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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. The present study used a density surface modelling approach with survey data from line transects and terrain metrics from multibeam acoustic bathymetry data, integrated with a Geographic Information System, to estimate the population density of Pacific Ocean perch *Sebastes alutus* (POP) within 6 sampling areas in the Gulf of Alaska (GOA) at 2 sampling scales: local and landscape. For adult POP, 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. 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 US$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

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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 Code of Federal Regulations [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 (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 GOA (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 *Sebastes alutus* (POP) and shortspine thornyhead *Sebastolobus alascanus* (SsT) 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 2 spatial scales: (i) local (10s to 100s of meters), and (ii) landscape (100s of meters to kilometers).

2. MATERIALS AND METHODS

2.1. Submersible line transect sampling

Line transect sampling data used in the distance analysis came from submersible dives that were originally part of 2 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 based on 2 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). In 2005, 33 dives were completed 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): 12 dives on the Hazy Islands mapped site, 9 dives on the Cape Ommaney mapped site, and 3 dives in the Gulf of Esquibel (Fig. 1). A total of 9 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 were 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 inverte-

Table 1. Dive transects for Cape Ommaney–Hazy Islands survey 2005, Eastern Gulf of Alaska ((EGOA) and for Albatross Bank survey 2005, Western Gulf of Alaska (WGOA). Study type refers to the purpose of each dive (Catchability: catchability experiment; Habitat: Inshore habitat dive) and location is provided with a 2 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 where applicable) for each transect

Dive no.	Study type	Region	Latitude (°N)	Longitude (°E)	Depth (m)	Transect length (m)
6462	Survey: HI	EGOA	55.8698	–134.8027	170	1700
6463	Habitat: HI	EGOA	55.8853	–134.8115	115–160	1801
6464	Habitat: HI	EGOA	55.8913	–134.8562	135–165	1801
6465	Habitat: HI	EGOA	55.8479	–134.8710	180–195	1801
6469	Habitat: HI	EGOA	55.7958	–134.5174	120–140	1817
6470	Habitat: HI	EGOA	55.8305	–134.4990	100–110	1200
6471	Habitat: HI	EGOA	55.8438	–134.6288	110–165	1001
6472	Habitat: HI	EGOA	55.8330	–134.7004	145–185	1601
6473	Habitat: HI	EGOA	55.9806	–134.7585	185–310	1105
6474	Habitat: HI	EGOA	55.9622	–134.6077	80–130	1801
6475	Habitat: HI	EGOA	55.9295	–134.6269	80–90	1500
6476	Habitat: HI	EGOA	55.9090	–134.6867	105–150	1801
6477	Survey: CO	EGOA	56.1791	–134.9556	185–190	1801
6479	Survey: CO	EGOA	56.2037	–135.0388	175	1801
6480	Habitat: GE	EGOA	55.5784	–133.4790	20–155	1000
6481	Habitat: GE	EGOA	55.5671	–133.6014	50–205	1001
6483	Habitat: GE	EGOA	55.6232	–133.5428	45–135	1000
6484	Habitat: CO	EGOA	56.1522	–134.8553	190–230	1801
6485	Habitat: CO	EGOA	56.1333	–134.9174	230–290	1801
6490	Habitat: CO	EGOA	56.1656	–134.9332	175–185	2001
6493	Habitat: CO	EGOA	56.1812	–134.8941	165–175	1801
6494	Habitat: CO	EGOA	56.2069	–135.0156	165–175	1801
6495	Habitat: CO	EGOA	56.2159	–135.1048	150–160	1851
6496	Habitat: CO	EGOA	56.2626	–135.0707	145–150	1801
6440	Habitat: AB1	WGOA	56.0234	–153.6544	70–75	1801
6441	Habitat: AB1	WGOA	55.9551	–153.5915	120–180	1620
6443	Catchability: AB1	WGOA	55.9388	–153.5926	300	1801
6445	Catchability: AB1	WGOA	55.9695	–153.5128	320	1802
6448	Catchability: AB1	WGOA	56.0083	–153.5180	260–265	1801
6452	Habitat: AB1	WGOA	56.0336	–153.8267	80	1802
6453	Habitat: AB2	WGOA	56.0276	–153.6109	75–80	1801
6459	Habitat: AB3	WGOA	56.3639	–152.3912	100–190	1802
6461	Habitat: AB2	WGOA	56.3240	–152.9231	70–80	1801

brate 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 2 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 were 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 1981) with ESRI ArcGIS software.

We included the following seafloor terrain metrics in the landscape-scale predictive density modeling

[1]Thales GeoSolutions (Pacific), Inc.

[2]National Ocean Service (surveys H11577, H11688, and H11690)

