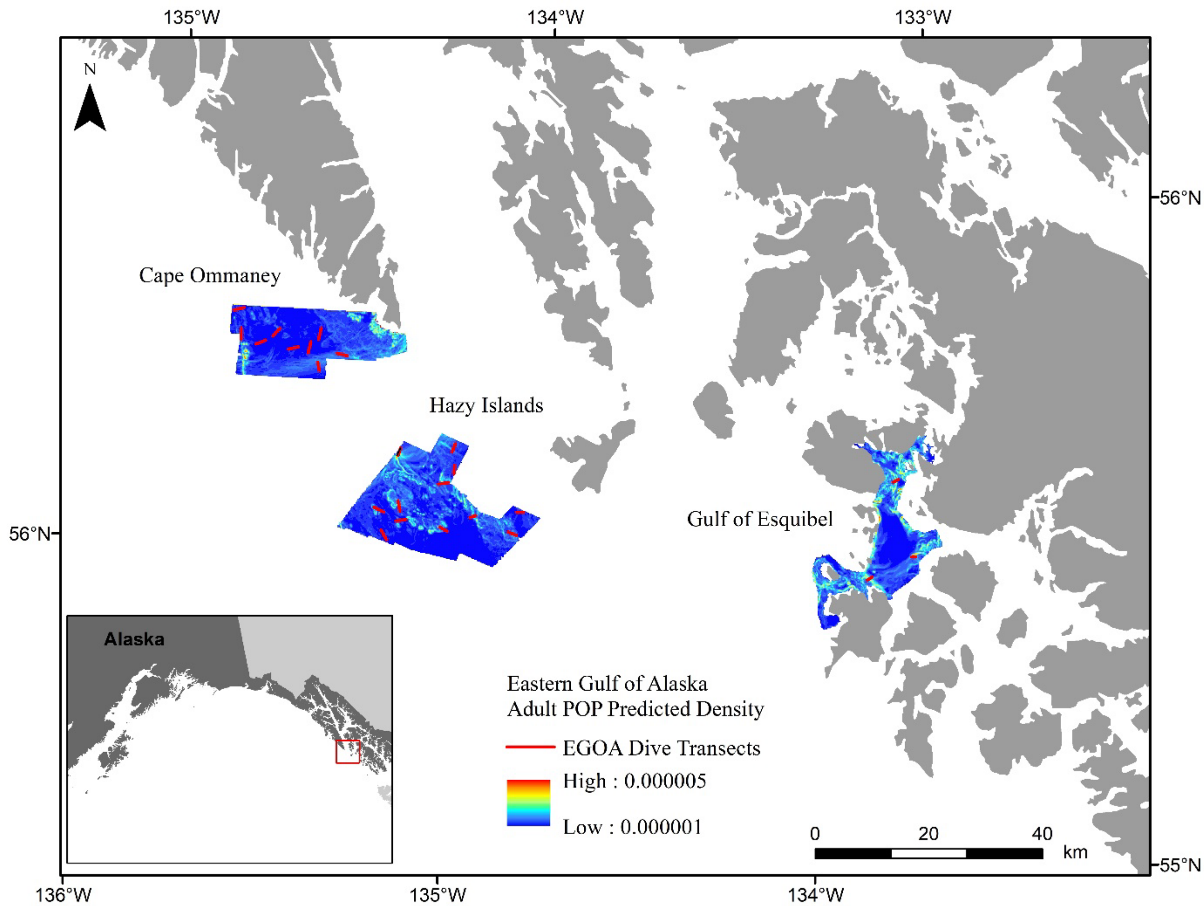


Figure 9. Smooth functions for the factors included in the best model for predicting density of adult Pacific ocean perch (POP) at the landscape scale in our study sites: Top row: plotted smooth function of aspect eastness (Avg_Sin; left panel) and estimated predicted density of adult POP at various levels of eastness (right panel). Middle row: plotted smooth function of the seafloor slope (Avg. Slope; left panel) and estimated predicted density of adult POP at various slope values (right panel). Bottom row: plotted smooth function of depth (m; left panel) and estimated predicted density (fish/m^2) of adult POP at various depths (m; right panel). Gray shading: approximate 95% confidence intervals. Covariate values as a rug plot are along the bottom of each left panel plot. Smooth panel plots are of the relationship between the covariate value and the linear predictor, with effective degrees of freedom.


