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Are fish associations with corals and sponges more than an affinity to structure? Evidence across two widely divergent ecosystems

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Abstract: The role of deep-sea coral and sponge ecosystems as habitat for marine fishes has been widely studied, with many finding significant associations, especially for rockfishes. However, rockfishes also thrive in areas largely devoid of corals and sponges. We compared the use of deep-sea corals and sponges by fish species in two ecosystems. Rockfishes (*Sebastes* spp.) and Pacific cod (*Gadus macrocephalus*) densities were significantly correlated to structured seafloors at the scale of transects across both regions. Regional effects were not significant for most rockfish species and Pacific cod. At smaller scales only Pacific cod and rockfishes had significant associations with structure. The size of the individual fish and the size of the structure both had significant impacts on the distance of fish from structure, with smaller fish closer to structure and closer to smaller structure. Over half of the individual fishes surveyed were associated with sponges. The implication of this research is that the presence of structure increases the density of rockfishes, and removal of deep-sea corals and sponges is likely to reduce the overall density of rockfishes.

Résumé : Le rôle des écosystèmes de coraux et d'éponges d'eau profonde comme habitat pour les poissons marins a été largement étudié, de nombreuses études relevant des associations significatives, en particulier avec des sébastes. Cependant, ces derniers occupent aussi des zones largement exemptes de coraux et éponges. Nous avons comparé l'utilisation de coraux et éponges d'eau profonde par différentes espèces de poissons dans deux écosystèmes. Les densités de sébastes (*Sebastes* spp.) et de morues du Pacifique (*Gadus macrocephalus*) sont significativement corrélées à des fonds marins structurés à l'échelle de transects traversant les deux régions. Les effets régionaux ne sont pas significatifs pour la plupart des espèces de sébastes et pour la morue du Pacifique. Ce n'est qu'à de plus petites échelles que la morue du Pacifique et les sébastes présentent des associations significatives avec la structure. La taille des poissons et la taille de la structure ont toutes deux des effets significatifs sur la distance séparant les poissons de la structure, les poissons plus petits se trouvant plus près de structures et plus près de structures plus petites. Plus de la moitié des poissons recensés présentent une association avec des éponges. La conclusion de l'étude est que la présence de structures accroît la densité de sébastes et que le retrait de coraux et d'éponges d'eau profonde se traduira probablement par une réduction de la densité globale de sébastes. [Traduit par la Rédaction]

Introduction

The association of deep-sea coral and sponge ecosystems with demersal marine fish and invertebrates has been widely studied. Broad-scale data sets, such as bottom trawl survey catches across large regions, have linked increased catches of many species of demersal fishes with increased catches of corals and (or) sponges (Rooper and Boldt 2005; Malecha et al. 2005; Kenchington et al. 2013; Laman et al. 2015). In Alaska, evidence from bottom trawl surveys suggests benthic-associated loosely schooling fishes, such as Atka mackerel (*Pleurogrammus monopterygius*) and Pacific ocean perch (*Sebastes alutus*), solitary demersal fishes, such as rougheye (*Sebastes aleutianus*), blackspotted rockfish (*Sebastes melanostictus*), and even flatfishes have been found to have higher catches in the presence of benthic invertebrates (Heifetz 2002; Malecha et al. 2005; Rooper and Martin 2012). Smaller-scale studies conducted with underwater cameras and underwater vehicles have also found associations between some fishes and corals–sponges (Auster 2005; Du Preez and Tunnicliffe 2011; Beazley et al. 2013; Linley et al. 2017). The specific mechanistic links between demersal fishes and structured benthic habitats are generally unresolved, but struc-

tured habitat, such as corals and sponges, has been documented as spawning substrates for some demersal fish species (Busby et al. 2006, 2012; Lauth et al. 2007; Baillon et al. 2012). The presence of corals and sponges has also been suggested to reflect or contribute to areas of higher productivity, possibly leading to enhanced feeding opportunities for demersal fish species that occur there (White et al. 2005). However, the majority of studies examining mechanistic links for an association between structured habitats and demersal fish species have focused on their role as refuges from predation, especially for juvenile life history stages (Love et al. 1991; Gotceitas et al. 1995; Ryer et al. 2004; Auster 2005; Pirtle et al. 2012). It is likely that multiple mechanisms may be resulting in observed associations between demersal fishes and structured habitat.

It is unclear to what degree observed associations of fishes with deep-sea corals and sponges are obligate for the fishes. For example, in areas where corals and sponges are sparse, but high-relief habitats occur, juvenile rockfishes (*Sebastes* spp.) are often common (Carlson and Straty 1981; Love et al. 2012). Additionally, an examination of individual invertebrates found fewer than 1% of

Fig. 1. Study areas of the eastern Bering Sea and Aleutian Islands large marine ecosystems in Alaska. Dots represent locations of underwater stereo-camera transects (n = 466) conducted in 2012 and 2014.

their associations were with fish and overall there were low levels of associations between fishes and invertebrates, with only 5.6% of fish species associated with invertebrates (Tissot et al. 2006). This result has led to some debate over the importance of the role that deep-sea corals and sponges play in the survival and productivity of their associated fishes (Cartes et al. 2013).

A further question with studies of habitat associations of rockfishes is the role of ontogeny or size in these associations. Juvenile and small rockfishes are the most commonly cited fish with tight associations with corals, sponges, and other complex habitats (Pearcy et al. 1989; Rooper et al. 2007; Laidig et al. 2009; Love et al. 2009; Love et al. 2012), whereas adult fishes of the same species may sometimes be found in association with bare sand habitats (Conrath et al., in press). However, there is also evidence for larger fishes being observed in association with the most complex habitats available (Yoklavich et al. 2000). The interaction between the size of fishes and the size or complexity of seafloor structure is also not well defined for most species groups. In part, the mixed results across a range of studies examining associations with deep-sea corals and sponges may reflect differences inherent among ecosystems and among species examined. For example, the majority of studies on rockfish associations with deep-sea corals and sponges have been completed in California and on the US west coast, which has >60 species of rockfishes, many of which have very different life history and habitat requirements (Love and Yoklavich 2006). The California region is also relatively depauperate in terms of deep-sea corals and sponges, when compared with the rest of the US west coast, British Columbia, and parts of Alaska (Hourigan et al. 2017).

Two ecosystems in Alaska, the eastern Bering Sea and the Aleutian Islands, share a number of commercially important fish and invertebrate species. These ecosystems also have very different seafloor characteristics, with the Aleutian Islands dominated by rocky hard substrates (Goddard et al. 2017; Wilborn et al. 2018) and the eastern Bering Sea dominated by unconsolidated substrates (Goddard et al. 2016; Rooper et al. 2016). Physical characteristics,

such as tidal currents, also vary (Ladd et al. 2005). Importantly for this comparison, the two systems have roughly two orders of magnitude difference in the overall abundance of corals and sponges (Rooper et al. 2016; Wilborn et al. 2018). The Aleutian Islands is home to some of the highest deep-sea coral and sponge densities and diversity in the world (Stone 2006; Stone et al. 2011), while the eastern Bering Sea has far less dense corals and sponges and far fewer species (Rooper et al. 2016; Stone and Rooper 2017).

Thus, the objective of this study was to compare transect-scale and individual-scale association of a wide variety of benthic and semipelagic fish species with benthic structure including deep-sea corals and sponges across two ecosystems. The goal was to determine whether different kinds of structure (e.g., rocks, emergent epifauna, or combinations of both) were equally associated with fishes. A secondary goal was to examine the association of fishes with seafloor structure of different sizes and to assess the levels of fish–structure association by fish size. Based on previously published research, we hypothesized that (*i*) the density of some species of fishes (especially rockfishes) would be higher where structure occurred, (*ii*) smaller individual fish would be closer to structure, (*iii*) larger structure would be associated with larger or more fishes, and (*iv*) fish would not prefer one type of structure over another. We conducted these analyses on two different scales by first testing whether there were significant habitat associations on a transect level for species shared across eastern Bering Sea and Aleutian Islands ecosystems. Then we tested for significant associations with seafloor structure for randomly selected individual fish by species and also compared these results between the two ecosystems.

Methods

Study areas
This study compares in situ observations from two of Alaska's large marine ecosystems, the eastern Bering Sea (EBS) and Aleutian Islands (AI) (Fig. 1). The EBS is dominated by a broad, shallow

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continental shelf that stretches east to west from the Alaska mainland to the shelf break roughly 700 km away (Fig. 1). The EBS shelf is commonly divided into three domains based on bathymetry and oceanographic fronts: the inner shelf (0 to 50 m), the middle shelf (50 to 100 m), and the outer shelf (100 to 180 m) (Coachman 1986). The shelf break is typically at 180 to 200 m depth, except at the northern edge of Bering Canyon, where the shelf break is at 500 m (Sigler et al. 2015). The seafloor substrates of the EBS are dominated by fine unconsolidated sediments (Smith and McConnaughey 1999; Rooper et al. 2016). This study focuses on the outer shelf and slope regions of the EBS.

Alaska's AI is an arc of volcanic islands that extend over 1700 km westward from the Alaska Peninsula, separating the North Pacific Ocean to the south from the Bering Sea to the north (Fig. 1). A generally steep continental slope borders the southern sides of the island chain, and the continental shelf is relatively deep (250 m). Substrates vary regionally along the island chain, from highly rugose rock walls, boulders, and bedrock to relatively flat sandy bottoms. Some form of hard bottom sediments comprise about 37% of the seafloor of the AI (Wilborn et al. 2018). Oceanic conditions dominate the area west of Samalga Pass (170°W), whereas the Alaska Coastal Stream brings lower salinity and higher velocities, heavily influencing environmental parameters along the coast east of Samalga Pass (Stabeno et al. 2002; Ladd et al. 2005). The Alaska Coastal Stream and Alaska Coastal Current flow westward on the Pacific side of the AI, while the Aleutian North Slope Current flows eastward on the Bering Sea side of the archipelago. Water transport through the many deep interisland passes moves mainly northward into the Bering Sea, but large tidal currents create a spatially and temporally complex environment in the areas immediately adjacent to the passes (Ladd et al. 2005).

