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ARTICLE

Predicting important rockfish (*Sebastes* spp.) habitat from large-scale longline surveys for southern British Columbia, Canada

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Abstract: Rockfish, particularly yelloweye (*Sebastes ruberrimus*) and quillback (*Sebastes maliger*), are vulnerable to overfishing because they mature late and have affinity for shallow water (50–200 m) habitats. Because studies relating habitat characteristics with the distribution and presence of rockfishes at large scales (100s of kilometres) remain scarce, we sought to investigate the relationships between benthic characteristics with the presence–absence and abundance of rockfishes caught in longline surveys in nearshore waters of southern British Columbia. Habitat parameters were calculated from a 20 m resolution bathymetry layer. Yelloweye and quillback were examined separately and combined with 19 other rockfish species in a species aggregate (total rockfish); occurrence data were fitted with generalized linear mixed effects models, and abundance data were fitted with zero-inflated mixed effects models. The relationship between rockfish abundance with presence–absence and slope, distance to rocky habitat, and fine bathymetric position index suggests that these species prefer rocky, steep habitat. While underwater visual observation data offer measures of visual fish habitat and abundance, longline surveys may be a more cost-effective method for large-scale studies.

Résumé : Les sébastes, en particulier les sébastes aux yeux jaunes (*Sebastes ruberrimus*) et les sébastes à dos épineux (*Sebastes maliger*), sont vulnérables à la surpêche en raison de leur maturité tardive et de leur affinité pour les habitats d'eau peu profonde (50–200 m). Comme les études qui relient les caractéristiques des habitats à la répartition et à la présence de sébastes à grande échelle (centaines de kilomètres) demeurent rares, nous avons examiné les relations entre les caractéristiques benthiques et la présence ou l'absence et l'abondance de sébastes capturés lors de relevés à la palangre dans des eaux littorales du sud de la Colombie-Britannique. Les paramètres associés à l'habitat ont été calculés à partir d'une couche bathymétrique d'une résolution de 20 m. Les sébastes à yeux jaunes et les sébastes à dos épineux ont été examinés séparément et combinés à 19 autres espèces de sébastes dans un regroupement d'espèces (sébastes totaux); les données sur la présence ont été calées sur des modèles linéaires généralisés à effets mixtes et les données d'abondance ont été calées sur des modèles à excès de zéros à effets mixtes. La relation entre l'abondance de sébastes avec présence–absence et la pente, la distance d'un habitat rocheux et l'indice de position bathymétrique fine indiquerait que ces espèces préfèrent les habitats rocheux à pente raide. Si les données d'observation sous-marines visuelles fournissent des mesures visuelles de l'habitat et de l'abondance des poissons, les relevés à la palangre pourraient s'avérer plus économiques pour les études à grande échelle. [Traduit par la Rédaction]

Introduction

Anthropogenic activities can cause water pollution, habitat degradation, and overfishing of many fish populations (Worm et al. 2006, 2009; Halpern et al. 2008) in many marine ecosystems. Consequently, a decline in biodiversity and ecosystem services, how natural systems fulfill human needs, has been reported in degraded marine systems (Holmlund and Hammer 1999; Worm et al. 2006). To date, the most conservative conservation strategy for protecting both the ecosystem and fish populations are spatial closures such as marine protected areas, whereby detrimental anthropogenic activities, such as fishing, are strictly controlled or forbidden (Halpern 2003; Edgar et al. 2014). Such closures can be an effective spatial management tool that serves to increase population size, individual fish size, species diversity; protect critical habitats; and enhance adjacent fisheries (Roberts et al. 2001; Haggarty et al. 2016*b*).

The relationship between organisms and their environment and therefore the distribution of species has been a key focus in

ecology for decades (Rushton et al. 2004). The underlying principle is that each species has a multidimensional environmental niche, and species are more abundant in the middle of (usually humped curved) an environmental gradient (Hutchinson 1959, 1991; Guisan and Thuiller 2005). Species distribution models (SDMs) are statistical tools to predict how species are distributed in the landscape over space and time (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Elith and Leathwick 2009). Moreover, SDMs can be extremely helpful for ecosystem management and conservation as spatial planning tools to create protected areas in both terrestrial and marine environments based on the predictive outcomes of the models (Lindholm et al. 2001; Le Pape et al. 2014).

Until recently, marine benthic habitats were described by direct observations of the environment and thus were limited to shallow waters (<30 m) over site-specific or limited spatial extents due to logistical and monetary constraints. In the last few decades, remote sensing techniques represent a more inexpensive way to map the marine floor over large spatial extents and at very high

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(<5 m) and medium (10–30 m) spatial resolution (Greene et al. 1999; Kostylev et al. 2001), facilitating the prediction of species distributions and abundance in deeper marine environments (Rubec et al. 1998, 2016b; Pittman and Brown 2011; Young and Carr 2015). Remote sensing collects physical data from the environment using the electromagnetic spectrum emitted either by the sun (passive) or by a source (active), such as multibeam sonars. The end product of multibeam data is a digital elevation model (DEM) raster data set with bathymetry values at defined regular intervals (Young et al. 2010).

Although SDMs are more common in terrestrial environments, the number of studies in freshwater environments (e.g., Lin et al. 2015) and the marine realm have increased considerably over time. Suitability models have been conducted for invertebrates such as shrimp (Rubec et al. 2016a, 2016b), corals, and sponges in Alaskan waters (Rooper et al. 2016, 2017) and in a number of demersal fish species, including rockfishes, in temperate waters of the Northeast Pacific (Young et al. 2010; Laman et al. 2015; Wedding and Yoklavich 2015; Young and Carr 2015; Pirtle et al. 2017). In general, there is consensus that habitat heterogeneity (i.e., the presence of biogenic or substrate structure) is related to an increase in either the probability of occurrence or the abundance of most species. However, studies for rockfishes in general, and yelloweye (Sebastes ruberrimus) and quillback (Sebastes maliger) in particular, remain scarce in British Columbia.

Rockfishes (genus Sebastes) are an important fishery resource in California, Washington, British Columbia, and Alaska waters. Most species are vulnerable to overfishing because they mature late in life and are sedentary animals with small home ranges (Love et al. 2002). In British Columbia and Puget Sound in Washington State waters, rockfish abundance has declined considerably due to overfishing by hook and line, longline, and trawl fisheries (Williams et al. 2010; Yamanaka and Logan 2010). As part of a strategy to recover the overfished populations of yelloweye rockfish (S. ruberrimus) and quillback rockfish (S. maliger) in nearshore waters of British Columbia, 164 rockfish conservation areas (RCAs) that are closed to fishing were established in 2007. The boundaries were created based on the best-available bathymetry data at the time (100 m resolution), together with georeferenced catch data from recreational and industrial fishing (Yamanaka and Logan 2010).

Several studies have quantified the abundance of rockfishes in relation to habitat using visual, in situ methods employing a remotely operated vehicle (Rooper et al. 2010; Du Preez and Tunnicliffe 2011; Wedding and Yoklavich 2015; Haggarty et al. 2016b) and SCUBA diving (Marliave et al. 2009; Haggarty et al. 2017). More recently, these visual and SCUBA-derived abundance estimates have been related to very high-resolution (3 m) bathymetry data on California's central coast (Young et al. 2010; Wedding and Yoklavich 2015; Young and Carr 2015). While these studies have been informative about how rockfish use their habitat, most of these studies are limited to small spatial extents (i.e., less than 100 km), generally due to operational costs. Studies over large spatial extents are rare for groundfish species in general and for rockfishes in particular. However, two large-scale studies have been conducted in Pacific waters; a study in the Aleutian islands evaluated the relationship of Pacific ocean perch (Sebastes alutus) collected with bottom trawls with biotic and abiotic factors (Laman et al. 2015), and a recent study in the Gulf of Alaska assessed the strength of the relationship between juvenile fish of several demersal species in relation to habitat structure heterogeneity (Pirtle et al. 2017). An alternative approach to using visual survey data is to use fishery-independent catch data collected using bottom trawling (e.g., Rooper and Martin 2009; Laman et al. 2015) or longlines over multiple years and large spatial extents (100s of kilometres) to inform species distribution questions. These approaches could narrow the gap between fish ecology

(habitat associations) and fishery management decision-making, especially for spatially explicit harvest refugia (Guisan et al. 2013).