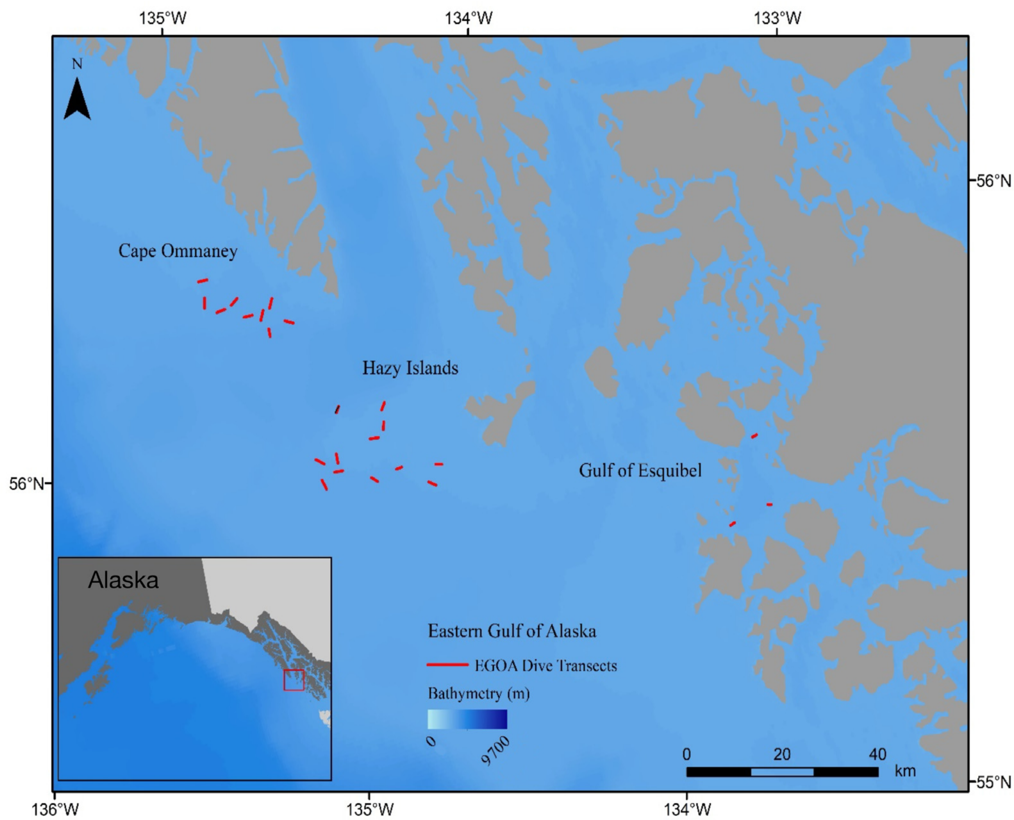


Fig. 1. Location of dive transects in the Eastern Gulf of Alaska sampling sites: Cape Ommaney, Hazy Islands, and Gulf of Esquibel. Map inset is for location reference. Each red line represents a dive transect

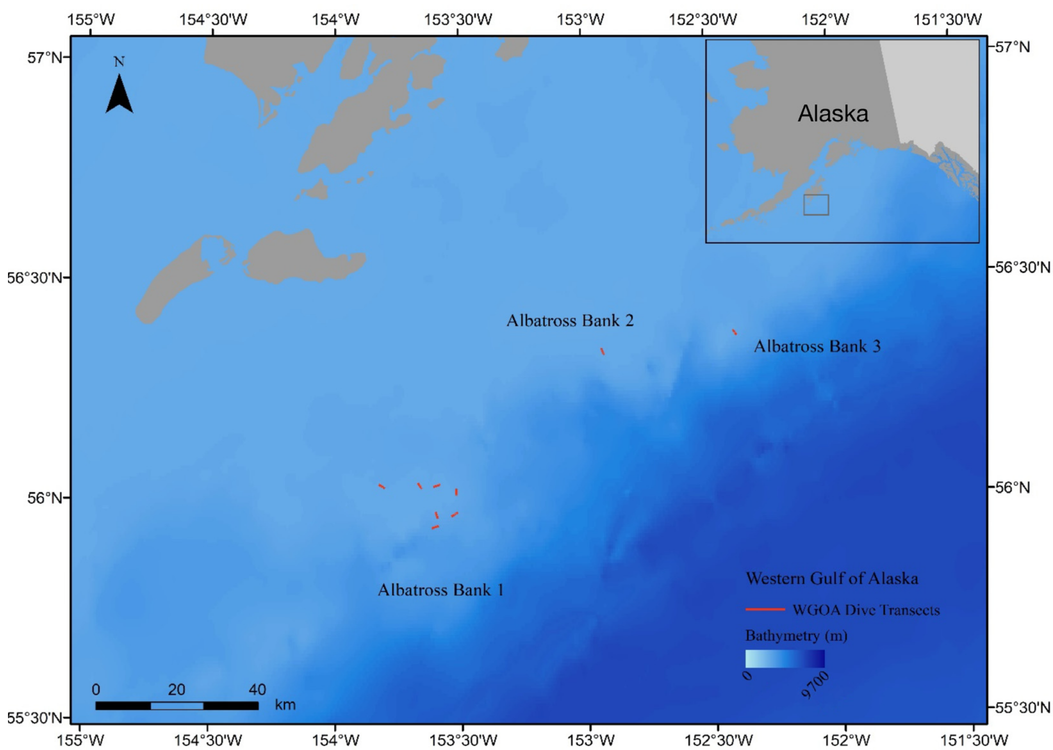


Fig. 2. Location of dive transects in the Western Gulf of Alaska, Albatross Bank sampling locations: Albatross Bank 1, Albatross Bank 2, and Albatross Bank 3. Map inset is for location reference. Each red line represents a dive transect

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) or line transect surveys (Transect)