135°W
134°W
133°W
136°W
135°W
134°W
56°N
56°N
55°N
N
Cape Ommaney
Hazy Islands
Gulf of Esquibel
Alaska
Eastern Gulf of Alaska
Adult POP Predicted Density
EGOA Dive Transects
High : 0.000005
Low : 0.000001
0
20
40
km

796

2

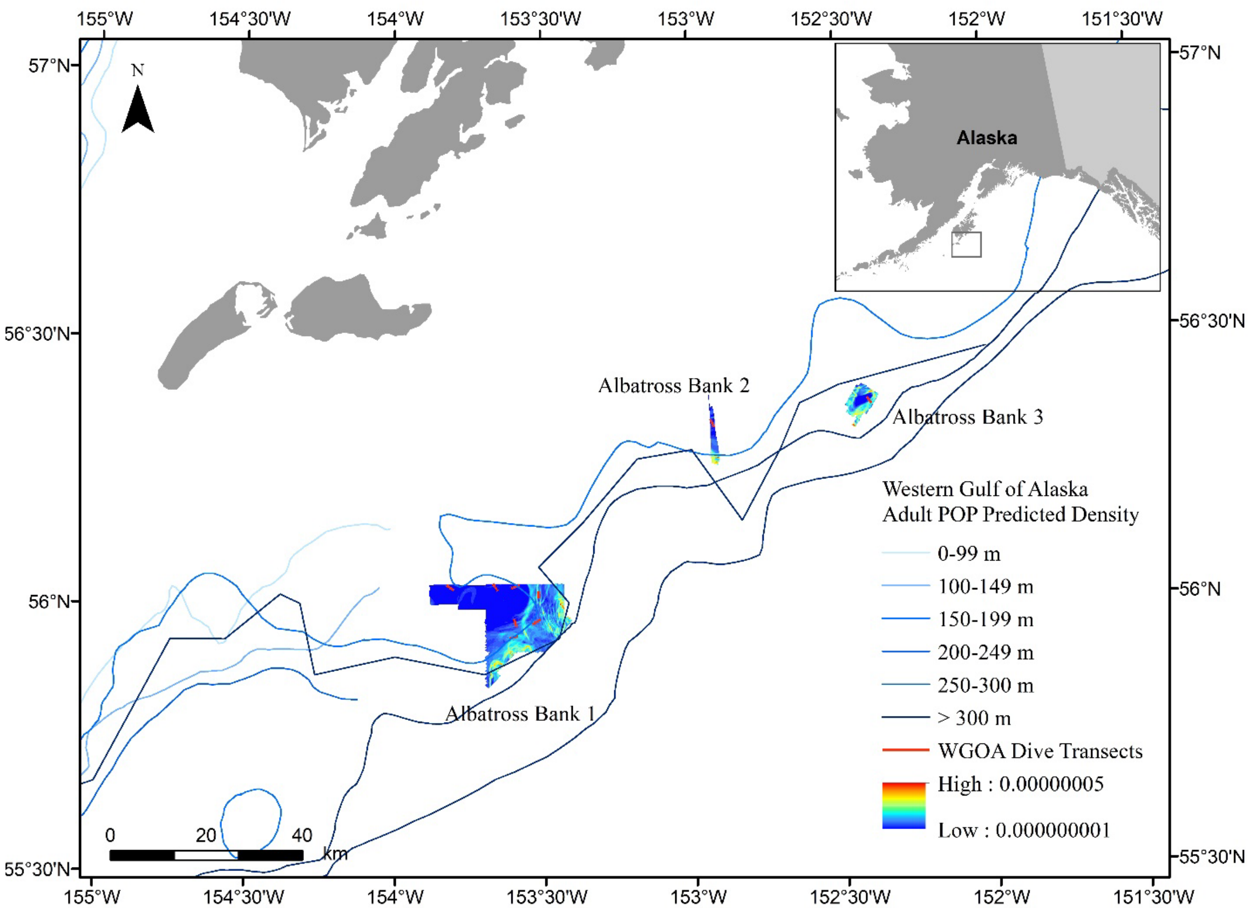


Figure 10. Mapped predicted density (number of fish/m^2) of adult Pacific ocean perch in the Eastern Gulf of Alaska study areas (top panel) and Western Gulf of Alaska study areas at the landscape scale. Note the different scale of density between the two plots.

8. TABLES

Table 1. Dive transects for Cape Ommaney – Hazy Islands survey 2005 and for Albatross Bank survey 2005. Study type refers to the purpose of each dive (e.g. catchability experiment = Catchability, Inshore habitat dive = Habitat) and location is provided with a two letter ID: CO = Cape Ommaney, GE = Gulf of Esquibel, HI = Hazy Islands, AB = Albatross Bank. Start latitude and longitude in decimal degrees are provided along with depth range for each transect when known.