Study design

Three research cruises were conducted from 14 to 28 August 2012 and 22 April to 13 May 2014 in the AI and from 8 August to 6 September 2014 in the EBS (see Goddard et al. 2016, 2017 for detailed transect descriptions). A total of 216 station locations were sampled from 2012 to 2014 in the AI and 250 stations were sampled in 2014 in the EBS (Fig. 1). These stations were randomly chosen within depth and (or) area strata based on a standard grid (1 ha) that was overlaid on each of the study areas.

The primary sampling tools for this study were two calibrated stereo drop-cameras deployed from a chartered fishing vessel (see Williams et al. 2010; Rooper et al. 2016; and Wilborn et al. 2018 for details on these systems). At each randomly chosen station, the drop-camera was deployed at the center of the grid cell and lowered to the seafloor. Once seafloor contact was made, the drop-camera drifted or was towed along the bottom for 15 min at a speed of 0.08–6.07 km·h⁻¹ (0.05–3.28 knots) in the direction of the prevailing current. The drop-camera was held approximately 1–2 m above the substrate with the cameras pointed slightly downward at an angle of approximately 35° off parallel to the seafloor. The position of the camera throughout the deployment was assumed to be the same as the research vessel's GPS. The deployment cable was held as near vertical as possible to improve positional accuracy, given weather and wind conditions. The distances traveled during deployments ranged from 21 to 1476 m (mean = 385 m, SE = 8.2 m). Only nine tows were less than 100 m long, and these were the result of equipment failure (such as dying batteries). Eighty percent of the deployments sampled distances between 200 and 600 m.

Transect-level image analyses

Postcruise image analysis was conducted to determine substrate types, species densities, and sizes of organisms for each transect. Image pairs collected at 1 s intervals during each deployment were viewed using SEBASTES stereo-image processing software developed in the Python programming language (Williams et al. 2016). To compute range and size information, we calibrated the cameras to correct for image distortion due to the lens and viewport optics and to solve for the epipolar geometry between the two cameras (Williams et al. 2010, 2016). The image analysis software then determined the three-dimensional coordinates corresponding to points identified in stereo-image pairs using a stereo-triangulation function. All measurements were made using the calibrated stereo-image pairs and SEBASTES software.

Structure-forming invertebrates (e.g., corals, sponges, and sea whips and sea pens (pennatulaceans)), fishes, and crabs were identified to the lowest possible taxonomic level and counted for each transect. The lowest possible taxonomic level was typically genus for corals and sea whips and order for sponges (Stone et al. 2011; Stone 2014; R. Stone, Alaska Fisheries Science Center, personal communication). Although sea whips (family Halipteridae) and sea pens (family Pennatulidae) are in the subclass containing corals (Octocorallia), sea whips and sea pens were considered separately from other corals due to differences in substrate preferences. Corals from the suborders Holaxonia (family Plexauridae) and Calcaxonia (families Primnoidae and Isididae) are found predominantly on rocky substrates (cobble, boulder, or exposed bedrock), while sea whips and sea pens have a preference for sandy, unconsolidated substrates. Careful examination and accounting of individual targets in adjacent frames ensured that objects were only counted once. Demosponges on 38 transects, corals on 20 transects, and hydrocorals on one transect were too numerous to individually count, so 135 image pairs were randomly subsampled and all of the individual sponges in these frames were enumerated and expanded to the unsampled frames. Sponges less than 10 cm (EBS) or 20 cm (AI) in height were difficult to discern from other small white- or yellow-colored items on the seafloor. To make the data comparable, we used the size distribution data from transects in the EBS to correct the abundance of sponges for the 10–20 cm individuals by removing the proportion of sponges in this size class from the transect. Thus, the sponge abundance used in the analyses of transect-scale data represents the density of individuals > 20 cm in height in both ecosystems.

The fish and crabs that were analyzed for associations at the transect scale are shown in Table 1. Species that were difficult to positively identify were combined into genus-level taxonomic groups, such as the arrowtooth and Kamchatka flounders (genus *Atheresthes*). For these transect-scale analyses, the unidentified rockfishes and the other rockfish groupings presented in Table 1 were also summed into a combined *Sebastes* spp. grouping.

Densities (no. of individuals·m⁻²) of individual taxa were calculated by dividing the count of the taxa on a transect by the area swept (distance observed × path width observed) on that transect. The median range (in cm) of all objects measured on a transect was assumed to be the distance from the camera where 100% of fishes and invertebrates were detected for that transect (Rooper et al. 2016). A swath width at the median range was calculated by combining the known viewing angle for each camera (fixed by the camera lens) and the median range to objects on a transect. The mean path width across all transects was 3.42 m (SE = 0.04 m), with a minimum of 1.55 m and a maximum of 6.32 m for any individual transect. The area viewed on each transect ranged from 80 to 4226 m² and averaged 1321 m² (SE = 33 m²).

The substrate observed in the underwater video transects was classified by a commonly used seafloor substratum classification scheme (Stein et al. 1992; Yoklavich et al. 2000) that consists of a two-letter coding of substratum type denoting a primary substratum with >50% coverage of the seafloor and a secondary substratum with 20%–49% coverage of the seafloor. There were eight identified substratum types: mud (M), sand (S), gravel–pebble (G, diameter < 6.5 cm), mixed coarse material (MC), cobble (C, 6.5 cm < diameter < 25.5 cm), boulder (B, diameter > 25.5 cm), exposed low relief bedrock (R), and exposed high relief bedrock (K).

Table 1. Sample sizes (numbers of fish) for each species (or group of species) used for analysis of individual fish habitat associations.

Common name(s)	Species name	Aleutian Islands	Eastern Bering Sea
Arrowtooth and Kamchatka flounders	***Atheresthes* spp.**	40	48
Blackspotted and rougheye rockfishes	*Sebastes melanostictus* and *Sebastes aleutianus*	18	14
Tanner and snow crabs	***Chionoecetes* spp.**	22	49
Giant grenadier	*Albatrossia pectoralis*	48	50
Pacific halibut	*Hippoglossoides stenolepis*	39	33
Northern rockfish	*Sebastes polyspinis*	135	65
Pacific cod	*Gadus macrocephalus*	53	22
Pollock	*Gadus chalcogrammus*	9	47
Pacific ocean perch	*Sebastes alutus*	114	132
Rex sole	*Glyptocephalus zachirus*	25	43
Rockfishes	*Sebastes* spp.	52	43
Thornyheads (shortspine and longspine)	*Sebastolobus* spp.	48	51
Shortraker rockfish	*Sebastes borealis*	6	44
Total		609	641

Note: The species and groupings are the same as were used in the analysis of transect-scale fish habitat associations (n = 466 transects). Names in bold are used throughout the manuscript to identify the species or taxonomic grouping.

By this classification, a section of seafloor covered primarily in cobble, but with boulders over more than 20% of the surface, would receive the substratum code cobble–boulder (Cb) with the secondary substratum indicated by the lowercase letter. The substratum code was only changed if a substratum encompassed more than 10 sequential images. The size of each substrate was estimated from the viewing path width or by direct measurement using stereo imagery. The proportion of rocky habitat on each transect was calculated by the percentage of the transect that included boulder, high or low relief bedrock, or cobble as either a primary or secondary substrate type. Other substrate types (sand, mud, gravel–pebble, mixed coarse material) were classified as unconsolidated substrate.

Individual-level image analysis

For analyzing individual patterns in animal associations with seafloor structure, we randomly chose individual fishes and crabs from a number of species that were shared between EBS and AI ecosystems (Table 1). Up to 150 individuals for each species were randomly chosen in approximately equal numbers between the two ecosystems. For some species, such as walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*), there were a limited number of observations; therefore, all measurable individuals from each ecosystem were analyzed. Difficult species to positively identify were combined into groups, such as the blackspotted (*Sebastes melanostictus*) and rougheye (*Sebastes aleutianus*) rockfishes. Unidentifiable rockfishes (*Sebastes* spp.) were also randomly sampled and their associations with seafloor structure examined

For each randomly selected individual fish or crab, the presence of seafloor structure within the image frame was noted, and the distance to the nearest seafloor structure was measured. If there was no seafloor structure within 200 cm of the fish or crab, that individual was deemed to have no association. For a fish or crab that did occur within 200 cm of seafloor structure, up to the three closest objects were identified and the closest distance to each of these seafloor structures was measured from a central point on the fish or crab. The height of each seafloor structure was also measured. For individual fish, the length of the fish was also measured. Crab carapaces were not measured. All measurements were to the nearest millimetre using stereo-image analysis software. It is important to note that for these analyses of individual fish associations, sponges less than 20 cm in height were identified

and included for both ecosystems (as opposed to the transect-level analyses above).