In this study, we combine medium-resolution (20 m) remote sensing imagery and multiyear fishery-independent longline survey catch data within a GIS framework to quantify relationships between fish presence–absence and abundance with habitat parameters using generalized linear mixed models (GLMMs) for presence–absence data and zero-inflated models for count data. While studies over large spatial extents combining fishery-independent data and derived bathymetric layers exist, to our knowledge this is one of the first studies conducted in British Columbia. The main objective of this study is to create informative models for spatial fishery management to achieve conservation objectives for rockfishes in inshore waters of British Columbia. To do so, we had two specific goals: (i) analyze relationships between benthic habitat characteristics derived from remote sensing with presence–absence and abundance data for two species of rockfishes, yelloweye and quillback, caught in research longline surveys and (ii) evaluate the performance of these species distribution models over large spatial extents.

Methods

Fish sampling

We used annual research longline survey catch data collected by Fisheries and Oceans Canada (DFO) as part of the Inshore Rockfish research and assessment program. Longline surveys were conducted in the summer (usually in August) during 21 consecutive days in inside waters of southern British Columbia for yelloweye and quillback stock assessments (Fig. 1). On even years (e.g., 2010), northern areas were sampled, while the southern waters were sampled in odd years. Usually four longline sets a day were fished, two in the morning and two in the afternoon. For this study, we used all the available survey data collected from 2003 to 2015, excluding 2006, when a survey was not conducted. Sites were chosen using depth-stratified sampling that classified two depths intervals, shallow (41–70 m) and deep (71–100 m). Each year, a predetermined number of 2 km × 2 km survey blocks for both shallow and deep depth intervals were randomly selected from a gridded map, and one longline set was fished within each selected block. When deploying the longline fishing gear, the aim was to fish on hard bottom to target rockfish (Yamanaka and Lacko 2004); however, this was not always accomplished over the entire length of the longline.

Each longline (~550 m in length) consists of 225 circle hooks baited with ~30 g of squid, each separated by approximately 2.67 m (8 feet) along a weighted groundline that is anchored at each end. Rockfishes are demersal and piscivorous (Love et al. 2002) and thus are attracted to bait mainly by visual cues. The longline gear used is similar to that used by the commercial fishery for rockfish and is selective for larger, adult fish. The longline was soaked for 2 h starting from the time of the last anchor deployed over the side of the fishing vessel when setting the gear until the first anchor was hauled on board the fishing vessel to retrieve the gear. Start and end points are recorded by the vessel's GPS system when the first and last anchor are set overboard (Yamanaka and Lacko 2004). All rockfish were weighed (g) and measured (total length, cm), dissected to determine sex and gonad maturity, and sampled for tissue and otolith samples for DNA and age analysis, respectively. For each set, presence or absence and abundance of each species were determined.

We created presence–absence and abundance data sets for all rockfish species caught and separately for yelloweye and quillback. We examined yelloweye and quillback independently because they occur throughout British Columbia and are caught in commercial longline fisheries. These rockfishes are the most valuable and abundant rockfish species caught on longlines (Table 1),

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Fig. 1. Map of the study area depicting all the sets fished from 2003 to 2015 (excluding 2006). Base map was provided by the Canadian Hydrographic Service (unpublished data).
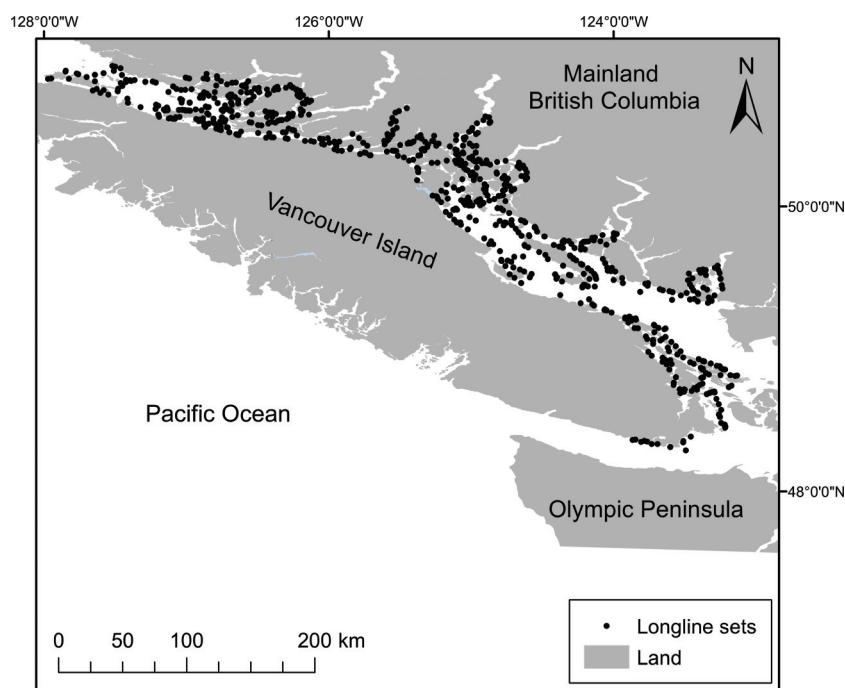
Table 1. List of rockfish species and total fish caught across all sampling years included in the study.

Rockfish	Species	Total abundance
Black	*Sebastes melanops*	12
Blue	*Sebastes mystinus*	4
Canary	*Sebastes pinniger*	150
China	*Sebastes nebulosus*	11
Copper	*Sebastes caurinus*	265
Greenstripped	*Sebastes elongatus*	177
Harlequin	*Sebastes variegatus*	2
Quillback	*Sebastes maliger*	4286
Redstripe	*Sebastes proriger*	10
Rosethorn	*Sebastes helvomaculatus*	6
Sharpchin	*Sebastes zacentrus*	2
Silvergray	*Sebastes brevispinis*	19
Tiger	*Sebastes nigrocinctus*	60
Vermelion	*Sebastes miniatus*	4
Widow	*Sebastes entomelas*	1
Yelloweye	*Sebastes ruberrimus*	2045
Yellowtail	*Sebastes flavidus*	54

and as a consequence, there has been considerable population declines due to overfishing (Yamanaka and Logan 2010).

Spatial data collection and processing

We used a 20 m² resolution DEM constructed from a combination of point sounded data and nautical charts provided by the Canadian Hydrographic Service under a sharing agreement. Such a DEM was used to obtain six different raster layers (see Haggarty and Yamanaka 2018 for complete methods), curvature, slope, rugosity, and bathymetric position index (BPI; see definitions in Table 2). To include potential latitudinal effects, we created a 20 m² spatial resolution latitude raster layer by kriging interpolation using the start latitudes from the sets surveyed. We calculated the area in square metres with the "tabular area" tool for four different substrates (rock, mixed coarse, sand, and mud) under each pixel that intersected each longline from a substrate

model (D. Haggarty, unpublished data). Finally, we calculated the Euclidean distance to rock and to mixed, coarse substrate from the same substrate model and produced two new raster layers (Table 2). If a longline overlapped a rock or mixed substrate, the distance was defined as zero.

To sample the raster layers at each longline location, we drew a straight line between the start and end coordinates with the "XY to line" tool in Arcmap 10.1. Next, we calculated the mean value of each habitat parameter for all cells that the longline intersected. We used this approach for two main reasons: first, because the length of a longline is greater than one pixel (20 m), and thus, sampling one unique pixel would not reflect the habitat characteristics under the entire line; second, because it provides a better habitat description for all the fish caught on the longline. A new data set with the mean value of each explanatory variable for each longline was created, together with the area (m²) of each substrate.