Dive #	Study Type	Region	Latitude	Longitude	Depth (m)	Transect Length (m)
6462	Survey: HI	EGOA	55.869808	-134.802740	170	1,700.46
6463	Habitat: HI	EGOA	55.885300	-134.811543	115-160	1,801.45
6464	Habitat: HI	EGOA	55.891283	-134.856245	135-165	1,800.92
6465	Habitat: HI	EGOA	55.847872	-134.871000	180-195	1,800.56
6469	Habitat: HI	EGOA	55.795792	-134.517400	120-140	1,816.6
6470	Habitat: HI	EGOA	55.830523	-134.498977	100-110	1,200.28
6471	Habitat: HI	EGOA	55.843825	-134.628847	110-165	1,000.49
6472	Habitat: HI	EGOA	55.833038	-134.700410	145-185	1,600.48
6473	Habitat: HI	EGOA	55.980625	-134.758510	185-310	1,105.02
6474	Habitat: HI	EGOA	55.962207	-134.607745	80-130	1,801.03
6475	Habitat: HI	EGOA	55.929503	-134.626905	80-90	1,500.37
6476	Habitat: HI	EGOA	55.909030	-134.686748	105-150	1,800.53
6477	Survey: CO	EGOA	56.179142	-134.955605	185-190	1,801.22
6479	Survey: CO	EGOA	56.203712	-135.038843	175	1,800.79
6480	Habitat: GE	EGOA	55.578407	-133.478975	20-155	1,000.37
6481	Habitat: GE	EGOA	55.567120	-133.601440	50-205	1,000.57
6483	Habitat: GE	EGOA	55.623243	-133.542792	45-135	1,000.44
6484	Habitat: CO	EGOA	56.152218	-134.855268	190-230	1,800.89
6485	Habitat: CO	EGOA	56.133323	-134.917352	230-290	1,800.58
6490	Habitat: CO	EGOA	56.165612	-134.933195	175-185	2,001.33
6493	Habitat: CO	EGOA	56.181182	-134.894082	165-175	1,800.69
6494	Habitat: CO	EGOA	56.206903	-135.015572	165-175	1,800.53

6495	Habitat: CO	EGOA	56.215893	-135.104807	150-160	1,850.8
6496	Habitat: CO	EGOA	56.262610	-135.070705	145-150	1,800.72
6440	Habitat: AB1	WGOA	56.0234	-153.6544	70-75	1,800.94
6441	Habitat: AB1	WGOA	55.9551	-153.5915	120-180	1,619.96
6443	Catchability:	WGOA	55.9388	-153.5926	300	1,800.8
6445	Catchability:	WGOA	55.9695	-153.5128	320	1,801.7
6448	Catchability:	WGOA	56.0083	-153.5180	260-265	1,801.05
6452	Habitat: AB1	WGOA	56.0336	-153.8267	80	1,801.58
6453	Habitat: AB2	WGOA	56.0276	-153.6109	75-80	1,800.6
6459	Habitat: AB3	WGOA	56.3639	-152.3912	100-190	1,802.03
6461	Habitat: AB2	WGOA	56.3240	-152.9231	70-80	1,801.05

Table 2. Covariates used for estimating the detection function (DF) and the final density surface models (DSM) at the landscape and local scale. Data source: bathymetry data from multibeam acoustic seafloor mapping surveys (Bathymetry) and line transect surveys (Transect).

Covariate	Definition	Data Source	Analysis	Model scale
Substrate Types				
Mud	noticeable organic particles	Transect	DF	-
Sand	grains distinguishable	Transect	DF	-
Gravel	≥ 4 mm and < 2 cm	Transect	DF	-
Pebble	≥ 2 cm and < 6.5 cm	Transect	DF	-
Cobble	≥ 6.5 cm and < 25.5 cm	Transect	DF	-
Boulder	diameter ≥ 25.5 cm	Transect	DF	-
Exposed bedrock	noticeable exposed bedrock	Transect	DF	-
Terrain Metrics				
Depth	Depth from the gridded bathymetry data (10 m resolution).	Bathymetry	DSM	Landscape
Bathymetric Position Index (BPI_15)	Bathymetric Position Index derived at a spatial scale of 150 m (10 m resolution bathymetry data and 15-cell neighborhood).	Bathymetry	DSM	Landscape
Vector Ruggedness Measure (VRM_15)	Vector Ruggedness Measure of seafloor ruggedness derived at a spatial scale of 150 m.	Bathymetry	DSM	Landscape
Multiscale Aspect Northness (ACos_M)	Multiscale Aspect Northness (cosine of aspect) derived at spatial scales from 30-450 m (Dolan & Lucieer 2014 Table 2 Method 5).	Bathymetry	DSM	Landscape
Multiscale Aspect Eastness (ASin_M)	Multiscale Aspect Eastness (sine of aspect) derived at spatial scales from 30-450 m.	Bathymetry	DSM	Landscape