Data analysis

Generalized additive models (GAMs) were used to test for significant associations between species and deep-sea coral or sponge habitat on a transect-scale level. For this analysis, the density of fish and crab taxonomic groups (listed in Table 1) on camera transects was used as the dependent variable. Densities were log-transformed to best meet the assumption of normality in residuals, and camera transects were used as replicates. A constant of ½ of the minimum positive density value was added to each density measure prior to log transformation, as this provided the best fit to normality for residuals. A log transformation with constants of 1% and 10% of the mean catch per unit of effort (CPUE) and a direct fourth-root transformation of the density data were also evaluated, but these resulted in larger residual deviations from normality. The following were used as explanatory variables in the model: the percentage of rocky substrate on a transect, density of corals, density of sponges, and density of pennatulaceans (including sea pens and sea whips). Densities of corals, sponges and pennatulaceans were also log-transformed (plus a constant of ½ the minimum positive density value). The environmental covariates mean depth and mean temperature recorded on the camera during the transect were also included in the model, as well as a factor for region (AI or EBS). In nine cases the temperature was not measured due to instrument failure, and the nearest transect at a similar depth on the same date was used. Correlations and variance inflation factors (Zuur et al. 2009) were calculated among explanatory variables to determine multicollinearity in the explanatory data. Variance inflation factors were 3.6 and less for all variables, and correlations were less than 0.8 (see online Supplemental Material 1[1]). Prior to model development, relationships between density and explanatory variables were explored graphically (see Supplemental Material 2[1]). The full model equation was

$$y_i = s(\text{Depth}) + s(\text{Temperature}) + s(\text{Percent rocky substrate})$$
$$+ \, s[\log(\text{Coral density})] + s[\log(\text{Sponge density})]$$
$$+ \, s[\log(\text{Pennatulacean density})] + \text{Region} + \varepsilon$$

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where y is the density of species i, and s indicates a thin plate regression spline smoothing function (Wood 2006). In each case, the basis degrees of freedom used in the smoothing function was limited to ≤5. Separate analyses were conducted for each fish or invertebrate species (Table 1). Backwards stepwise elimination was used to remove insignificant variables. Initially a full model containing all independent variables was fit to the data. Then the least significant variable was removed from the model, provided it had $p > 0.05$, the generalized-cross-validation (GCV) score was lower with the elimination of the variable, and the estimated degrees of freedom of the variable was not equal to 1 (Weinberg and Kotwicki 2008). The resulting reduced model was refit to the data. Stepwise variable removal was continued until all variables were significant in the model or removal of additional variables resulted in a higher GCV score. The remaining variables in the best model were determined to have significant effects on the log-transformed density of that species. Residuals of the model fit and model diagnostics examined for the magnitude of deviations from normality assumptions (see Supplemental Material 3[1]).

A secondary analysis examined the effect of coral, sponge, and pennatulacean mean height at each transect on the density of fish and crabs. This analysis was conducted for a subset of transects where the mean height of a structure-forming invertebrate was measured ($n = 245$) and prior analyses identified a significant relationship between a fish or crab species and the abundance of the structure-forming invertebrate. Correlations and variance inflation factors (Zuur et al. 2009) were calculated among explanatory variables to determine multicollinearity in the explanatory data. Variance inflation factors were 3.3 and less for all variables, and correlations were less than 0.8 (see Supplemental Material S1[1]). Prior to model development, relationships between density and explanatory variables were explored graphically (see Supplemental Material 2[1]). The same type of GAM analyses outlined above was used, but an additional factor of mean height of structure-forming invertebrates was added so that

$$y_i = s(\text{Depth}) + s(\text{Temperature}) + s(\text{Percent rocky substrate})$$
$$+ \ s[\log(\text{Coral density})] + s[\log(\text{Sponge density})]$$
$$+ \ s[\log(\text{Pennatulacean density})] + s(\text{Invertebrate height})$$
$$+ \ \text{Region} + \varepsilon$$

As in the previous GAM, data were log-transformed and backwards stepwise variable elimination was used to determine the best-fitting model. Residuals of the model fit and model diagnostics examined for the magnitude of deviations from normality assumptions (see Supplemental Material 3[1]).

Independent of transects, associations of individual fishes with structure were also analyzed to determine whether patterns in association among species differed between the regions. For this analysis a generalized linear model (GLM) was used (R Development Core Team 2016) with the randomly selected individual fish from each species (Table 1) as the replicates. A binomial response variable (y) with a logit-link indicated whether there was (1) or was not (0) an association with structured habitat (regardless of type of structure) for each of the 1250 individuals. The factors used as independent variables in the GLM were region (either AI or EBS) and species, as well as an interaction term between species and location to indicate differences in association patterns among species between regions, so that

$$y = \text{Region} + \text{Species} + \text{Species} \times \text{Region} + \varepsilon$$

For fish species found to have individual associations with structure (rockfishes and Pacific cod), the effect of fish length, structure height, and structure type on distance to their associated structure was tested for individuals. In this analysis, a GAM was used and the independent variables were structure height (for the closest structure to the individual), individual fish length, structure type (for the closest structure to the individual), ecosystem (AI or EBS), and fish species. The dependent variable was untransformed distance from the fish to the closest seafloor structure. Because of the small sample size for measured distances to pennatulaceans, these seafloor structures were included in the "other" category for this analysis: $y_i = s(\text{Structure height}) + s(\text{Fish length}) + \text{Structure type} + \text{Region} + \text{Species} + \varepsilon$. An identity link was used for the model, and a residual diagnostic plot can be found in Supplemental Material 3[1].

Finally, to test for equivalent use of structure among the available types, we used a χ^2 test implemented in the R software. This analysis used the distinct structure types that were available to each randomly selected fish. These structure types were categorized as rock, sponge, coral, or other, which primarily included hydrocorals, basket stars, bryozoans, hydroids, anemones, sea whips, and sea pens. For each structure type, the frequency it was chosen was compared with the frequency that it was available (present) in the same frame as the fish using a χ^2 test. Significance was judged at $p < 0.05$. Pairwise comparisons of the results were conducted using a Bonferroni-adjusted p value for multiple comparisons. Chi-squared tests were conducted for all rockfishes and Pacific cod combined across regions, rockfishes and Pacific cod within regions, and rockfishes only and Pacific cod only to determine if patterns were similar across regions and species. Only individual rockfishes and Pacific cod found to have seafloor structure associations were used in these analyses.

Results

In total, there were 23 173 individual fish and crabs observed in underwater camera transects in the EBS (13 089) and AI (10 084) representing 56 individually identified species. The AI fish fauna were dominated by rockfishes (5503 individuals) and Atka mackerel (1020 individuals), followed by sculpins (694), searchers (656), eelpouts (449), grenadiers (441), flatfishes (322), gadids (178), crabs (143), and skates (120). In the EBS the most common taxonomic groups were crabs (2848), eelpouts (2155), grenadiers (2068), rockfishes (2056), sculpins (1169), flatfishes (867), snailfishes (613), poachers (604), skates (168), searchers (154), and gadids (114). For many of the species analyzed, there were large differences in overall density between ecosystems (Fig. 2). However, GAM modeling of the effect of habitat on fish and crab densities indicates that the two ecosystems are perhaps more similar than would be expected by simply examining the density of fish and invertebrate groups shared in common. When examined across transects, depth was a significant predictor of density for all species in the GAM models (Table 2; Supplemental Material 4[1]). Each species inhabited a relatively specific depth zone, ranging from the relatively shallow distribution of northern rockfish to the deep distribution of *Sebastolobus* spp. and grenadier species (Fig. 3). Temperature was a significant predictor of density for the *Sebastes* spp. group, northern rockfish, Pacific cod, Pacific halibut, and crabs. The proportion of rocky habitat, coral abundance, and (or) sponge abundance were significantly correlated to all rockfish groupings. Negative relationships were found between the proportion of rocky habitat and log-transformed density of *Atheresthes* spp. There were also negative relationships between coral and sponge abundance and rex sole and *Chionoecetes* crab abundance. A negative relationship between coral abundance and Pacific ocean perch (POP) density was also found, but POP were positively related to sponge abundance. Regional differences in density were significant for shortraker rockfish, walleye pollock, *Atheresthes* spp., and *Chionoecetes* crabs. Region was not significant for other fish groups. Models explained between 4% and 57% of the variability of log-transformed densities for the species groups examined (Table 2). When the mean height of the structure forming invertebrates on the transect was included in the GAM models and the species with associations were examined, the significant terms in the models for most species

Fig. 2. Mean density (± standard error) of taxa at underwater stereo-camera transects (n = 466) in the eastern Bering Sea (EBS) and Aleutian Islands (AI).
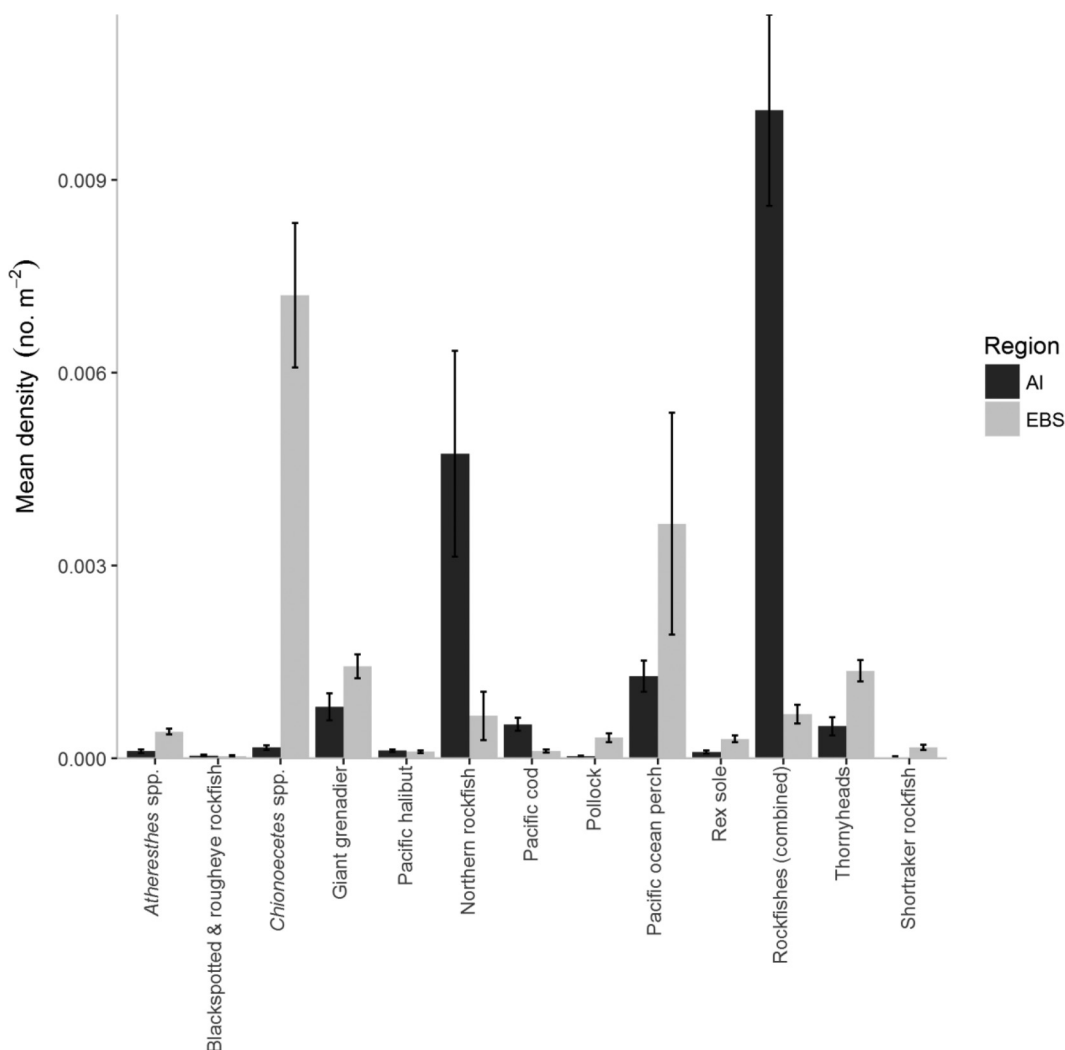