When overlaying the longline data sets with the bathymetry layer, some sites appeared to be on land rather than in the water (i.e., bathymetry values >0). To avoid this problem, we eliminated all sets with mean depth values <20 m, and thus our analysis included 743 sets across all years.

Statistical analyses

General modeling process

We used GLMMs with a binomial distribution and logit link function (Guisan et al. 2002; Zuur et al. 2009) to model presence–absence for total rockfishes, yelloweye, and quillback presence–absence. We used zero-inflated negative binomial (ZINB) models (Martin et al. 2005) to predict abundance because there was an excess of zeros in the three data sets (24%, 52.5%, and 32.8% of sets for total rockfish, yelloweye, and quillback, respectively). Prior to the modeling process, the explanatory variables were scaled and centered to have a mean of 0 and a standard deviation of 1 (Legendre and Legendre 2012) to obtain standardized effect sizes. Collinearity among predictor variables was tested, and highly correlated variables were not included in the same model. A global model including all explanatory variables was created, and alternative reduced models derived from the global model were used

Table 2. Description of the 11 explanatory variables derived from the digital elevation model and calculated from the substrate model (Haggarty and Yamanaka 2018) that were included in the modeling process for both the presence–absence and abundance analysis.

Variable	Definition
Depth (m)	Obtained from a digital elevation model; raster data set that contains elevation values for each pixel.
Curvature	Rate of change of the bathymetric slope (Haggarty and Yamanaka 2018). Negative values indicate a convex surface at that pixel; a positive value indicates a concave surface at that pixel; and a 0 indicates a flat surface.
Slope	Rate of change in depth between any given cell and the neighbour cells. Values are in degrees: the higher the value, the higher the slope.
Rugosity	Index of surface complexity calculated by dividing the contoured distance by the planar distance (Du Preez 2014). Values range between 0 (flat terrain) and 1 (high roughness).
Bathymetric Position Index*	
BBPI (500 m × 5000 m); MBPI (200 m × 200 m); FBPI (60 m × 500 m)	BBPI captures large characteristics within the landscape, while MBPI (medium BPI) captures features at a lower scale and FBPI (fine BPI) captures fine-scale bathymetric characteristics (Wright et al. 2012; Haggarty and Yamanaka 2018). Negative values describe valleys, positive BPI values are ridges, while 0 values are either flat surfaces or constant slopes.
Latitude	A raster data set that covers the entire study area where each cell has a latitude value.
Distance to rock	A raster data set that calculates the distance to rock substrate. Values are in metres.
Distance to mixed substrate	A raster data set that calculates the distance to mixed substrate. Values are in metres.
Substrate area	
Rock	Area (in m²) of bedrock and boulder under each longline.
Mixed substrate	Area (in m²) of cobble and gravel under each longline.
Sand	Area (in m²) of sand under each longline.
Mud	Area (in m²) of mud under each longline.

Note: All spatial variables had a 20 m spatial resolution, while the substrate area calculations were calculated in square metres.

*Inner and outer neighborhoods are shown in metres.

to determine the best model based on Akaike's information criterion (AIC). If two or more models were within two units of the best model, the model with the fewest explanatory covariates was chosen (Burnham and Anderson 2003). Once the best model was selected, the variance inflation factor (VIF) was computed to corroborate that the predictors within a model were not collinear (Zuur et al. 2007, 2009). Last, spatial autocorrelation in the residuals was evaluated for each of the best models by using semivariograms for presence–absence models and Moran-I correlograms for abundance models (refer to online Supplemental Material[1]). Spatial autocorrelation occurs when close values are more similar than values further apart. If spatial autocorrelation is present, the independence assumption is violated and the spatial structure must be accounted for to prevent this issue (Legendre 1993; Dormann et al. 2007). All GLMMs were fitted using the "lme4" package (Bates et al. 2015), while ZINB models were constructed in the "glmmAMD" package (Skaug et al. 2016). Spatial autocorrelation was evaluated with "ncf" and "gstat" packages (Benedikt et al. 2016; Bjornstad 2016). All analyses were conducted using R statistical software (R Core Team 2014).

Presence–absence

A site was classified as a "presence" if there was at least one rockfish, or yelloweye, or quillback, while an "absence" occurred when there were no rockfish caught on a longline. We randomly divided the data set into training data (70%, $n = 520$) and test data (30%, $n = 223$). Training data were used to model the response variable with the predictors, while test data were used to evaluate the accuracy of the models (Roberts et al. 2010; Young et al. 2010). The presence–absence data were analyzed in two separate steps. First, we used GLMMs to obtain the best model, and secondly, we used a generalized linear model (GLM) with the same terms of the GLMM but excluding the random effect (year) to construct a predictive raster layer using the Marine Geospatial Ecology Tools (MGET) in ArcGIS, because to date, MGET does not run predictive models with random effects. MGET is a toolset that incorporates ArcGIS with the R statistical package to create predictive raster layers from the modeling process (Roberts et al. 2010). However,

one limitation of the toolset is that it does not run GLMMs. There were no differences in the significance or direction of the relationship in the GLMM versus the GLM for all species (Fig. 2). We ran the GLM model with the training data and then created a predictive raster. For each species, the raster data set was reclassified with values of 1 (presence) and 0 (absence) with a cutoff of 0.7. This cutoff was selected based on the analysis of the receiver operating characteristics for true positives and true negatives (Iampietro et al. 2008) and are within the ranges used for similar species (Iampietro et al. 2008; Young et al. 2010). To test the accuracy of the model, we calculated the agreement between the training data and the test data with Cohen's Kappa statistic within the MGET toolset in ArcGIS (Roberts et al. 2010; Young et al. 2010). The Kappa index ranges from 0 to 1, whereby 1 is a perfect agreement between train and test data, while 0 represents no agreement between data sets. Values in between represent slight (0–0.2), fair (0.21–0.40), moderate (0.41–0.60), substantial (0.6–0.80), and almost perfect agreement (Landis and Koch 1977).

Abundance

The number of total rockfishes, yelloweye, and quillback were counted for each line, and the relationship to the environmental variables was modeled with ZINB. ZINB models have been demonstrated to improve the fit relative to Poisson or negative binomial distributions in the presence of excess of zeros (Potts and Elith 2006). We selected zero-inflated over hurdle models because we wanted to distinguish between false zeros and true zeros. False zeros occur when the habitat is suitable but a fish is not found, while true zeros can occur when the habitat is not suitable (Martin et al. 2005; Potts and Elith 2006).

Results

A total of 743 longline sets were fished between 2003 and 2015, 76% of which caught at least one rockfish. On average, 8.85 rockfish (SD = 10.81) per set were recorded, ranging from 0 to 60 individuals. Quillback were caught on 67.3% of sets, which was the most abundant species caught (4286 individuals) across all years