Covariate	Definition	Data source	Analysis	Model scale
Substrate type				
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 metric				
Depth	Gridded bathymetry data (10 m resolution)	Bathymetry	DSM	Landscape
Bathymetric Position Index (BPI_15)	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)	Seafloor ruggedness derived at a spatial scale of 150 m	Bathymetry	DSM	Landscape
Multiscale Aspect Northness (ACos_M)	Cosine of aspect derived at spatial scales of 30–450 m (Dolan & Lucieer 2014; their Table 2, Method 5)	Bathymetry	DSM	Landscape
Multiscale Aspect Eastness (ASin_M)	Sine of aspect derived at spatial scales of 30–450 m	Bathymetry	DSM	Landscape
Multiscale Slope (Slope_M)	Derived at spatial scales of 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

analysis to describe attributes of rockfish habitat: depth, bathymetric position index (BPI) (Guisan et al. 1999, Weiss 2001), 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 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). VRM is a measurement that incorporates the heterogeneity of both slope and aspect (Sappington et al. 2007). Values of VRM can range from 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 (1981) method. The measure may be useful in determining colonization as flat areas can better 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 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; their Table 2, Method 5) in ArcGIS at increasing spatial scales and analysis windows of 30 to 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 2 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.

2.3.1. 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), sand (S), gravel (G), pebble (P), cobble (C), boulder (B), and exposed bedrock (R; Table 2). The vertical relief scale was defined as (0) no vertical relief, (1) low, (2) moderate, and (3) high (Table 2). 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.

2.3.2. 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 (Table 2), 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% and that 75% 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 seastars, 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 2-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. 2015). 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 (Miller et al. 2019) in R v.3.6.1. 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. 2013a). 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 4 cosine adjustment terms. The following covariates were included in the determination of the detection function: primary substrate type (factor covariate with 7 levels: boulder, gravel, cobble, pebble, sand, mud, and rock) and depth (factor covariate with 6 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. 2015). 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:

$$\hat{D} = \frac{n}{a\hat{P}_a} \tag{1}$$

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 DSM, transect lines were divided into T unequal segments, based on a change in the primary substrate type (as defined in Section 2.3) (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 2 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 models (DSM)

Data were then fit, for each species/life stage, to GAMs 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 (Miller et al. 2013a,b) in R v.3.6.1. The following is the general formulation:

$$E\left(\widehat{D_i}\right) = \hat{P}_{ai} \exp\left[\beta_0 + \sum_k f_k\left(z_{ik}\right)\right], \; i = 1, \ldots, T \qquad (2)$$

where f_k are smooth functions of the covariates, β_0 is an intercept term, and T is the number of segments. Estimated detection probability, P_a, within segment i was allowed to vary for each animal, j, using the Horvitz-Thompson-like estimator (Hedley & Buckland 2004):

$$\widehat{D_i} = \sum_{j=1}^{n_j} \frac{1}{\widehat{\hat{P}_{a\,ij}}}, \; i = 1, \ldots, T \qquad (3)$$

Selection for the smooth terms was performed via restricted maximum likelihood, 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 2863 POP and SsT observations were made across 33 transects: 40 juvenile POP, 99 juvenile SsT, 463 adult SsT, and 2261 adult POP. Group abundance ranged from 1 to 27 fish, but the majority of rockfish were observed alone (1974 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 2 species of rockfish (Fig. 5). SsT 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 EGOA occurred at depths between 150 and 200 m, with relatively equal sampling among boulder, cobble, and rock habitats. In the WGOA, 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 EGOA (Cape Ommaney; n = 4) and

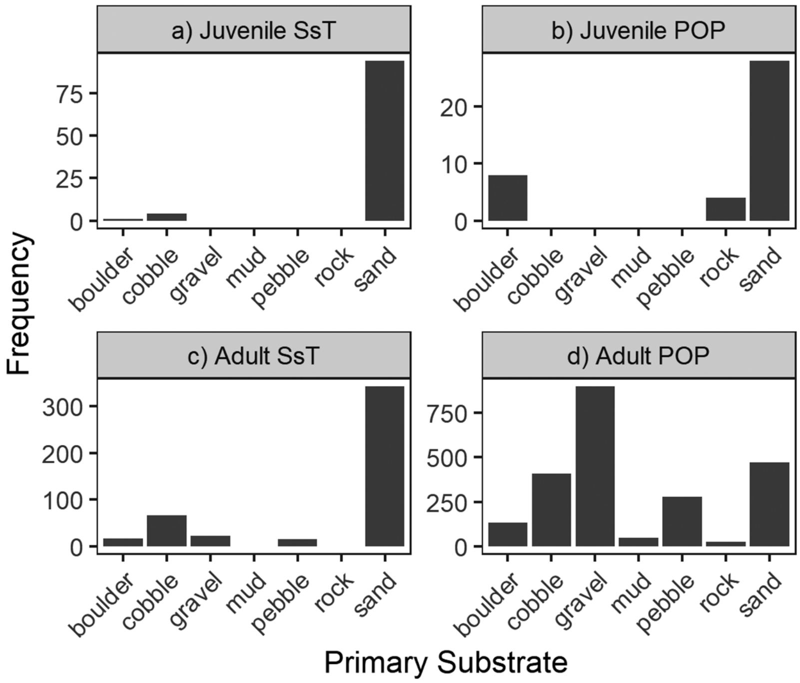


Fig. 3. Frequencies of observed (a,b) juvenile and (c,d) adult (a,c) shortspine thornyhead (SsT) and (b,d) Pacific Ocean perch (POP) by substrate type. See Table 2 for substrate type descriptions. Note different frequency scales between the panels