Table 2. Best-fitting generalized additive models (GAMs) for density of fish and invertebrates by taxonomic grouping.

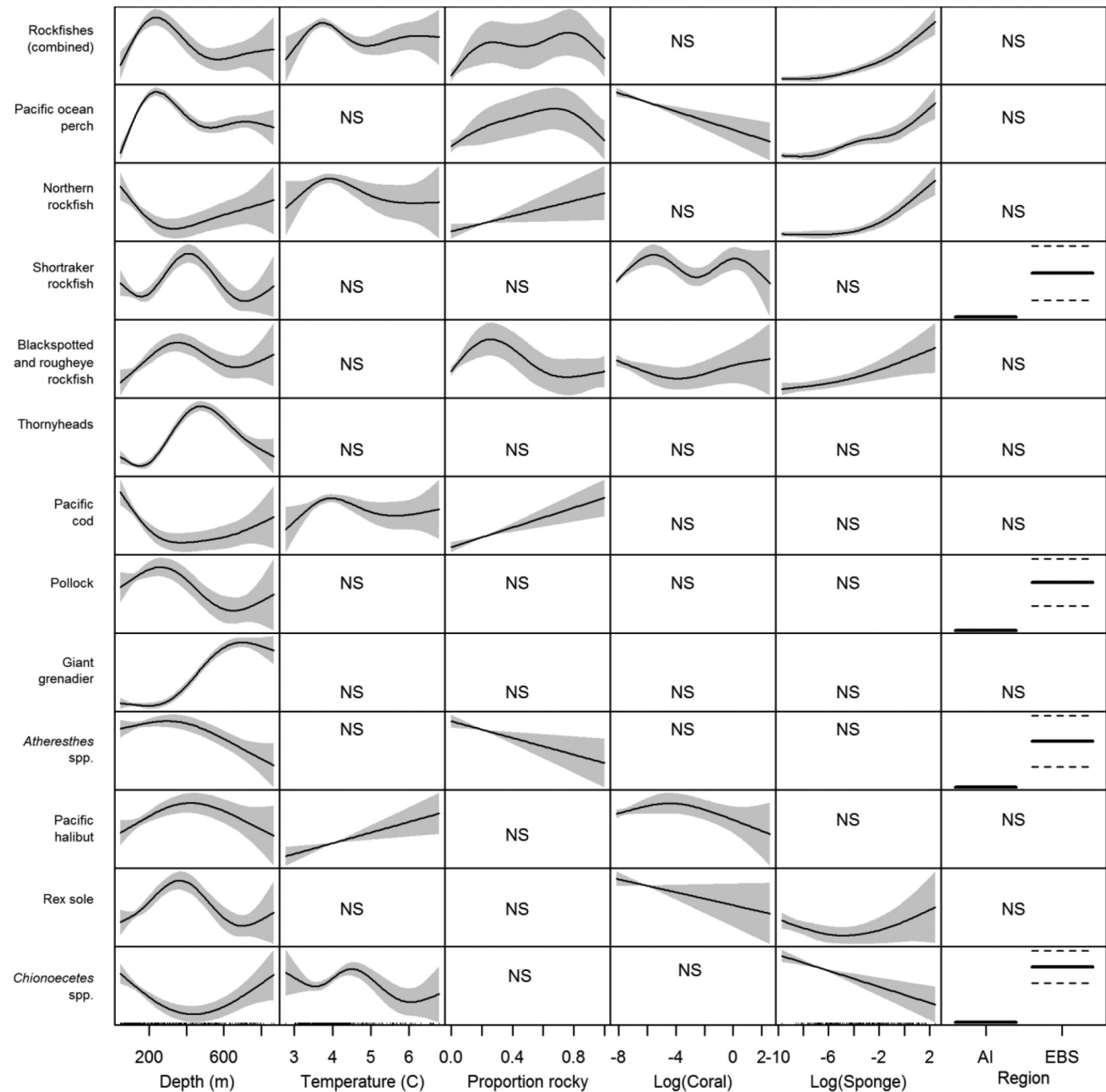| Species	GAM	Deviance explained (%)	Est. df	R^2
Rockfishes (combined)	s(Depth) + s(Temperature) + s(Proportion_rocky) + s[log(Coral)] + s[log(Sponge)]	49.5	3.6, 3.6, 2.5, 2.1, 3.7	0.48
Pacific ocean perch	s(Depth) + s(Proportion_rocky) + s[log(Coral)] + s[log(Sponge)]	35.0	3.9, 2.7, 1.0, 3.8	0.33
Northern rockfish	s(Depth) + s(Proportion_rocky) + s[log(Coral)] + s[log(Sponge)]	34.8	2.8, 1.0, 2.2, 3.6	0.33
Shortraker rockfish	s(Depth) + s(Proportion_rocky) + s[log(Coral)] + s[log(Sponge)]	20.1	3.9, 2.8, 3.8, 3.6, 1.0	0.17
Blackspotted and rougheye rockfishes	s(Depth) + s(Proportion_rocky) + s[log(Coral)] + s[log(Sponge)]	12.2	3.5, 3.4, 2.3, 2.3	0.10
Thornyheads	s(Depth)	43.1	3.9	0.43
Pacific cod	s(Depth) + s(Temperature) + s(Proportion_rocky)	16.8	3.2, 3.3, 1.0	0.15
Pollock	s(Depth) + Region	8.7	3.2, 1.0	0.08
Giant grenadier	s(Depth)	56.9	3.8	0.57
Atheresthes spp.	s(Depth) + s(Proportion_rocky) + Region	11.5	2.2, 1.0, 1.0	0.11
Pacific halibut	s(Depth) + s(Temperature) + s[log(Coral)]	5.2	2.2, 1.0, 2.0	0.04
Rex sole	s(Depth) + s[log(Sponge)]	12.0	3.7, 2.3	0.11
Chionoecetes spp.	s(Depth) + s(Temperature) + s[log(Sponge)] + Region	33.2	2.4, 3.7, 1.0, 1.0	0.32

Note: Best-fitting GAM equation, the percentage of deviance explained, the estimated degrees of freedom (Est. df) for each variable, and the R^2 value for each model are shown.

did not change (Table 3; Supplemental Material 4[1]). The only species with significant relationships to mean invertebrate heights were POP, rex sole, and *Chionoecetes* crabs. POP density decreased linearly with increasing invertebrate height. Rex sole densities increased with increasing mean height to about 50 cm, at which point densities decreased. Crab densities peaked bimodally at structure forming invertebrate (SFI) heights of about 25 and 125 cm (Fig. 4).

For randomly sampled individual fishes (Table 1), the GLM model indicated there were significant fish–structure differences

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Fig. 3. Plots of log-transformed density for each fish group against depth, temperature, substrate type, and log-transformed densities of coral and sponge from generalized additive models. Shaded area and dotted horizontal lines indicate ±1 SE; NS indicates the variable was not significantly ($p \geq 0.05$) related to log-transformed density.

among species, regions, and within species among regions (Table 4). The species with significantly higher probability of having associations were rockfishes ($p = 0.0001$), POP ($p < 0.0001$), northern rockfish ($p < 0.0001$), and Pacific cod ($p = 0.03$; Table 4). There was also a significant difference between regions, with the AI having significantly higher probability of fish–structure associations than the EBS ($p = 0.031$). The results indicated that the interaction term (species × region) was only significant for Pacific cod ($p = 0.02$), indicating that Pacific cod had significantly higher probability of being associated with structure in the AI than the EBS. There was a higher proportion of nonassociated individuals in the EBS (95% of individuals were not associated with structure) relative to the

AI (34% of individuals were not associated with structure; Fig. 5). When Pacific cod were removed from the analysis, the results were unchanged from the previous analyses for the remaining species; rockfishes ($p = 0.0001$), POP ($p < 0.0001$), and northern rockfish ($p < 0.0001$) had a significantly higher probability of associations with structure, the probability of associations with structure were higher in the AI ($p = 0.03$), and there were no significant interaction terms when Pacific cod was removed (see Supplemental Material 5[1]). The raw data from individual fishes indicates that only rockfish groups had proportions of association with seafloor structure (e.g., rocks, corals, sponges, etc.) >0.50 when aggregated across ecosystems (Fig. 5). When split into regions, a few species

Table 3. Best-fitting generalized additive models (GAMs) for density of fish and invertebrates by taxonomic grouping.