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Fig. 2. Standardized coefficients to predict probability of occurrence using both generalized linear model (GLM) and generalized linear mixed model (GLMM) approaches for (*a*) total rockfish, (*b*) yelloweye rockfish, and (*c*) quillback rockfish from inshore waters of southern British Columbia. Horizontal lines represent 95% confidence intervals. Positive values show a positive correlation, while negative values represent a negative relationship. Values are significant ($p < 0.05$) if confidence intervals do not overlap with 0 (vertical dashed line) and are represented with a circle, while variables that are nonsignificant are represented with a triangle.
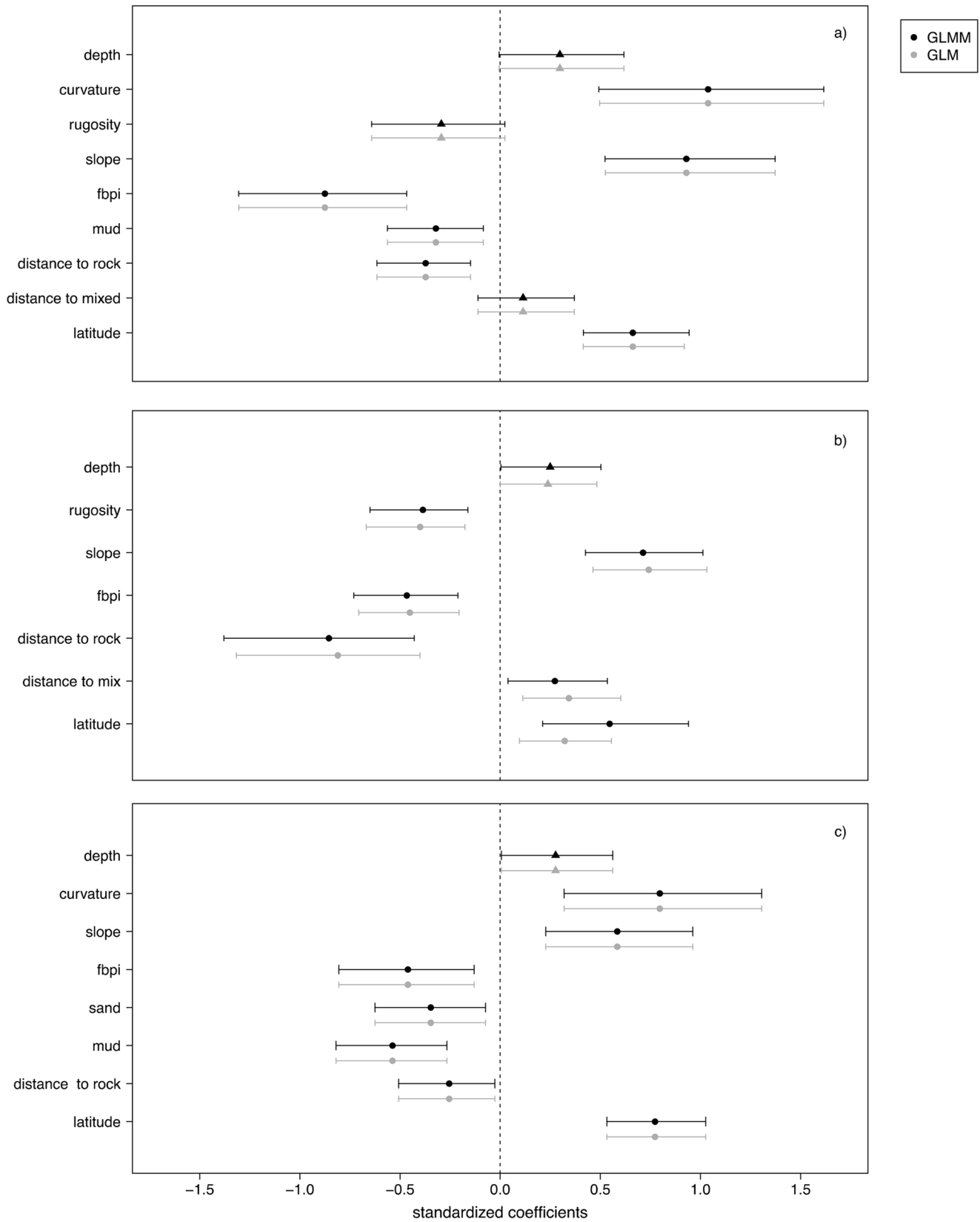
Fig. 3. Standardized coefficients of the predictor variables retained by the best binomial GLMM model based on AIC scores for (*a*) total rockfish, (*b*) yelloweye rockfish, and (*c*) quillback rockfish. Horizontal lines represent 95% confidence intervals. Positive values show a positive correlation, while negative values represent a negative relationship. Values are significant (*p* < 0.05) if confidence intervals do not overlap with zero (vertical dashed line) and are represented with a circle, while nonsignificant variables are represented with a triangle.
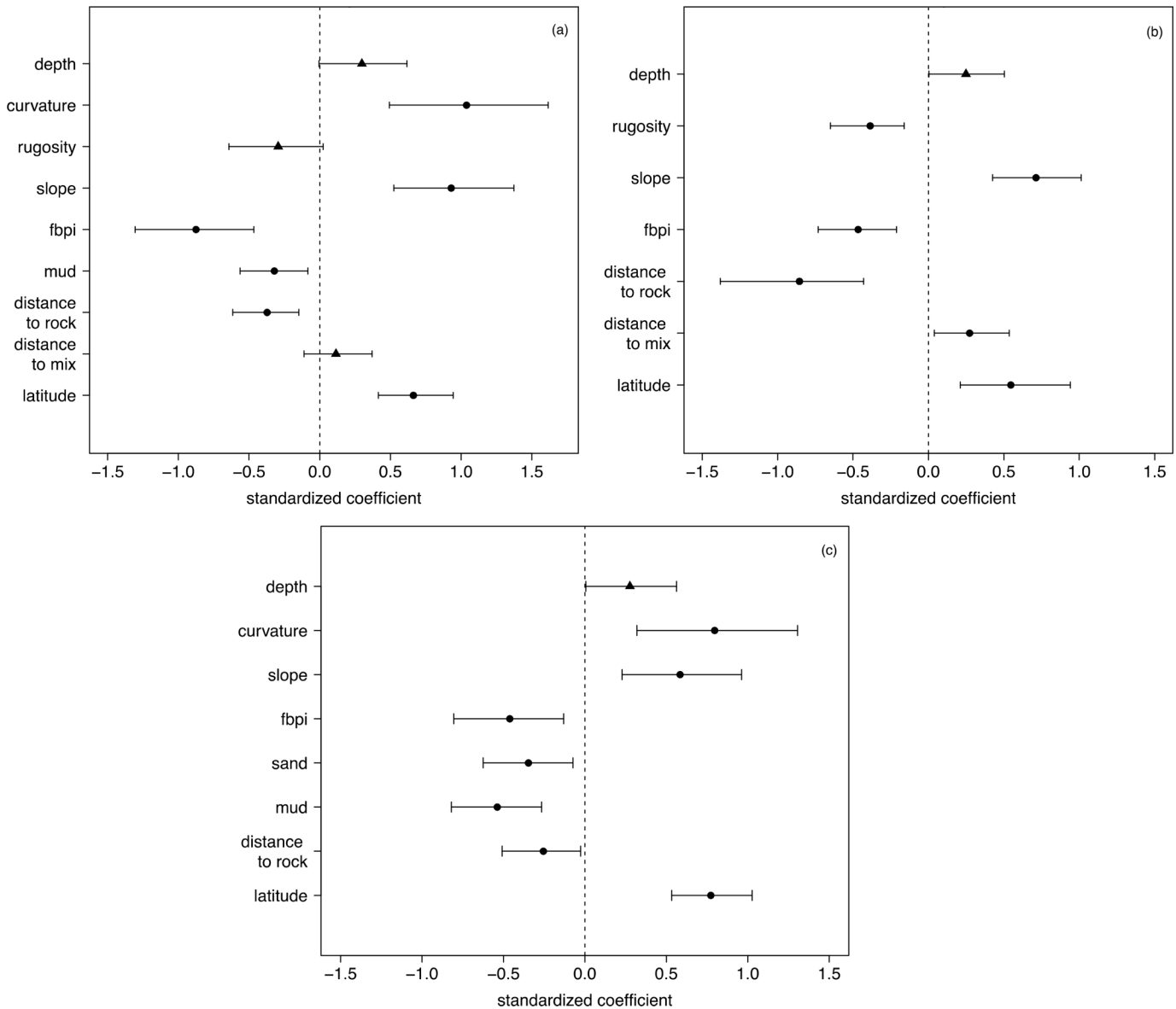
ranging from 0 to 56 individuals (mean = 5.37, SD = 7.98). Yelloweye were caught on 47.5% of the longlines and represented the second most abundant species (2045 individuals). The mean number of yelloweye per set was 2.53 (SD = 4.44). In total, 17 different rockfish species were caught across all years (Table 1). Rockfish species richness ranged from 0 to 8 species, with a mode of 3 rockfish species. The set with the highest richness (i.e., 8 species) was fished in 2007 where 47% of all reported species where caught.