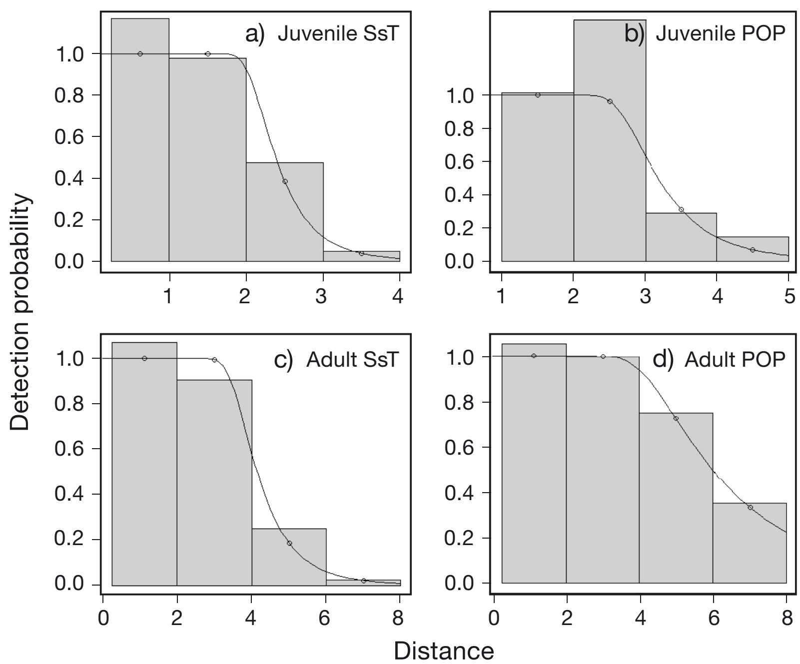


Fig. 4. Distribution of perpendicular detection distances (m) from submersible of (a) juvenile shortspine thornyhead (SsT), (b) juvenile Pacific Ocean perch (POP), (c) adult SsT, and (d) adult POP in sampled sites observed during submersible transect surveys with the fitted (hazard-rate) detection function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

WGOA (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 ($P_a = 1$) until approximately 2.5 m, where it dropped dramatically ($P_a < 0.2$; 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 EGOA (Hazy Islands and Cape Ommaney; n = 8) and WGOA (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 and 2.5 m ($P_a > 1$), where it dropped dramatically ($P_a < 0.2$; 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. 6b), 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

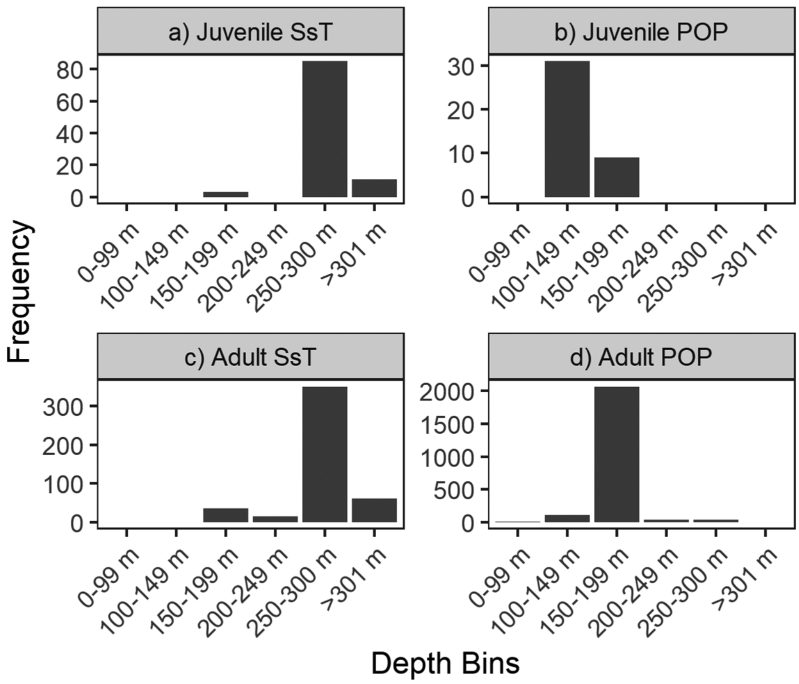


Fig. 5. Frequencies of observed (a,b) juvenile and (c,d) adult (a,c) shortspine thornyhead (SsT) and (b,d) Pacific Ocean perch (POP) by depth: 0–99 m, 100–149 m, 150–199 m, 200–249 m, 250–300 m, and >301 m. Note different frequency scales between the panels

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 are mud (M), sand (S), gravel (G), pebble (P), cobble (C), boulder (B), and exposed bedrock (R)

Primary substrate	Segment count WGOA	Segment count EGOA	Depth (m)	Segment count WGOA	Segment count 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			

low confidence in model results and convergence warnings. Adult SsT observations from the EGOA (Cape Ommaney and Hazy Islands; n = 125) and WGOA (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_a > 0.6; Fig. 4c). The majority of adult SsT were observed on sandy habitat (Fig. 3c) at depths between 250 and 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 EGOA (Cape Ommaney and Hazy Islands; n = 1399) and the WGOA (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_a > 0.6; Fig. 4d). Adult POP were primarily observed on gravel (Fig. 3d), at depths of 150 to 199 m (Fig. 5d), and with approximately 30 to 50% invertebrate (Fig. 6d) and little to no (<10%) coral 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. 8a) and depth (Fig. 8c), 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 high sponge coverage (>75%; Fig. 8b) and at depths between 100 and 200 m (Fig. 8d). Note that error surrounding areas of highest density increases greatly for both sponge coverage (Fig. 8b) and depth (Fig. 8d). Also, results of the sponge smooth function (Fig. 8a) 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. 9a), seafloor slope (Fig. 9c), and depth (Fig. 9e), 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. 9d) eastern