Species	GAM	Deviance explained (%)	Est. df	R^2
Rockfishes (combined)	s(Depth) + s(Temperature) + s(Proportion_rocky) + s[log(Sponge)]	48.4	3.5, 3.5, 2.1, 2.4	0.46
Pacific ocean perch	s(Depth) + s(Proportion_rocky) + s[log(Coral)] + s[log(Sponge)] + s(Invertebrate height)	34.8	3.9, 2.0, 1.0, 1.1, 1.0	0.32
Northern rockfish	s(Depth) + s[log(Coral)] + s[log(Sponge)]	33.3	2.5, 2.0, 1.9	0.32
Shortraker rockfish	s(Depth) + s(Proportion_rocky) + s[log(Coral)] + s[log(Sponge)] + Region	21.4	3.3, 1.4, 3.7, 1.0, 1.0	0.18
Blackspotted and rougheye rockfishes	s(Depth) + s(Proportion_rocky) + s[log(Coral)] + s[log(Sponge)]	15.3	3.4, 3.3, 2.0, 1.0	0.12
Pacific halibut	s(Depth) + s(Temperature)	7.7	2.4, 1.0	0.06
Rex sole	s(Depth) + s(Temperature) + s[log(Coral)] + s[log(Sponge)] + s(Invertebrate height)	16.6	2.6, 1.0, 1.3, 2.1, 3.1	0.13
Chionoecetes spp.	s(Depth) + s(Temperature) + s[log(Coral)] + s(Invertebrate height) + Region	40.8	2.7, 3.2, 1.7, 3.9, 1.0	0.38

Note: In this case, the data include height of structure-forming invertebrates and include only transects where height data were available ($n = 245$). Best-fitting GAM equation, the percentage of deviance explained, the estimated degrees of freedom (Est. df) for each variable, and the R^2 value for each model are shown.

Fig. 4. Plots of log-transformed density for each fish group against depth, temperature, substrate type, log-transformed densities of coral and sponge, and height of structure-forming invertebrates from generalized additive models. These data are a subset of transects where invertebrate heights were available for analysis ($n = 245$). Shaded area and dotted horizontal lines indicate ±1 SE; NS indicates the variable was not significantly ($p \geq 0.05$) related to log-transformed density.
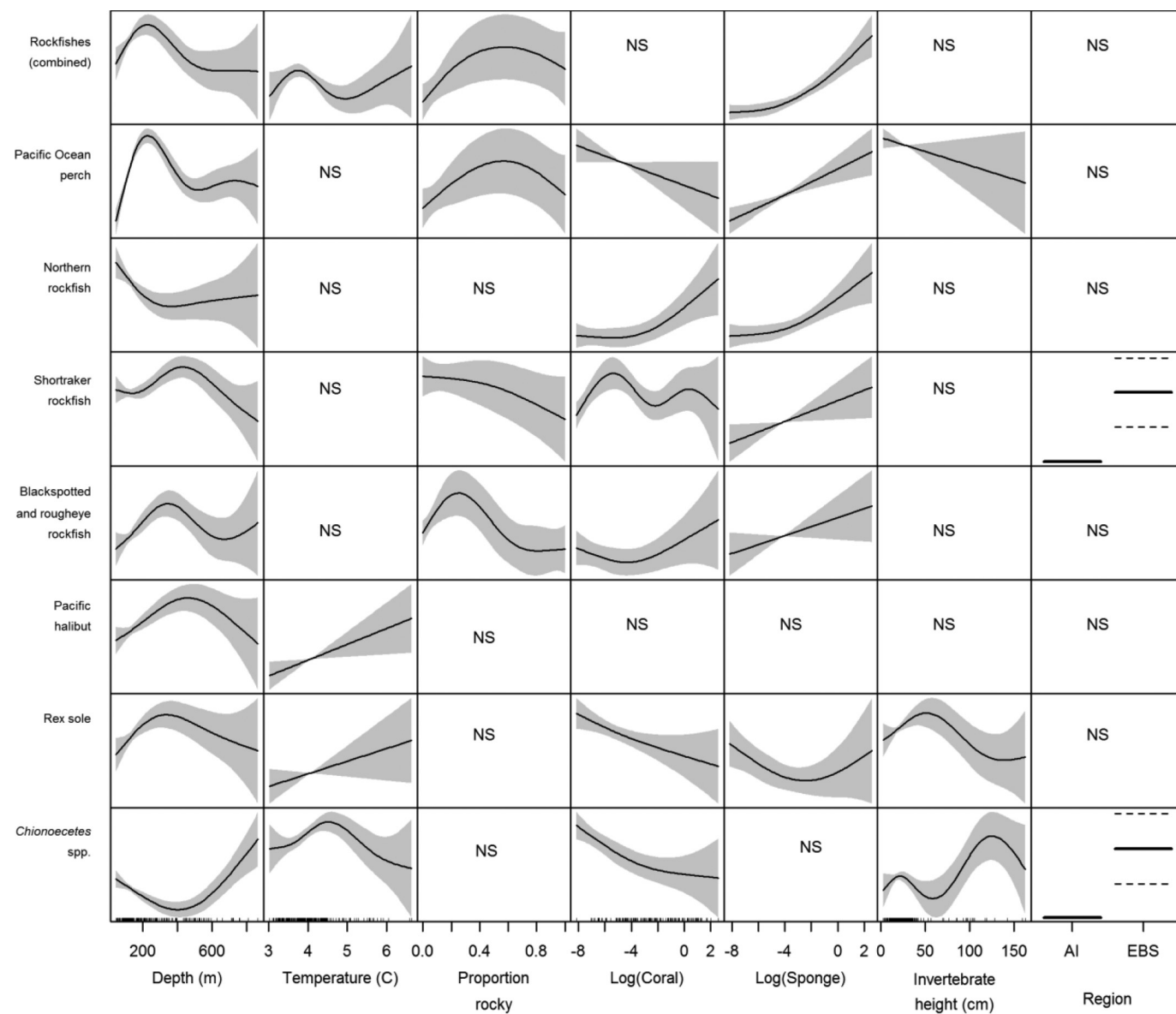
Table 4. Results and parameter estimates for general linear model predicting presence or absence of association for randomly selected individual fishes between regions and among species groupings (n = 1250).

	df	Deviance	Residual df	Residual deviance
Null model	—	—	1249	1704.5
Species	12	416.6	1237	1288.6
Region	1	101.8	1236	1186.1
Species × Region	12	21.7	1224	1164.4
	Estimate	Std. error	z value	p value
Intercept	−0.3023	0.3198	−0.9450	0.3446
Atheresthes spp.	—	—	—	—
Chionoecetes spp.	−0.9215	0.6009	−1.5330	0.1252
Giant grenadier	0.3857	0.4310	0.8950	0.3709
Pacific halibut	0.3536	0.4527	0.7810	0.4348
Northern rockfish	**2.8280**	**0.4586**	**6.1670**	**0.0000**
Pacific cod	**0.9673**	**0.4318**	**2.2400**	**0.0251**
Pollock	0.5254	0.7432	0.7070	0.4796
Pacific ocean perch	**3.1930**	**0.5275**	**6.0530**	**0.0000**
Blackspotted and rougheye rockfishes	16.8700	565.6000	0.0300	0.9762
Rex sole	−0.1032	0.5186	−0.1990	0.8423
Rockfishes	**2.0070**	**0.5000**	**4.0140**	**0.0001**
Thornyheads	0.3023	0.4309	0.7020	0.4829
Shortraker rockfish	16.8700	979.6000	0.0170	0.9863
Aleutian Islands (AI)	—	—	—	—
Eastern Bering Sea (EBS)	**−1.033**	**0.478**	**−2.160**	**0.031**
Atheresthes spp. × EBS	—	—	—	—
Chionoecetes spp. × EBS	0.2871	0.8230	0.3490	0.7273
Giant grenadier × EBS	−0.8660	0.6915	−1.2520	0.2105
Pacific halibut × EBS	0.0006	0.6957	0.0010	0.9993
Northern rockfish × EBS	−0.2200	0.6662	−0.3300	0.7412
Pacific cod × EBS	**−2.6770**	**1.1660**	**−2.2950**	**0.0217**
Pollock × EBS	−0.9334	0.9200	−1.0150	0.3103
Pacific ocean perch × EBS	−0.6339	0.6691	−0.9470	0.3434
Blackspotted and rougheye rockfishes × EBS	−15.5300	565.6000	−0.0270	0.9781
Rex sole × EBS	−0.1994	0.7523	−0.2650	0.7909
Rockfishes × EBS	0.3958	0.7060	0.5610	0.5751
Thornyheads × EBS	−0.6490	0.6784	−0.9570	0.3387
Shortraker rockfish × EBS	−14.9700	979.6000	−0.0150	0.9878

Note: Bold font indicates statistically significant result ($p < 0.05$).

(pollock, giant grenadier, Pacific halibut, and Pacific cod) had proportions of associations around 0.50 in the AI (Fig. 5), but in the EBS the associations were much lower for these species (<0.25), which explains the significance of the region term in the GLM (Table 4). So, although the overall levels of associations were higher in the AI than in the EBS (likely due to differences in abundance of sponges and corals), rockfish species were the only taxonomic groupings where >50% of the individuals exhibited affinities for structure in both regions. Based on these results, only rockfish species and Pacific cod (because of the statistical significance of the interaction term) were included in further analyses.