Presence–absence models

For total rockfishes, the best model based on AIC scores retained nine predictors. (Fig. 3*a*). The probability of occurrence of any species of rockfish was positively related to curvature (1.04, 95% CI: 1.61, 0.49), slope (0.92, 95% CI: 1.37, 0.52), and latitude (0.66, 95% CI: 0.94, 0.41) while negatively correlated with mud area (−0.32, 95% CI: −0.08, −0.56), distance to rock (−0.37, 95% CI: −0.14, −0.61), and fine bathymetric position index (FBPI) (−0.37, 95% CI: −0.47, −1.3) (Fig. 3*a*). The Kappa index for the agreement between the test and train data was 0.46. Presence was correctly predicted at an 80% rate, while absences were predicted at 69.7%. Model accuracy was higher in Johnstone Strait and nearby inlets where a large proportion of presences was accurately predicted (Fig. 4*a*). The best model equation for total rockfishes is

$$\text{presence–absence} = 1.8 + (0.19 \times \text{depth}) + (1.05 \times \text{curvature}) - (0.34 \times \text{rugosity}) + (0.95 \times \text{slope}) - (1.01 \times \text{FBPI})$$
$$- (0.38 \times \text{distance to rock}) + (0.07 \times \text{distance to mix}) + (0.69 \times \text{latitude})$$

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Fig. 4. Maps of inshore waters of southern British Columbia showing locations where probability of occurrence is low (absence) and high (presence) based on the predictors from the GLM model for (*a*) total rockfish, (*b*) yelloweye rockfish, and (*c*) quillback rockfish. Insets depict zoomed-in areas, where black circles represent absence of rockfish, while white circles represent presence of rockfish. White circles overlaid on purple or black circles overlaid on brown show agreement between train and test data. In contrast, when white circles overlay a brown area or black circles overlay a purple area the agreement is incorrect (i.e., model prediction is poor). Base map was provided by the Canadian Hydrographic Service (unpublished data). [Colour online.]
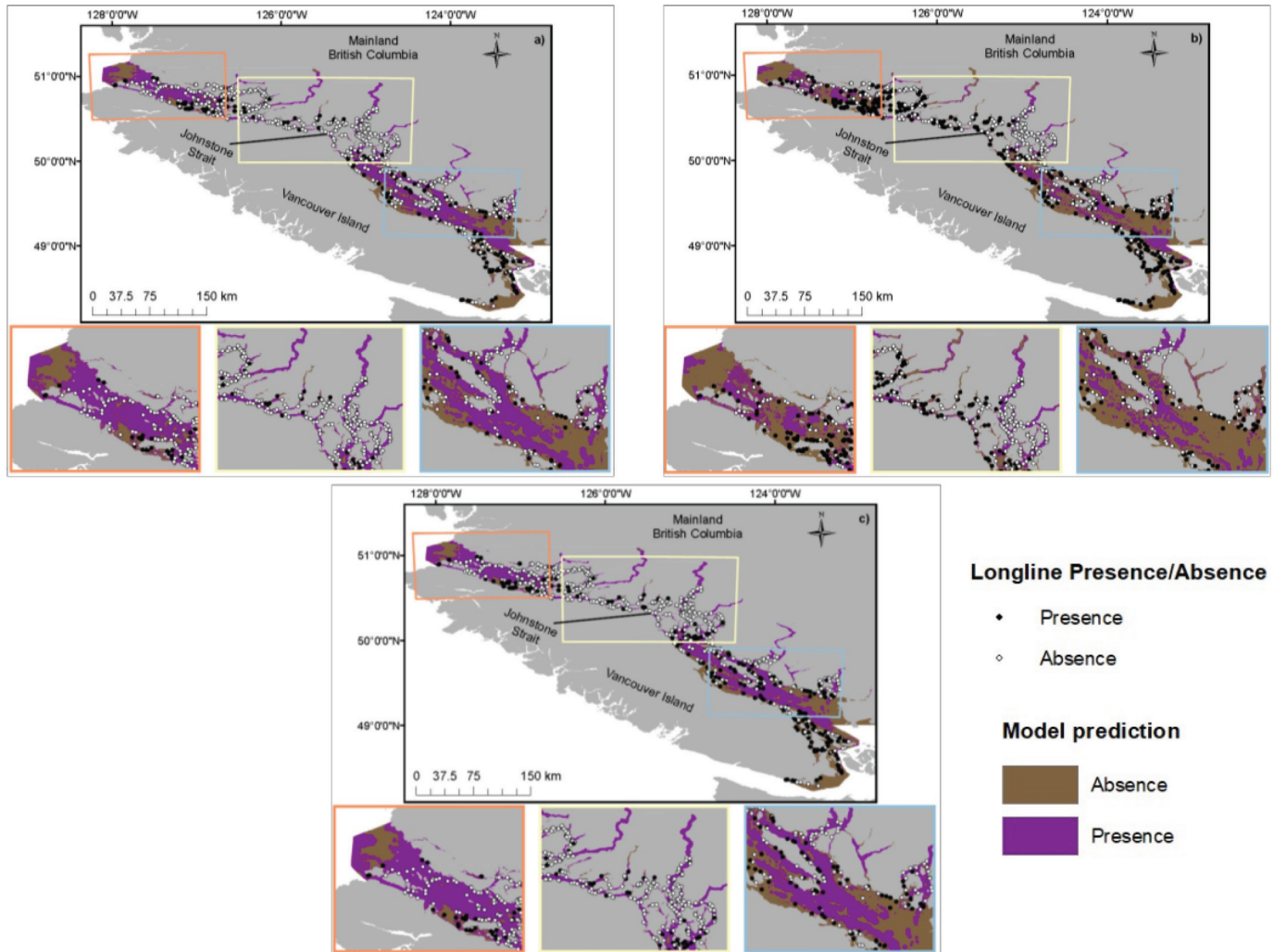
Based on AIC scores, the model for yelloweye retained seven covariates. Slope, latitude, and distance to mixed substrate were positively correlated with rugosity, while FBPI and distance to rock substrate were negatively correlated with the probability of occurrence. Though positive, distance to mix substrate showed a small effect size (0.27, 95% CI: 0.0039, 0.53), unlike in total rockfish. Rugosity was significant for yelloweye while nonsignificant for total rockfish, and the distance to rock effect size was larger in

yelloweye (−0.85, 95% CI: −0.43, −1.38) compared with total rockfish (−0.37, 95% CI: −0.15, −0.61) (Fig. 3*b*). The Kappa index for the agreement between the train and test data was 0.45. Yelloweye had a lower percentage of presences correctly predicted (68%) compared with absences (76%). Like for total rockfish, the majority of presence agreements for yelloweye were in the inlets in Johnstone Strait (Fig. 4*b*). The equation obtained for the best model for yelloweye is

$$\text{presence–absence} = -0.13 + (0.25 \times \text{depth}) - (0.38 \times \text{rugosity}) + (0.71 \times \text{slope}) - (0.47 \times \text{FBPI}) - (0.86 \times \text{distance to rock})$$
$$+ (0.27 \times \text{distance to mix}) + (0.55 \times \text{latitude})$$