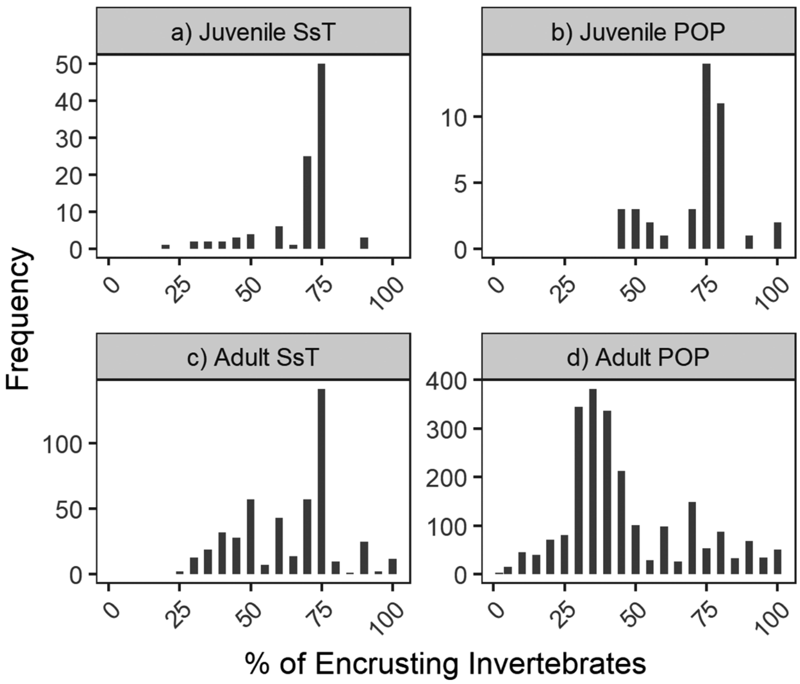


Fig. 6. Frequencies of observed (a,b) juvenile and (c,d) adult (b,d) shortspine thornyhead (SsT) and (b,d) Pacific Ocean perch (POP) by percentage of encrusting invertebrate coverage. Note different frequency scales between the panels

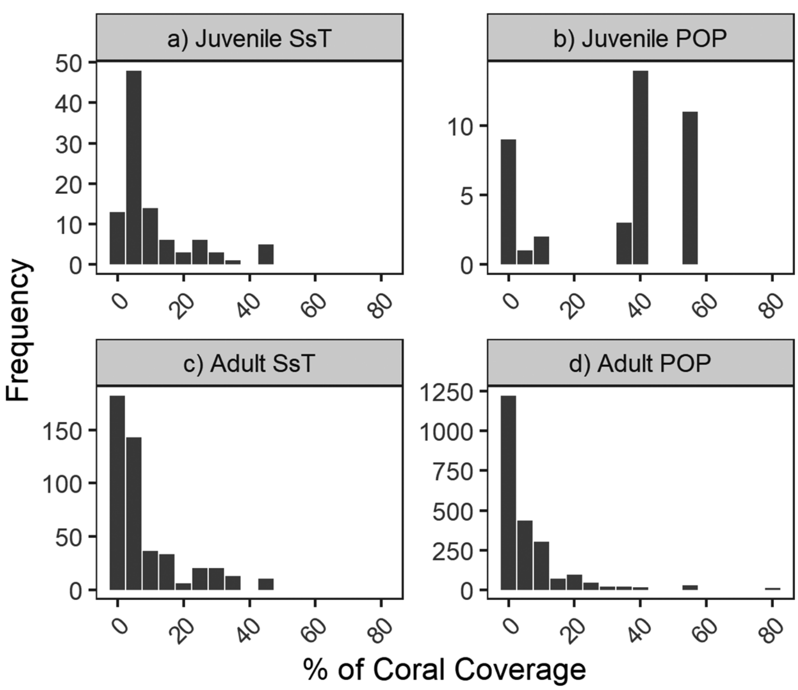


Fig. 7. Frequencies of observed (a,b) juvenile and (c,d) adult (a,c) shortspine thornyhead (SsT) and (b,d) Pacific Ocean perch (POP) by percentage of coral coverage. Note different frequency scales between the panels

facing slopes (Fig. 9b) at depths of 100 to 200 m (Fig. 9f). 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. 10a).

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 POP 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. POP 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, there is little confidence in these results for reasons further discussed.

When designing a line transect survey, there are many considerations that must be included to ensure