A GAM to test for differences in the distance of individual fishes from the closest seafloor structure revealed that interspecies differences were not significant (Table 5; Fig. 6). The results also showed an insignificant difference in average fish distance from structure between regions ($p = 0.47$), indicating that on average individual fish were not closer to structure in the EBS versus the AI. The distance to structure was not significantly different among different types of structure either. It should be noted that in this data there were only measurements available for a single sea pen and a single sea whip, so these two data points were combined into the "other" category for this analysis. Individual fish length and structure height did have a significant effect ($p = 0.0003$ and $p = 0.032$, respectively) on the distance between a fish and a structure on the seafloor (Fig. 7). Smaller fishes were closer to objects,

at least for fishes < 60 cm in length. Above 60 cm in length, the relationship between fish length and distance from an object leveled off, possibly indicating these fish had less affinity to structure. Observed fishes greater than 60 cm long were exclusively Pacific cod. The height of an object was linearly related to the distance from an individual fish for objects < 2 m in height (Fig. 7), so that fish were likely to be found closer to small objects and farther from larger objects.

Owing to the significant relationship between fish size and distance to structure, we also compared the average size of a subset of species of rockfishes (POP, northern rockfish, rougheye, and blackspotted rockfish) and Pacific cod with associations and without associations where length measurements were available. Individual fish with a seafloor structure association were on average 18 cm smaller than individual fish without a seafloor structure association (Fig. 8). A t test indicated that this difference was significant ($p < 0.0001$, df = 252, $t = 5.59$). However, this difference was largely due to the over-representation of Pacific cod in the "no association category". When Pacific cod were removed from the analysis and only the three species of rockfish were considered, the difference was only 2 cm (Fig. 8) and the t test was not significant ($p = 0.373$, df = 204, $t = 0.893$). The sample size of individuals measured for length in the "no association category" when only rockfish were considered was small ($n = 17$).

For individual rockfish and Pacific cod, the most commonly associated structures were sponges (51% of individual rockfish as-

Fig. 5. The proportion of randomly sampled individual fish associated with six types of benthic structure and those with no association. The aggregated panel represents both the eastern Bering Sea and Aleutian Islands ecosystems combined. [Colour online.]
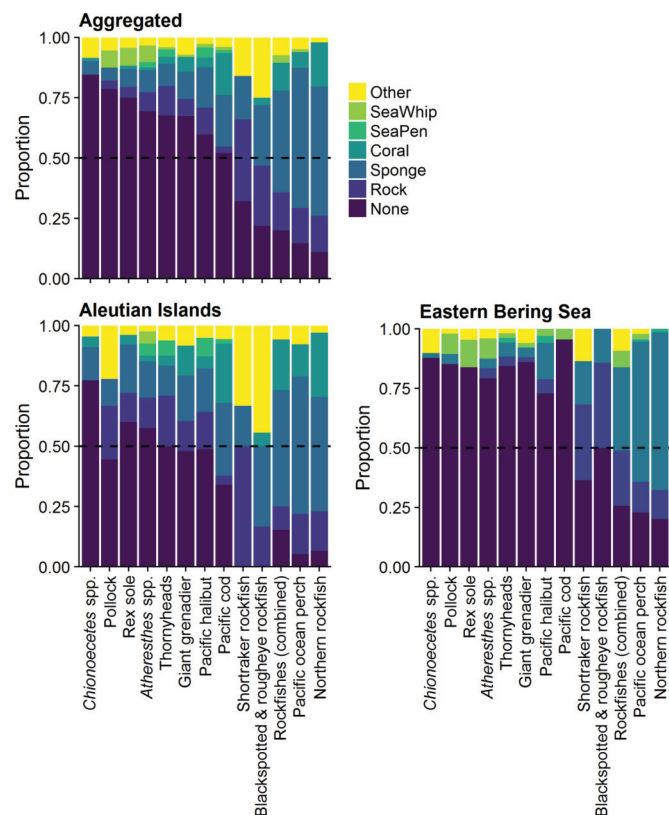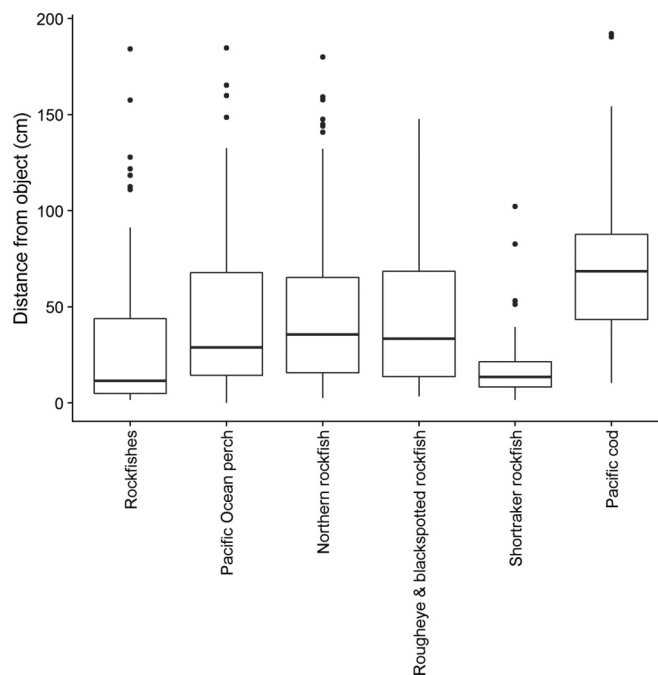

Fig. 6. Distance from seafloor structure for rockfish species and Pacific cod in the eastern Bering Sea and Aleutian Islands across all sizes of fish.

Table 5. Results of generalized additive model predicting distance of individual fish from seafloor structure (for those fish found to have an association; $n = 246$) for Pacific cod and rockfish species in the Aleutian Islands and eastern Bering Sea.

Term	Estimate	Std. error	t value	p value
(Intercept)	49.2376	6.9583	7.0760	<0.0001
Coral	—	—	—	—
Other structure	2.5623	10.90329	0.235	0.814
Rock	0.0194	9.2606	0.0020	0.9980
Sponge	10.2888	7.1595	1.4370	0.1520
Aleutian Islands	—	—	—	—
Eastern Bering Sea	−7.2763	10.1048	−0.7200	0.4720
Northern rockfish	—	—	—	—
Pacific cod	−15.0054	15.1649	−0.9890	0.3230
Pacific ocean perch	−6.5141	6.6605	−0.9780	0.3290
Blackspotted and rougheye rockfishes	−10.5876	12.6501	−0.8370	0.4030
Rockfishes	4.2709	10.4564	0.4080	0.6830
Shortraker rockfish	−18.6158	14.0112	−1.3290	0.1850
	Est. df	Ref. df	F	p value
Fish length	1.881	1.986	9.306	0.0003
Structure height	1.804	1.962	3.978	0.0319
Generalized-cross-validation score	1758.1			
Deviance explained (%)	14.2			

sociations), followed by rocks (23% of associations) and corals (17% of associations), with the remainder of associations with other types of structures (Table 6). Chi-squared tests showed that there were significant differences ($\chi^2 = 16.71$, df = 3, $p = 0.0008$) in the

types of structure used by fishes when the association data were combined. Post hoc tests showed that the differences were due to higher levels of association with sponge than all other structure types (Table 7; Fig. 9). When the areas were tested individually, the results were similar, with significant differences observed for the EBS ($\chi^2 = 13.45$, df = 3, $p = 0.0011$) and the AI ($\chi^2 = 104.84$, df = 3, $p < 0.0001$). However, the post hoc tests showed that associations with sponge were again significantly higher in the AI (Table 7), and both coral and sponge had higher associations than rock. The opposite was true for the EBS, where rocks had the highest levels of association, but only significantly higher than the other category (Fig. 9). Interestingly, Pacific cod were associated with rock significantly less than the other types of structure, which were roughly equal in importance for Pacific cod (Table 7). This was a different pattern than for rockfishes (Fig. 9).

Data collected on the height of individual fishes off the seafloor may explain the pattern in preference against rocks for Pacific cod (Fig. 10). The data show that Pacific cod were much more likely to be observed higher off the seafloor than rockfish. About ⅔ of rockfish were laying on the seafloor or within 20 cm of the seafloor, whereas the cod were more evenly spread among heights off the seafloor. Since sponges and corals use rocks or hard bottom substrates for attachment, they are likely to reach heights off the seafloor that exceed those of rocks (e.g., if sponges and corals are growing on top of rocks). Therefore, Pacific cod that are found higher in the water column are more likely to have an association (defined as being within 2 m) with sponges or corals that are growing on top of rocky substrate. In contrast, rockfishes that are more likely to be near the seafloor would be more likely to be associated with rocks.

Discussion

This study examined the potentially confounding associations between fishes and benthic invertebrates by evaluating the habitat use of several species across two ecosystems and two different scales. The results indicate rockfish densities have a positive association with coral and sponge densities and an affinity for areas where the proportion of rocky habitat is higher. The results of this

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Fig. 7. Additive effects of fish length and structure height from generalized additive model predicting the distance of an individual fish from a seafloor structure. These data are for individual fish where an association with seafloor structure was observed (*n* = 246). Shaded area indicates ±1 SE.
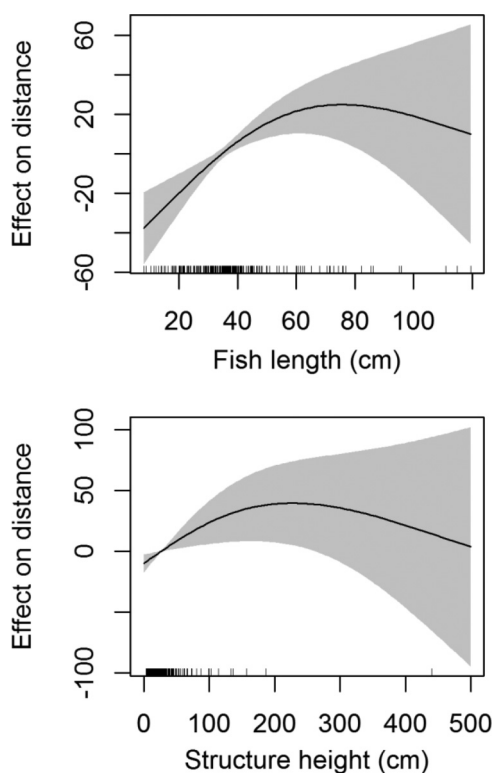