The best model obtained by AIC for quillback showed that curvature (0.79, 95% CI: 0.32, 1.31), slope (0.58, CI: 0.23, 0.96), and latitude were positively correlated, while FBPI (−0.46, CI: −0.81, −0.13), sand, mud, and distance to rock had a negative relationship (Fig. 3*c*; also see equation below for quillback). The latitude effect was larger (0.77, 95% CI: 1.02, 0.53) than for total

rockfish (0.66, 95% CI: 0.94, 0.41) or yelloweye (0.55, 95% CI: 0.94, 0.21), while the distance to rock was significant, but the effect size was small (Fig. 3*c*). As for total rockfish and yelloweye, depth was not significant. The agreement between the train and test data based on the Kappa index was 0.49. Presence was correctly predicted 71.6% of the time, whereas absence was

predicted correctly 81.7% of the time. The greatest agreement between longline data and the model output was in Johnstone Strait, resembling the patterns observed for yelloweye and total rockfish (Fig. 4b). For the three species, and according to the predictors, there is more suitable habitat in northern waters and inlets of the inshore waters separating Vancouver Island from the mainland (Fig. 4). For quillback, the equation for the best model is

$$\text{presence–absence} = 1.03 + (0.28 \times \text{depth}) + (0.79 \times \text{curvature}) + (0.58 \times \text{slope}) - (0.46 \times \text{FBPI}) - (0.35 \times \text{sand area}) - (0.54 \times \text{mud area}) - (0.25 \times \text{distance to rock}) + (0.77 \times \text{latitude})$$

Abundance models

The best models obtained based on AIC scores retained six covariates for total rockfish, eight for yelloweye, and seven for quillback. Unlike for the presence–absence models, positive but weak relationships were observed between depth and total rockfish (0.11, 95% CI: 0.04, 0.18), yelloweye (0.13, 95% CI: 0.03, 0.24), and quillback (0.16, 95% CI: 0.08, 0.24) abundances (Fig. 5).

Slope showed a positive relationship with abundance for the three species, but was strongest for yelloweye (0.39, 95% CI: 0.26, 0.51) followed by total rockfish (0.95, 95% CI: 0.55, 1.39) and weakest for quillback (0.09, 95% CI: 0.009, 0.19). Similarly, abundance increased with latitude for all species, but the effect was largest for quillback (0.83, 95% CI: 0.63, 1.04). Yelloweye abundance peaked in the inlets of Johnstone Strait, while quillback abundance continued to increase northward (Fig. 6). However, the geographical location where the peak abundance was found was similar. Nonetheless, the maximum number of yelloweye (31) and quillback (56) per set also differed (Figs. 6b and 6c).

In contrast with latitude and slope, distance to rock had a strong negative effect for the three species, but was strongest for yelloweye (−0.61, 95% CI: −0.9, −0.33) relative to quillback and total rockfish, suggesting the importance of rocky habitat for rockfishes. FBPI showed a negative relationship with abundance for all three species, suggesting that abundance decreases in flat areas such as top of rocks. However, these effects were small in comparison with the effects of distance to rock (Fig. 5). The equations obtained from the best models based on the coefficient estimates are

$$\text{total rockfish abundance} = 2.0 + (0.11 \times \text{depth}) + (0.16 \times \text{slope}) - (0.07 \times \text{rugosity}) - (0.11 \times \text{FBPI}) - (0.44 \times \text{distance to rock}) + (0.43 \times \text{latitude})$$

$$\text{yelloweye abundance} = 0.57 + (0.13 \times \text{depth}) - (0.10 \times \text{curvature}) - (0.15 \times \text{FBPI}) - (0.08 \times \text{rugosity}) + (0.39 \times \text{slope}) - (0.61 \times \text{distance to rock}) + (0.14 \times \text{distance to mix}) + (0.37 \times \text{latitude})$$

$$\text{quillback abundance} = -40.31 + (0.16 \times \text{slope}) - (0.09 \times \text{FBPI}) - (0.09 \times \text{rugosity}) + (0.1 \times \text{slope}) - (0.045 \times \text{distance to rock}) - (0.09 \times \text{distance to mix}) + (0.83 \times \text{latitude})$$

Discussion

We found strong evidence for the importance of habitat heterogeneity for both presence–absence and abundance for total rockfish, yelloweye, and quillback. While there were some differences in the predictors obtained by presence–absence and abundance models, there are similar patterns across both approaches. For example, slope (except for quillback in zero-inflated models), FBPI, distance to rock, and latitude were consistently important predictors across species and model types.

The most noticeable difference between the two sets of models was the lack of significance of depth in the presence–absence approach, but its positive correlation in the abundance models. A possible explanation for the lack of significance of depth in the presence–absence models could be related to the sample design used in the longline surveys. The sets were divided into shallow (41–70 m) and deep (71–100 m), which does not span the entire depth range of yelloweye (up to 500 m) or quillback (up to 275 m) (Love et al. 2002). It also does not include the depth ranges of the other rockfish species included in the total rockfish category. In contrast, depth was a significant predictor for the probability of occurrence of three different adult rockfish species in Cordell Bank, California, using presence–absence data (Young et al. 2010) and for some juvenile demersal species in the Gulf of Alaska (Pirtle et al. 2017) with presence only data. However, a broader depth range was sampled in those studies compared with ours. When predicting abundance, depth had a positive effect, though the magnitude was small, for all three species. Our findings are consistent with the results obtained by Young and Carr (2015) using visual surveys in California for various rockfish species, by Williams and Ralston (2002) using trawl surveys in California and Oregon for a number of groundfish species including rockfish, and for Pacific ocean perch in the Aleutian islands (Laman et al. 2015). This suggests that abundance models are better than presence–absence models at highlighting a depth effect. Higher abundance in deeper waters could also be related to lower fishing pressure because deeper waters are harder to fish. As a consequence, depth may be a better predictor for other life history traits such as size, because many rockfish species migrate from shallow nursery habitats to deep habitats as they grow (Love et al. 1991; Johnson et al. 2003; Yamanaka et al. 2006a, 2006b; Pirtle et al. 2017). Unfortunately, the gear used and its selectivity for adults only allows us to describe adult rockfish habitat. As such, future studies should focus on sampling all age classes of rockfish together with well-known nursery areas such as seagrass meadows and kelp forests (Love et al. 1991). In doing so, the SDMs and resulting spatially explicit conservation plans would become more robust.

FBPI was defined by a 60 m inner radius and 500 m outer radius (Table 2) and was retained as an important covariate for all species. This suggests that over this scale, the terrain's habitat heterogeneity (Lundblad et al. 2006) is related to rockfish occurrence and abundance within inshore waters of southern British Columbia. While BPIs at different scales can describe different habitat types (Young et al. 2010; Pirtle et al. 2017), FBPI may be the most accurate for rockfish species in inshore waters of British Columbia because of their small home ranges. As such, BPIs at local