Multiscale Slope (Slope_M)	Multiscale Slope derived at spatial scales from 30-450 m.	Bathymetry	DSM	Landscape
Invertebrates				
Coral	Coral coverage	Transect	DSM	Local
Sponge	Sponge coverage	Transect	DSM	Local
Anemone	Anemone coverage	Transect	DSM	Local
% Invertebrate Coverage				
None (0)	No invertebrate coverage	Transect	DSM	Local
Light (1)	20 – 50% coverage	Transect	DSM	Local
Moderate (2)	< 50 – 75%	Transect	DSM	Local
Heavy (3)	> 75%	Transect	DSM	Local
Vertical Height (of substrate and invertebrates)				
0	No vertical relief	Transect	DSM	Local
1	vertical relief < 0.5 m	Transect	DSM	Local
2	vertical relief ≥ 0.5 m and < 2 m	Transect	DSM	Local
3	vertical relief ≥ 2 m	Transect	DSM	Local

Table 3. Number of segments (segment count) sampled in the Western Gulf of Alaska (WGOA) and Eastern Gulf of Alaska (EGOA) of each primary substrate and depth (m). Primary substrate types: mud (m), sand (s), gravel (g), pebble (p), cobble (c), boulder (b), and exposed bedrock (r).

Primary Substrate	Segment count		Depth (m)	Segment count	
	WGOA	EGOA		WGOA	EGOA
m	8	58	1-99	239	94
s	104	122	100-149	19	239
g	40	64	150-199	11	404
p	23	66	200-249	2	37
c	62	184	250-299	52	42
b	94	159	>299	29	4
r	20	162			

Table 4. Results of the final detection functions for juvenile shortspine thornhead (juv SST), juvenile Pacific ocean perch (juv POP), adult shortspine thornyhead (adult SST), and adult Pacific ocean perch (adult POP), and results for density surface models at the local and landscape scale for adult POP. Detection function: species/life stage, number of observations (n), the range of observations included in the analysis (distance range, m), model type (hazard-rate key function), covariates included in the detection function (depth, m), AIC value used for model selection, region (Albatross Bank – Western Gulf of Alaska, Cape Ommaney – Eastern Gulf of Alaska, Hazy Islands – Eastern Gulf of Alaska), area size (m^2) included in the detection function, and density estimation per meter squared with standard error in parentheses. Local and landscape scale density surface models (DSM): species/life stage, final DSM model (invertebrate coverage, coral coverage, sponge coverage, depth (m), vector ruggedness measure (VRM_15), bathymetric position index (BPI_15), seafloor slope (Avg_Slope), aspect eastness (ASin_Avg), and aspect northness (ACos_Avg).

Detection function								
	n	Distance range (m)	Model	Covariates	AIC	Region	Area size (m^2)	Est. Density
Juv SST	95	0.25 - 4	HZ	--	220	Albatross Bank	29,106	0.005 (0.0008)
Juv POP	20	1 – 5	HZ	--	49	Albatross Bank	13,304	0.003 (0.0014)
Adult SST	382	0.25 - 8	HZ	Depth (m)	868	Albatross Bank	74,812	0.008 (0.0015)
						Cape Ommaney	47,909	0.0008 (0.0003)
						Hazy Islands	14,130	0.003 (0.0007)
Adult POP	1,649	0.25 - 8	HZ	--	4,382	Albatross Bank	8,403	0.009 (0.001)
						Albatross Bank	94,164	0.003 (0.001)

						Cape Ommaney	142,706	0.12 (0.002)
						Hazy Islands	60,506	0.002 (0.0003)

Local Scale DSM

	Final Model	R^2 (adj)	Deviance Explained
Adult POP	density.est ~ s (x, y) + s (Sponge) + s (Avg_Depth)	0.691	83.9%

Landscape Scale DSM

	Final Model	R^2 (adj)	Deviance Explained
Adult POP	density.est ~ s(x, y) + s (Avg_Depth) + s (ASin_Avg) + s (Sl ope_Avg)	0.7	85%