Fig. 8. Mean size of rockfish and Pacific cod that had an association with seafloor structure (associated) and did not have an association with seafloor structure (no association). The numbers within the barplots indicate sample sizes where lengths were measured for each group; data are shown for groupings of all fish and only rockfishes (i.e., with Pacific cod data excluded).
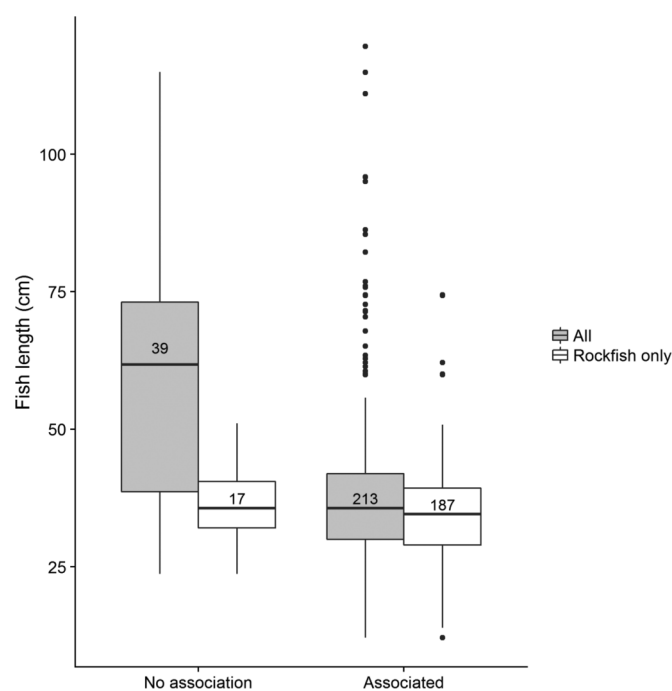

Table 6. Contingency table for counts of randomly selected individual rockfishes and Pacific cod and the types of structure-forming invertebrates used for association.

Area	Species	Coral	Sponge	Rock	Other
Aleutian Islands	Pacific cod	13 (27)	16 (34)	2 (32)	4 (8)
	Rockfishes	63 (227)	161 (297)	52 (288)	26 (134)
Eastern Bering Sea	Pacific cod	—	—	—	1 (1)
	Rockfishes	1 (1)	25 (55)	33 (60)	5 (32)

Note: The number of individuals that chose the type of structure are shown, with the number of times that structure was available to the fish in parentheses.
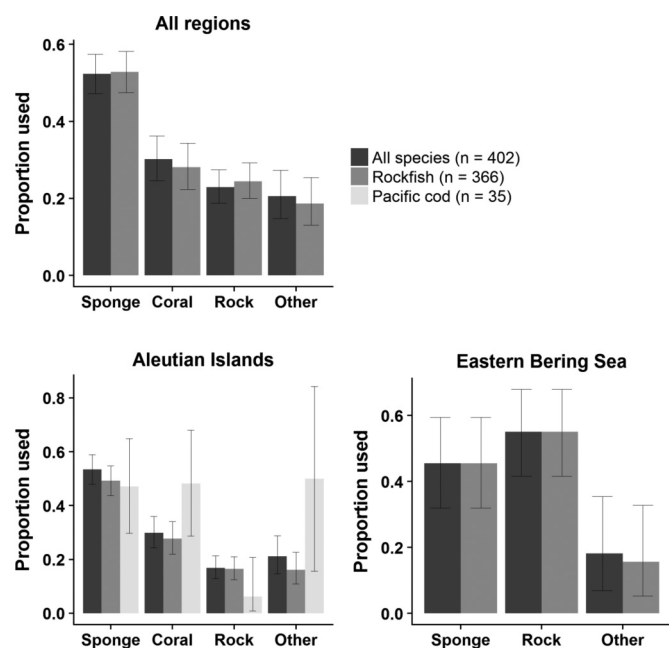
Table 7. Results of post hoc comparisons of χ^2 test for significance among structure-forming invertebrate groups.

Data	Post hoc comparisons	p.Chisq	p.adj.Chisq
All data combined	Coral: other	0.0343	0.2060
	Coral: rock	0.0490	0.2940
	Coral: sponge	0.0000	0.0000*
	Other: rock	0.6150	1.0000
	Other: sponge	0.0000	0.0000*
	Rock: sponge	0.0000	0.0000*
Eastern Bering Sea only	Other: rock	0.0013	0.0038*
	Other: sponge	0.0182	0.0546
	Rock: sponge	0.4030	1.0000
Aleutian Islands only	Coral: other	0.0755	0.4530
	Coral: rock	0.0003	0.0019*
	Coral: sponge	0.0000	0.0000*
	Other: rock	0.3360	1.0000
	Other: sponge	0.0000	0.0000*
	Rock: sponge	0.0000	0.0000*
All regions rockfishes only	Coral: other	0.0420	0.0630
	Coral: rock	0.3790	0.3790
	Coral: sponge	0.0000	0.0000*
	Other: rock	0.1780	0.2140
	Other: sponge	0.0000	0.0000*
	Rock: sponge	0.0000	0.0000*
Eastern Bering Sea rockfishes	Other: rock	0.0006	0.0018*
	Other: sponge	0.0096	0.0289*
	Rock: sponge	0.4030	1.0000
Aleutian Islands rockfishes	Coral: other	0.0985	0.5910
	Coral: rock	0.0118	0.0708
	Coral: sponge	0.0000	0.0000*
	Other: rock	0.8440	1.0000
	Other: sponge	0.0000	0.0000*
	Rock: sponge	0.0000	0.0000*
Aleutian Islands Pacific cod only	Coral: other	1.0000	1.0000
	Coral: rock	0.0007	0.0043*
	Coral: sponge	1.0000	1.0000
	Other: rock	0.0109	0.0654
	Other: sponge	1.0000	1.0000
	Rock: sponge	0.0006	0.0034*

Note: *p* values for pairwise tests (p.Chisq) corrected for multiple comparisons using a Bonferroni adjustment (p.adj.Chisq) were used to determine significant differences among pairs (indicated by *).

study indicate that structure of any type is important to rockfishes, and more structure (including rocks, corals, or sponges) leads to increased rockfish densities. This result has important implications for the management of both rockfishes and deep-sea corals and sponges in that less benthic structure (e.g., deep-sea corals and sponges) is correlated to reductions in the density of rockfishes that support commercial fisheries. The results also showed that smaller rockfish are more likely to be nearer to seafloor structure, and there were no differences found among the species of rockfishes examined. It was difficult to separate the differences in effects of the different types of structure-forming invertebrates from the effects of rocky habitat in this study, as the two are highly linked. There were only five cases where rocks

Fig. 9. Proportion of times each type of available seafloor structure was used by rockfish and Pacific cod for individual rockfish and Pacific cod. Only one Pacific cod in the eastern Bering Sea had an association with seafloor structure, so this species was only included in the Aleutian Islands panel.
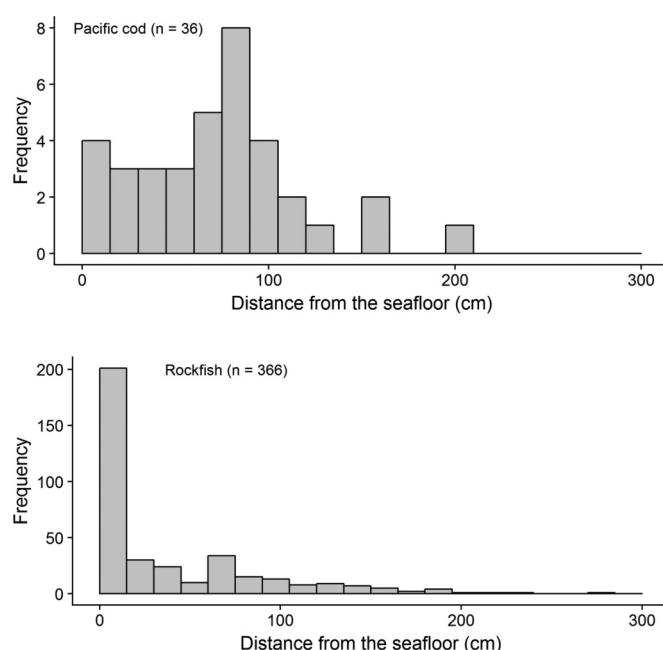

Fig. 10. Frequency of occurrence of height off the seafloor for individual Pacific cod (upper panel) and rockfish (lower panel) observed to have an association with seafloor structure. The distance from the seafloor was measured for individuals using the underwater stereo-camera system and are grouped into 20 cm bins.

devoid of any structure-forming invertebrates were available and were chosen for association. However, the results of this study show that sponges are chosen as associated structure significantly more than other types of structure.