Fig. 5. Standardized coefficients for the count portion of the best zero-inflated model based on the AIC scores for (*a*) total rockfish, (*b*) yelloweye rockfish, and (*c*) quillback rockfish. Horizontal lines represent 95% confidence intervals. Positive values show a positive correlation, while negative values represent a negative relationship. Values are significant ($p < 0.05$) if confidence intervals do not overlap with 0 (vertical dashed line) and are represented with a black circle, while variables that are not significant are represented with a black triangle.
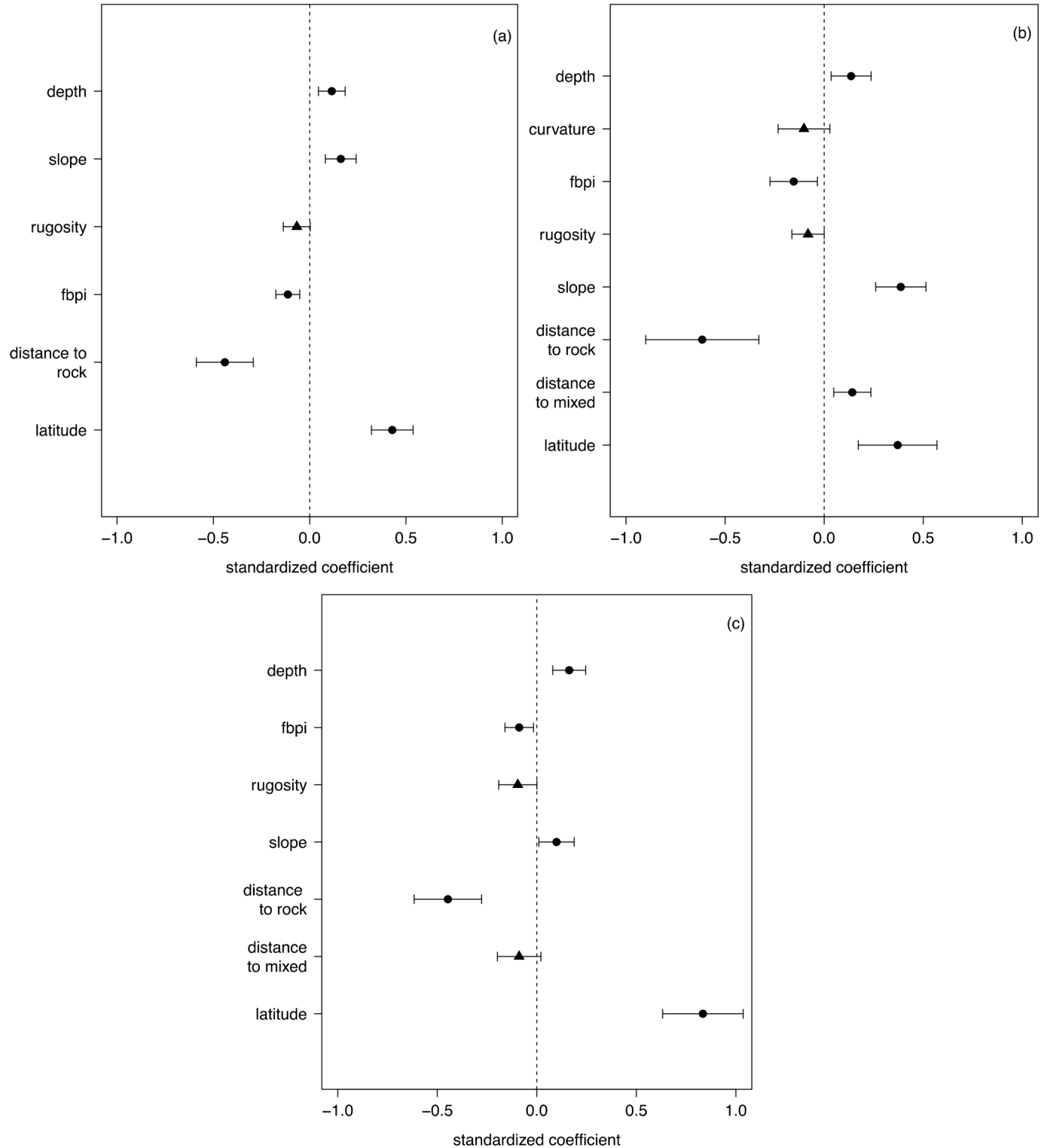

scales can better describe their habitat compared with BPI at medium and large scales in our study area.

Areas with steeper slopes better predicted the occurrence and had higher abundance for the three data sets. The magnitude of the effect was largest for yelloweye and second for quillback. Un-

derwater video observations (UVOs) of yelloweye and quillback have found them on vertical walls in complex habitats in Alaska (Johnson et al. 2003), while other rockfish species have also been associated with vertical habitats in Monterey Bay, California (Yoklavich et al. 1999), and British Columbia (Richards 1986),

Fig. 6. Spatial distribution and abundance of (*a*) total rockfish, (*b*) yelloweye rockfish, and (*c*) quillback rockfish in inshore waters of southern British Columbia. Insets depict zoomed-in areas. Base map was provided by the Canadian Hydrographic Service (unpublished data). [Colour online.]
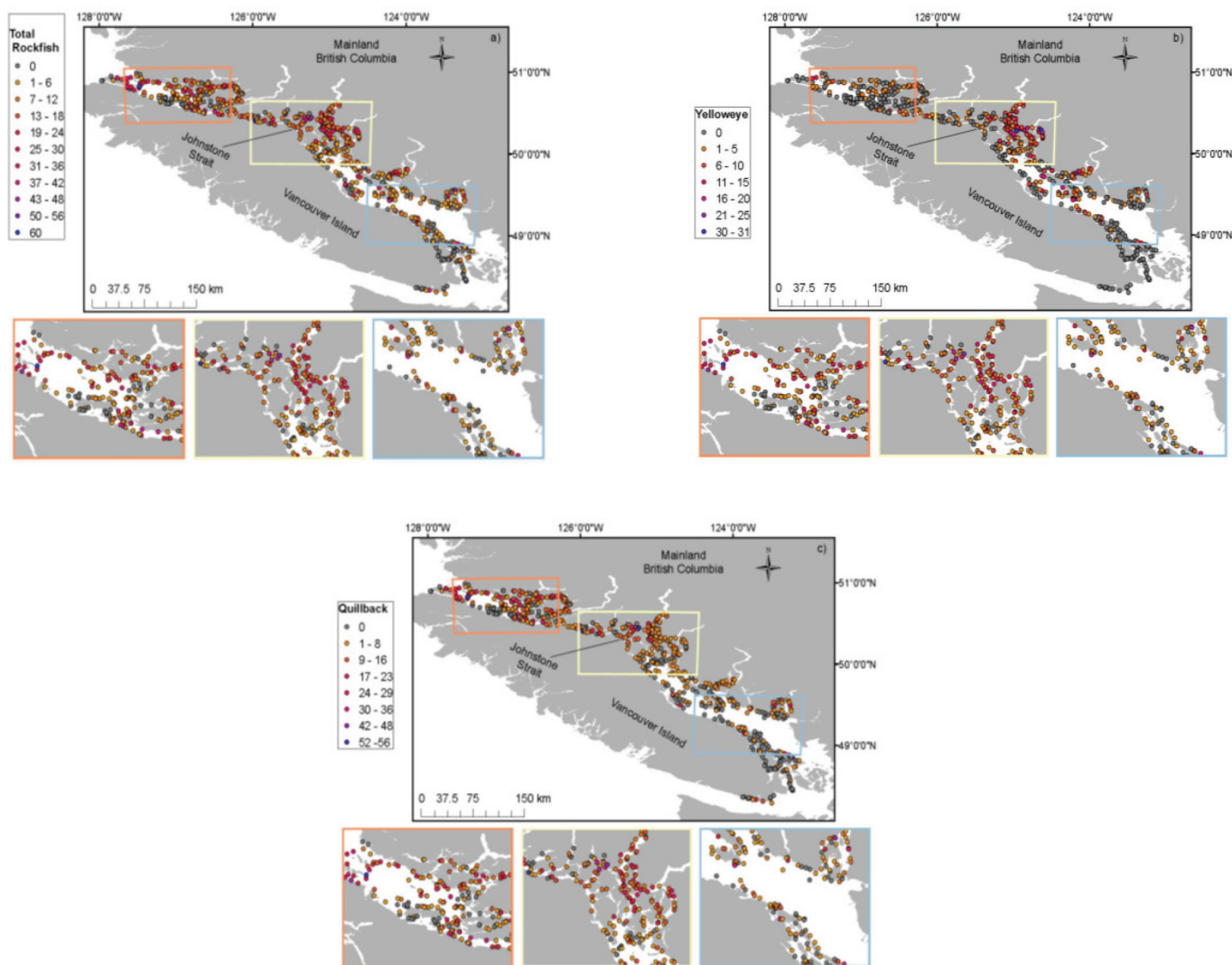
likely because many of these habitats have crevices that are used as refuges (Yoklavich et al. 1999). Given the geology of our study area, it is likely that the areas of high slope are areas of rock walls, and while the number of crevices are not visible with remote sensing techniques, our results were consistent with studies conducted with UVO in similar areas in British Columbia and California.