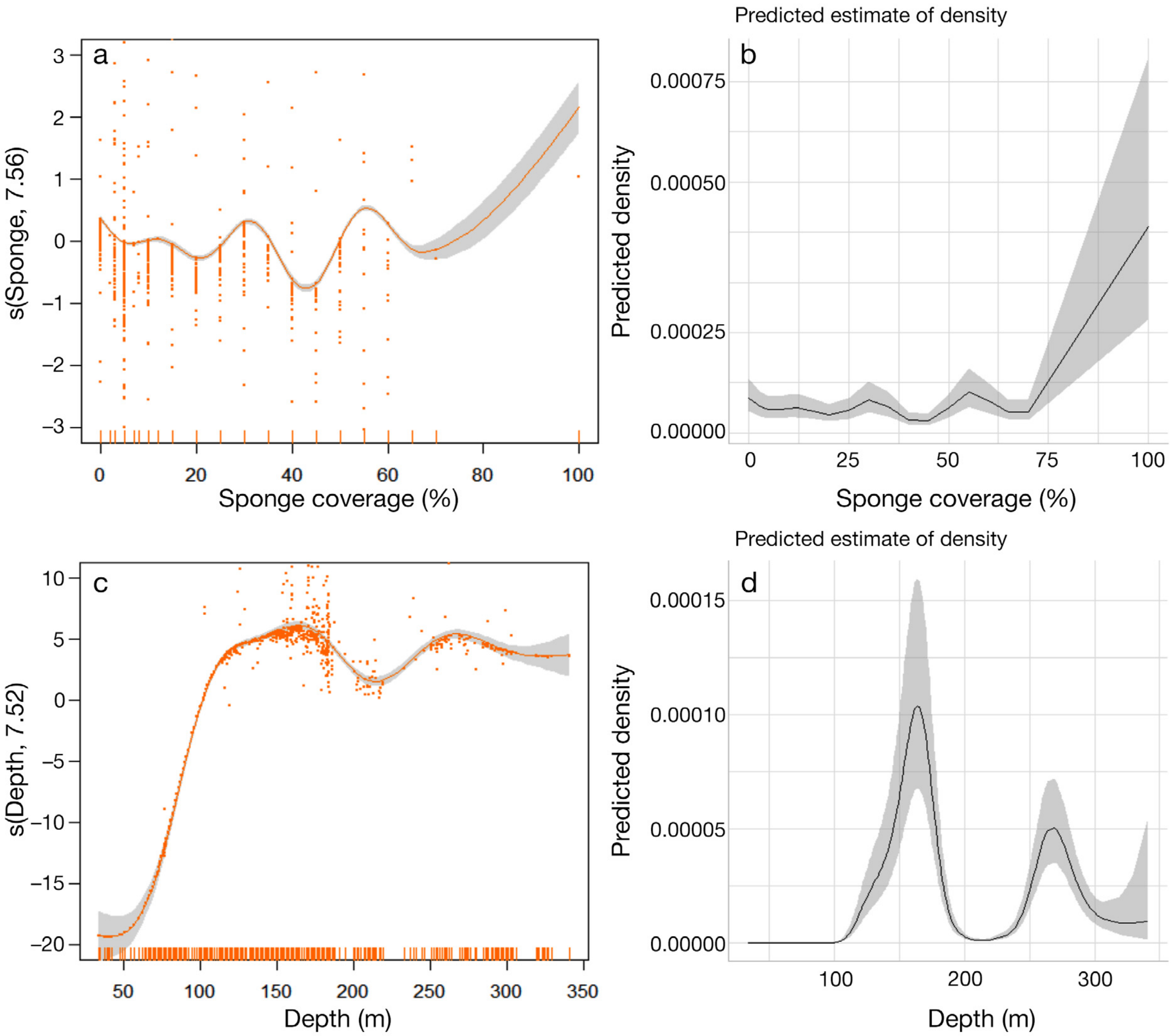


Fig. 8. Smooth functions for the factors included in the best model for predicting density of adult Pacific Ocean perch (POP) at the local scale in our study sites. (a) Smooth function of the percentage of sponge coverage and (b) estimated predicted density (fish m^{-2}) of adult POP at various sponge coverage. (c) Smooth function of depth (m) and (d) estimated predicted density of adult POP at various depths (m). 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

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-

Table 4. Final detection functions for juvenile (juv) and adult shortspine thornhead (SsT) and Pacific Ocean perch (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, location (Albatross Bank, Western Gulf of Alaska; Cape Ommaney and 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 (sponge coverage, depth (Avg_Depth, m), seafloor slope (Avg_Slope), and aspect eastness (ASin_Avg). Dash (–) indicates no covariates were included in the detection function

	n	Distance range (m)	Model	Covariates	AIC	Location	Area size (m^2)	Est. density
Detection function								
Juv SsT	95	0.25–4	HZ	–	220	Albatross Bank	29106	0.005 (0.0008)
Juv POP	20	1–5	HZ	–	49	Albatross Bank	13304	0.003 (0.0014)
Adult SsT	382	0.25–8	HZ	Depth (m)	868	Albatross Bank	74812	0.008 (0.0015)
						Cape Ommaney	47909	0.0008 (0.0003)
						Hazy Islands	14130	0.003 (0.0007)
Adult POP	1649	0.25–8	HZ	–	4382	Albatross Bank	8403	0.009 (0.001)
						Albatross Bank	94164	0.003 (0.001)
						Cape Ommaney	142706	0.12 (0.002)
						Hazy Islands	60506	0.002 (0.0003)

	Final model	R^2 (adj)	Deviance explained
Local scale DSM			
Adult POP	density.est ~ $s(x, y)$ + s(Sponge) + s(Avg_Depth)	0.691	83.9%
Landscape Scale DSM			
Adult POP	density.est ~ $s(x, y)$ + s(Avg_Depth) + s(ASin_Avg) + s(Slope_Avg)	0.7	85%

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; Figs. 1 & 2). Sampling was disproportioned among the depth bins and various substrate types (Table 3). The majority of the sampling effort in the EGOA occurred at depths between 150 and 200 m, with relatively equal sampling among boulder, cobble, and rock habitats. In the WGOA, 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 (EGOA vs. WGOA, 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 Greene et al.'s (1999) 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