The findings of this research are consistent with previous studies on rockfishes and habitat associations in the North Pacific Ocean. Studies at many scales, including trawl survey analyses (Heifetz 2002; Rooper and Boldt 2005; Laman et al. 2015) and analyses of underwater video (Pearcy et al. 1989; Stein et al. 1992; Yoklavich et al. 2000; Rooper et al. 2007, 2010), have all shown that higher rockfish densities are associated with hard substrates as well as deep-sea corals and sponges. Juvenile POP and some other species of rockfishes have been found near structure in many systems (Carlson and Straty 1981; Matthews 1989; Love et al. 1991; Tissot et al. 2006; Rooper et al. 2007). Du Preez and Tunnicliffe (2011) found that the presence and large size of epifauna support higher densities of rockfish than bare seafloor or equivalent substrate with no epifauna. However, in a detailed analysis of individual epifaunal components, Tissot et al. (2006) found that of 108 fish species observed, only six species (all rockfishes) were associated more often with invertebrates than would be predicted based on their densities. Other studies have found that when substrate relief and the presence of epifauna are accounted for, there is no clear evidence fishes are choosing coral over other types of available structure (Auster 2005; Parrish 2006). These results are consistent with this study in that observed associations with deep-sea corals and sponges are not necessarily obligate for the fishes, as juvenile and adult fish will use other types of structure when available. The results of this study are also consistent with findings for other species in bottom trawl surveys and underwater visual studies. It has commonly been observed that flatfishes, grenadiers, thornyheads, and crabs are not associated with structured habitats (Stein et al. 1992; McConnaughey and Smith 2000; Yoklavich et al. 2000; Rooper and Martin 2009; DuPreez and Tunnicliffe 2011).
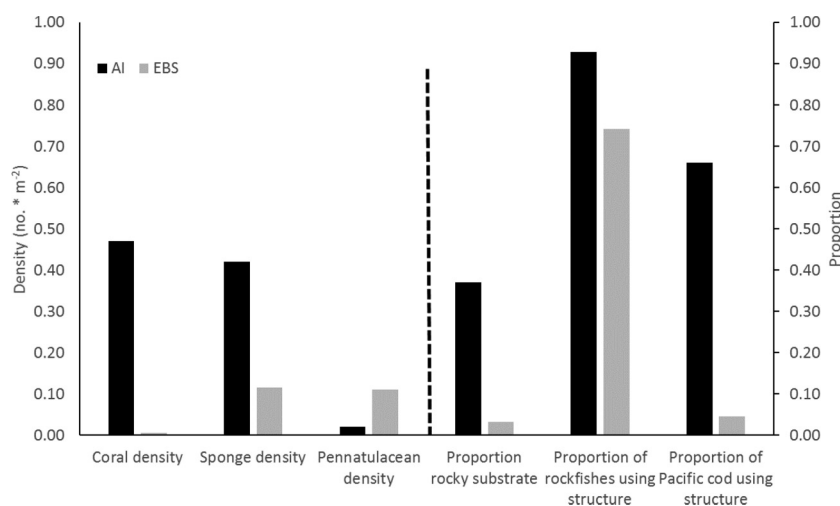
In field studies, it is difficult to control all the factors that may influence the data. In our case, rockfish behavior in response to

the underwater vehicle undoubtedly played a role in the distance measured between fishes and structure. Rooper et al. (2015) found that small rockfishes have a stronger reaction to the approach of an underwater vehicle than large rockfishes, with small rockfishes moving closer to the seafloor in response to an approaching vehicle. The effect was less pronounced when strobe lights were used (such as in this study) as opposed to constant white light (used in the other studies listed above). The observed effect of smaller rockfish staying close to substrates is consistent with an escape response. This escape response has been observed in underwater camera studies for rockfish found in the water column (Krieger and Ito 1999; Laidig et al. 2013), but less so when rockfish are observed near the seafloor (Else et al. 2002; Nasby-Lucas et al. 2002; Lauth et al. 2004; Love et al. 2006). If there were no escape response to the vehicle, a reduction of the strength of the associations (more fish may have been farther than 2 m from substrate) and a reduction of the effect of fish length on the strength of the association (if small fishes respond more strongly than large fishes) would be likely. It was also likely that for smaller fishes the detectability in complex substrate was reduced relative to less complex substrates. This would have affected the results of the transect-level analysis by potentially reducing the strength of the observed association with complex habitats (fish density would have been observed to be lower than the true density in more complex habitats). For the analysis of individuals, lowered detectability in complex habitats might have led undetected fish not being chosen randomly for the analysis. This in turn may have reduced the perceived strength of individual associations with seafloor structure (if fish close to structure were less likely to be detected). In a previous study using a similar type of camera in a similar range of habitats, we found that CPUE from trawl net catches was consistent with densities from underwater camera transects across habitats, indicating that each gear was reflecting differences in abundance rather than detectability for the most part (Rooper et al. 2007). Finally, the sampling was conducted in two seasons (August 2014 in the EBS and August 2012 and May 2014 for the AI). This may have had an effect on the results, although

Fig. 11. Regional-scale characteristics of the structure-forming invertebrates and fish associations for the Aleutian Islands (AI) and eastern Bering Sea (EBS). On the left axis are mean densities of structure-forming invertebrates from underwater camera surveys conducted in each region (data from Rooper et al. 2016 and Wilborn et al. 2018). On the right axis are the mean proportion of rocky substrate at underwater camera transects (data from Rooper et al. 2016; Goddard et al. 2017) and the overall proportion of randomly selected rockfishes and Pacific cod found in association with structure from this study.

any differences in the data between the two seasons within the AI were confounded with differences among spatial locations sampled and interannual differences, making seasonal effects impossible to determine. None of the fish used in the individual analyses of associations were young-of-the-year, and size effects were accounted for directly by using length as a covariate in some analyses. Research conducted in other regions of Alaska on rockfishes shows similar patterns in habitat use across seasons (Conrath et al., in press) and limited lifetime dispersal of 70–400 km (Palof et al. 2010), indicating a minimal effect of fish movement on these results.

One of the most interesting aspects of this study is the lack of significant differences between the two ecosystems (AI and EBS). This is striking when the characteristics of structure-forming invertebrates and rocky substrate are compared between the two ecosystems (Fig. 11). From previously published research using the same underwater camera survey data, the densities of sponges and corals were 3 and 100 times higher in the AI than in the EBS, respectively. This is likely in part due to the >10-fold difference in the abundance of rocky substrate for invertebrate attachment between the two ecosystems (Fig. 11). In the current analysis, the differences in the abundance of rocky substrate and structure-forming invertebrates were reflected in the proportion of Pacific cod using structure, in that there were significant differences found between ecosystems and the difference was in line with the different proportions of structure, with the proportion of Pacific cod using structure in the EBS roughly 15 times higher than in the AI (Fig. 11). This is in contrast with the results for rockfishes. No significant ecosystem effects were observed in the analyses on densities of rockfishes or individual rockfish associations, and the overall proportion of rockfish associated with structure declines only ~20% from the AI to the EBS, even though the decline in abundance of structure was precipitous (Fig. 11). This is consistent with other studies of rockfish and seafloor structure from single ecosystems, including other data sets from Alaska (e.g., Heifetz 2002; Malecha et al. 2005; Rooper and Boldt 2005; Laman et al. 2015), other data sets from the west coast of Canada (Murie et al. 1993; Marlieve and Challenger 2009; Du Preez and Tunnicliffe 2011), and other data sets on the US west coast from Washington to California (Pearcy et al. 1989; Love et al. 1991; Stein et al. 1992; Yoklavich et al. 2000). Even *Sebastes* species in the eastern and western Atlantic Ocean have been found to be more abundant in

areas with higher levels of seafloor structure (Husebo et al. 2002; Auster et al. 2003). There is also limited evidence that in otherwise unstructured areas, the addition of seafloor structure in an ecosystem where rockfish occur can increase the abundance of the taxa (Emery et al. 2006; Love and York 2006; Love et al. 2006). For POP, there are also indications that habitat limitation and habitat-related processes like growth in the juvenile stages can dampen recruitment variability (Iles and Beverton 2000; Rooper et al. 2012). Although intra-ecosystem comparisons of habitat use by fishes and invertebrates are fairly common in the literature, we could find no similar cross-ecosystem comparisons using the same groups of species and methodologies. The global consistency of the effects of structure on rockfish behavior within multiple ecosystems and at an individual scale suggests that differences in density at transects between ecosystems are influenced by the amount of available seafloor structure, although other factors such as food availability, competitors, and predator abundance undoubtedly have an effect.

For flatfishes, crabs, thornyheads, grenadiers, and pollock observed in this study, there was no evidence of positive association with seafloor structure at either the transect-level analysis or the individual analyses. For flatfishes, this is consistent with previous studies from around the world that indicate unconsolidated sediments are the preferred habitats for these species (Jager et al. 1993; McConnaughey and Smith 2000; Amezcua and Nash 2001), although there is some evidence that for smaller individuals emergent epifauna can be important in reducing predation risk (e.g., Ryer et al. 2004). Little is known of habitat associations for the two deep-water taxa (grenadiers and thornyheads), although some studies have found negative associations with seafloor substrates and specifically deep-sea corals and sponges (Else et al. 2002; Rooper and Martin 2009) and associations with sedimentary substrate (Stein et al. 1992; Lauth et al. 2004). The gadids examined in this study (Pacific cod and pollock) are less demersally associated than the other species. Both species are schooling, with pollock often forming large schools that are targeted by midwater fisheries. Both species are also migratory; for example, Pacific cod tagging studies have shown migration between the Gulf of Alaska and EBS (Shimada and Kimura 1994). Cod have shown some association with structured habitats as small juveniles (Tupper and Boutilier 1995; Abookire et al. 2007; Laurel et al. 2007), but the cod observed during this study were all larger than juvenile sizes,

which may have accounted for their relative indifference to structure-forming invertebrates. Pollock are not known to associate with structure-forming invertebrates even as juveniles, which is consistent with our findings.

This study and others have shown that rockfishes are strongly associated with seafloor structure. The results of the current study indicate that more structure results in a higher density of fish. The results also show that the size of the structure relative to fish size influences how close rockfish are to structure. The implication of this research is that the presence of more structure increases the density of Pacific rockfishes. Deep-sea corals and sponges provide additional structure in rocky habitats and a primary source of structure in otherwise flat, uniform substrates, making them an important ecosystem components for rockfishes. Removal of deep-sea corals and sponges during routine fishery operations using bottom-contacting gear reduces the total amount of structure and is likely to reduce the overall density of rockfishes. It also follows that if all other factors (food availability, larval supply, etc.) are equal, an increase in abundance and (or) size of corals and sponges is likely to support higher densities of rockfishes in a region.

Acknowledgements

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