Occurrence and abundance of total rockfish, yelloweye, and quillback decrease as the distance to rock increases. Young et al. (2010) found a similar relationship for yellowtail rockfish (*Sebastes flavidus*) and rosy rockfish (*Sebastes rosaceus*) in Cordell Bank, California. Similarly, many studies conducted by UVO have found that many species of rockfish are associated with boulder and bedrock in larger densities than in less complex habitats (O'Connell and Carlile 1993; Yoklavich et al. 1999; Johnson et al. 2003).

Both the probability of occurrence and abundance increased with latitude for the three data sets. Although the predictive raster layers (Fig. 4) show suitable habitat in the south, the probability of occurrence was low. Similarly, abundance for total rockfish, yelloweye, and quillback were lower in the south, where many longline sets failed to catch rockfish. However, the pattern differed between yelloweye and quillback rockfish in more northern

latitudes; although both yelloweye and quillback abundance peaked in the Johnstone Strait inlets, quillback abundance continued to be high northward (Fig. 6), explaining the larger effect size of latitude for quillback with respect to yelloweye. One possible explanation for this pattern is that latitude is correlated with other important environmental variables (Young and Carr 2015) not accounted for in this study. Indeed, the inshore waters of southern British Columbia have complex oceanographic dynamics (Burd et al. 2008) driven by freshwater flows (e.g., from the Fraser River) and tidal regimes that could explain such patterns. However, studies in Alaska have shown that yelloweye and quillback are tolerant of fluctuating oceanographic conditions (Johnson et al. 2003). An alternative and perhaps more plausible explanation is that southern Vancouver Island and the British Columbia mainland have a higher human population than northern latitudes, which may have negatively impacted rockfish populations by exerting a larger fishing pressure and (or) other types of human stressors (Frid et al. 2016). Such patterns have also been suggested in Alaska's inshore waters to explain rockfish distribution (Johnson et al. 2003).

All of our Kappa values for the presence–absence models fell within 0.41 and 0.60, suggesting moderate agreement between

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training and test data (Landis and Koch 1977). These values were lower than those measured for UVO observations of Yellowtail and rosy rockfish in California, where almost perfect agreement between train and test data were obtained (Young et al. 2010). Instead, our Kappa values (0.42) were similar (0.39 and 0.54) to those obtained for quillback and yelloweye by Iampietro et al. (2008) but in a different study site and sampling with remotely operated vehicles, a different UVO sampling technique. Differences in agreement may be a function of both the DEM resolution and the sampling technique. For example, with UVO exact coordinates for presence–absence can be extracted and then related to high-resolution DEMs (e.g., 3 m). We did not relate hook by hook to a specific pixel in the bathymetry and derived layers. Rather, we estimated an average under the pixels that intersected the line for each layer. Although high-resolution DEMs have been successfully used in California to model occurrence and abundance of some rockfish species (Young et al. 2010; Wedding and Yoklavich 2015; Young and Carr 2015), coarse (100 m) resolution DEMs have been as successful to model Pacific ocean perch in Alaska (Laman et al. 2015). The medium-resolution DEM (20 m) used in our study also proved to be successful for rockfish species. In fact, the scale of the DEM used does not seem to be as important as the scales of the ecological processes observed. For example, high-resolution DEM is extremely effective at small extents whereby interspecific interactions are observed, while medium-resolution DEMs at large extents (100s of kilometres) provide a larger overall picture of the species' distribution in an area (Guisan and Thuiller 2005). Increased Kappa values can be obtained by validating the model with in situ ground-truth data as opposed to using the 30% randomly selected test data from the whole data set. The test data are subject to the same sampling bias as the train data because they are not independent from the data set (Rooper et al. 2016).

An advantage of our study is that we were able to assess rockfish distribution and abundance at a much larger spatial extent relative to studies conducted with UVO surveys. While large spatial extent studies could be possible with UVO, a major limitation to this approach is the high costs of transporting and operating the underwater vehicle compared with obtaining the fishery-independent data because surveys are annually conducted for stock assessment purposes. However, studies conducted with UVO techniques may classify rockfish habitats as biogenic or abiotic (Du Preez and Tunnicliffe 2011), thus providing additional resolution to habitat. Nonetheless, the development of algorithms to predict accurately some of the habitat characteristics observable with visual techniques has improved considerably and has helped to characterize habitat based on remotely sensed data.

While longline surveys have some advantages over UVOs, this methodology has some limitations. For example, these particular longline surveys cause 100% rockfish mortality. Although the surveys were conducted for stock assessment purposes and thus all fish where kept for biological sampling, rockfish survival rate would be low due to barotrauma (Hannah and Matteson 2007). The anchors and the line may cause some habitat destruction that may affect demersal fish communities; however, this effect is low compared with bottom trawling. Longline catch rates can also be affected by oceanographic variables such as currents. For example, when the line is set in the same direction of the water currents, catches decline but when lines are set in the opposite direction of the current, catch rates increase because fish are more likely to sense the bait plume (Løkkeborg and Pina 1997). While seafloor impact is minor with UVOs, fish behavior may be modified by the underwater vehicle, affecting the fish count and resulting in over- or underestimations (Wedding and Yoklavich 2015). Conversely, UVOs allows for a larger fish size class sampling compared with the narrow size class obtained with selective fishing gear. The longline data used to construct these models are biased towards large fish because they sample adult rockfish in deep habitats. As a result, other habitats that may also contain

rockfish species are likely undersampled. For example, Laman et al. (2015) found that vertical biogenic habitat was important to predict abundance for Pacific ocean perch by sampling habitats with trawl surveys. As such, untrawlable habitats like rocky habitats were not sampled. There are trade-offs in the sampling methods used and the habitats sampled that can affect model performance.

Our results are important for rockfish conservation and marine spatial planning in British Columbia waters. We identified suitable habitat based on rockfish occurrence and abundance, and such habitats can be considered for spatial population recovery purposes. This information can be used to create new RCAs or reevaluate and reconfigure existing RCA boundaries. To date, RCAs in inshore waters of southern British Columbia have not contributed substantially to the recovery of rockfish populations in the southern areas of the coast (Haggarty et al. 2016b). However, there is some evidence of recovery in British Columbia's central coast (Frid et al. 2016). On the British Columbia southern coast there is lack of compliance by fishers to RCA regulations, and this may be a factor affecting rockfish population recovery (Lancaster et al. 2015; Haggarty et al. 2016a; Lancaster et al. 2017). It is also possible that RCAs may need more time to show recovery because rockfish are very long-lived. These study findings also contribute to describe rockfish habitat better, which is a critical aspect of ecosystem-based fishery management (EBFM). EBFM includes habitat, species interactions, and environmental variables in a common framework to better manage target species (Pikitch et al. 2004). As a result, an enhanced rockfish habitat understanding provides valuable information towards achieving an EBFM. These models and SDMs in general can have a positive impact on EBFM by expanding our knowledge of the species use of the ecosystem. While SDMs can be used as powerful information tools for conservation and management purposes by decision makers, these tools require articulate discussions among managers, decision makers, and scientists to properly fine-tune the models and better exploit such tools (Guisan et al. 2013).

Our study is one of the first studies to integrate multiyear fishery-independent longline catch data and remote sensed imagery at large spatial extents (100s of kilometres) to predict the probability of rockfish occurrence and abundance. We found that total rockfish, yelloweye, and quillback are strongly related to habitat heterogeneity in inshore waters of southern British Columbia. These findings confirm the importance of rock and habitat heterogeneity for demersal species of the genus *Sebastes*, particularly yelloweye and quillback rockfish. The moderate agreement (Kappa values) between test and train data highlights the convenience of using inexpensive sampling techniques such as research longline surveys to sample large spatial extents and yet have accurate models to use for spatial planning and conservation purposes. Overall, our results are critical for marine spatial planning and conservation decision makers in Canada and will help efforts to improve rockfish spatial management and conservation.

Acknowledgements

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