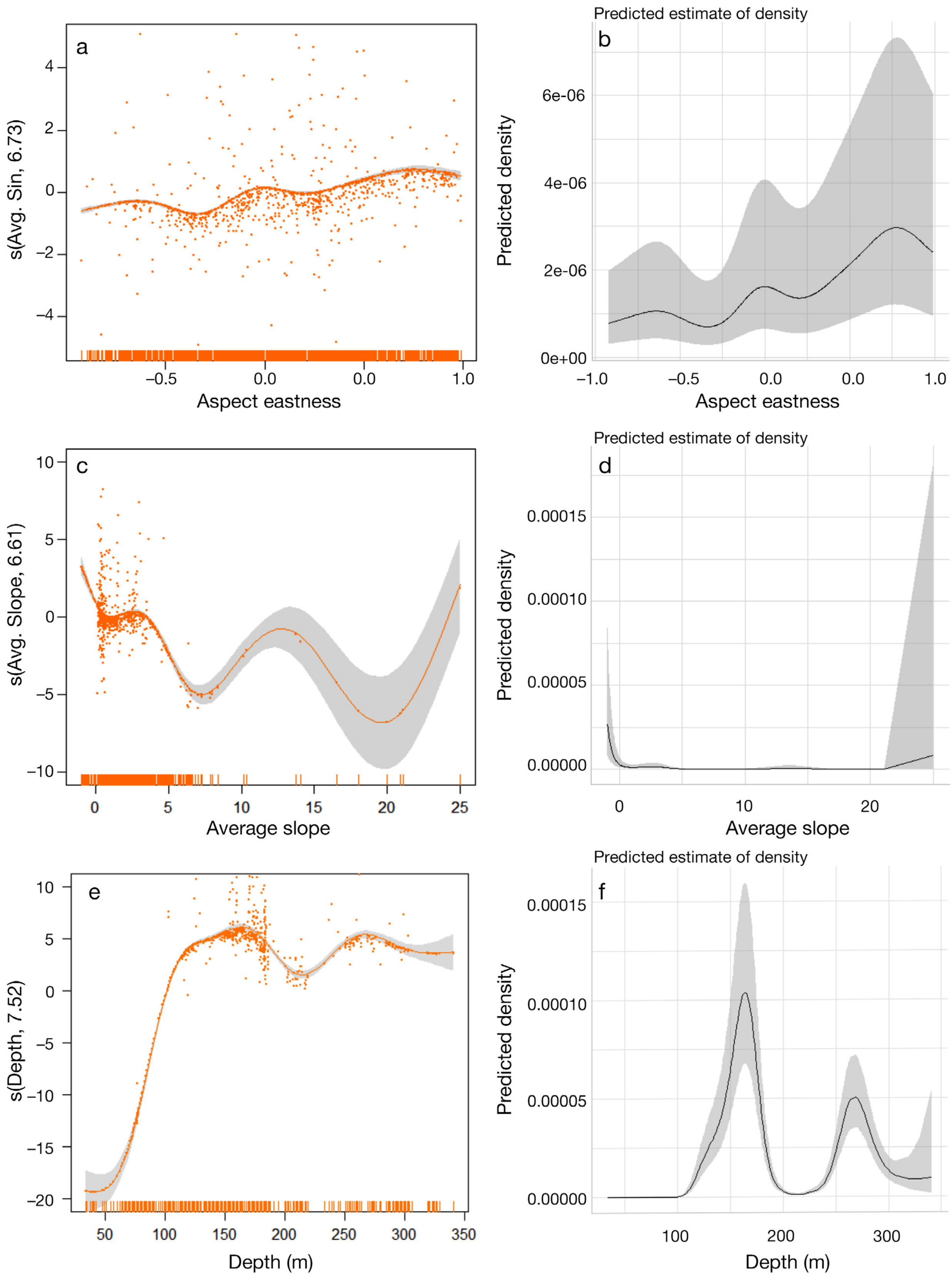
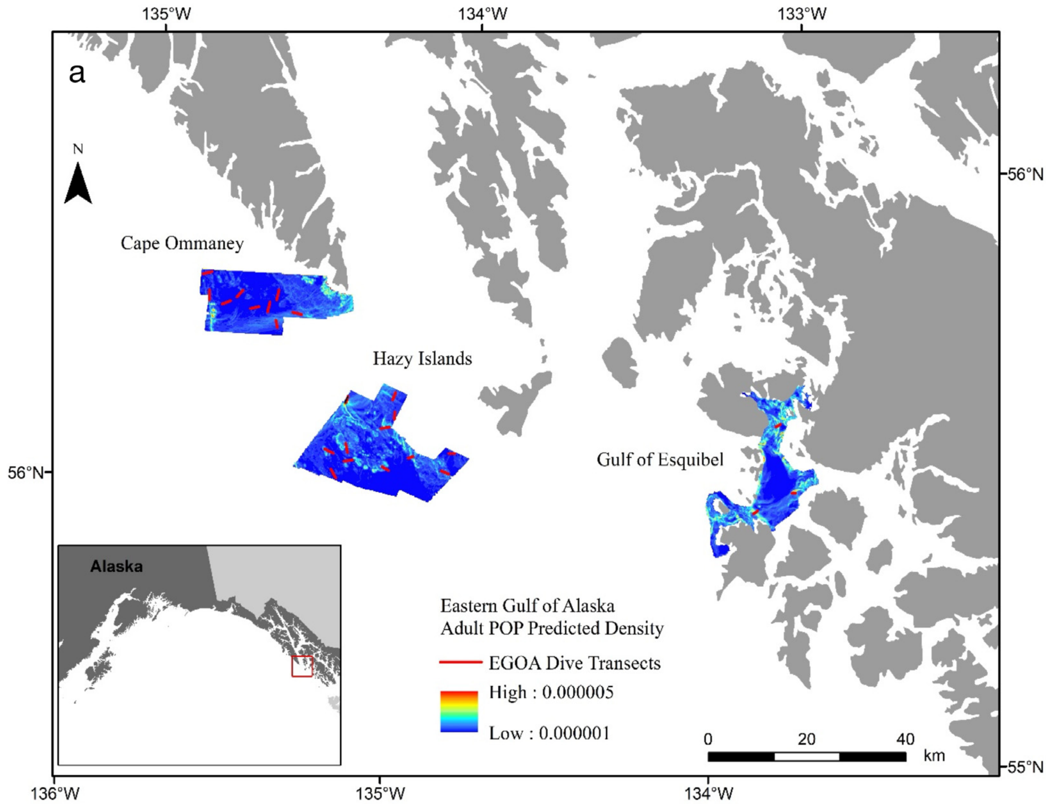


Fig. 9. Smooth functions for the factors included in the best model for predicting density of adult Pacific Ocean perch (POP) at the landscape scale in our study sites. (a) Smooth function of aspect eastness (Avg.Sin) and (b) estimated predicted density of adult POP at various levels of eastness. (c) Smooth function of the seafloor slope (Avg.Slope) and (d) estimated predicted density of adult POP at various slope values. (e) Smooth function of depth (m) and (f) estimated predicted density (fish m^{-2}) of adult POP at various depths (m). Other details as in Fig. 8



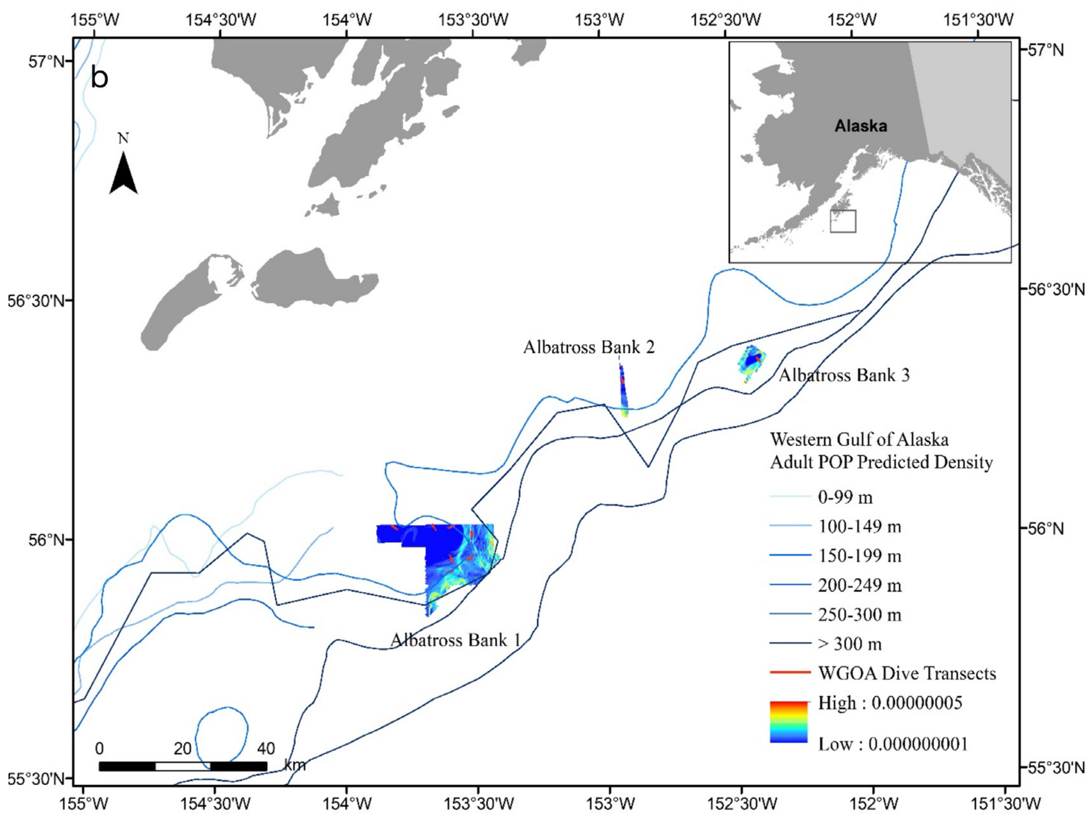


Fig. 10. Mapped predicted density (number of fish m^{-2}) of adult Pacific Ocean perch in (a) the Eastern and (b) Western Gulf of Alaska study areas at the landscape scale. Note the different scale of density between the 2 plots

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 an area for a rockfish species could result in unreliable density estimates, especially if spatial modeling has shown them to have 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 (WGOA, Central GOA, and EGOA) 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. Often 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 to 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. (2004) recommend a minimum of 60 to 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 MCDS 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, there was little confidence in model output for juveniles of both species in this study, 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 may 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. 2021). 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 SDMs 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, 2021) to help with abundance estimation of species such as rockfish that inhabit untrawlable areas. The results presented here should be considered exploratory and should 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 another ecosystem-based fisheries management (EBFM) 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 DSM could be used to fill sampling gaps for untrawlable areas in the current EFH SDMs (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 SDM 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 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 2 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 (WGOA, 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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