

The area–heterogeneity tradeoff applied to spatial protection of rockfish (*Sebastes* spp.) species richness

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Abstract

The “area–heterogeneity tradeoff” hypothesis predicts unimodal effects of habitat heterogeneity on species richness, implying that habitats with intermediate heterogeneity may be priority for spatial protection. Alternatively, if heterogeneity effects are positive, then protecting the most heterogeneous habitats may take precedence. We tested for unimodal effects of habitat heterogeneity on the species density (area-corrected richness) of rockfishes (*Sebastes* spp.): long-lived, benthic fishes vulnerable to over-exploitation. Inconsistent with predictions, topographic structural complexity had a strong linear effect on species density; other heterogeneity measures had weaker, positive effects and the only unimodal effect (depth range) was weak. The clear implication is that, to protect the highest density of rockfish species, marine protected areas should include the most topographically complex substrates. Our results can also help refine and test species distribution models needed to inform spatial planning where in situ surveys are lacking. The area–heterogeneity tradeoff generates useful predictions for which support may be context-dependent.

KEYWORDS

area–heterogeneity tradeoff, biogenic structural complexity, cold water corals, glass sponges, marine protected area network, Northern Shelf Bioregion, *Sebastes*, spatial protection, species richness, topographic structural complexity

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1 | INTRODUCTION

Since the 1960s, many studies have supported the hypothesis that species richness increases with greater habitat heterogeneity at local to regional scales. Mechanisms that might drive this relationship include an increase in the number of niches available due to habitat and resource complexity (Tews et al., 2004). The richness–heterogeneity relationship, however, may not always be linear or positive (Allouche, Kalyuzhny, Moreno-Rueda, Pizarro, & Kadmon, 2012).

One hypothesis is that, given a fixed total area, an increase in habitat heterogeneity reduces the sizes of habitats used by individual species, which increases the risk of stochastic extinction. Thus, even though more heterogeneous environments contain a greater number of habitats that could potentially support more species, an “area–heterogeneity tradeoff” may preclude this potential from being realized (Kadmon & Allouche, 2007). The effects of habitat heterogeneity, therefore, should be negative for species abundances, positive for extinction rates, and unimodal for species richness. These effects should weaken, however, as niche breadth increases (Allouche et al., 2012). At a landscape scale, evidence from bird communities has supported these predictions (Allouche et al., 2012). Area–heterogeneity tradeoffs might also occur at smaller spatial scales. On marine rocky reefs, the richness–heterogeneity relationship was unimodal for benthic fishes sampled within 120 m² transects (Paxton, Pickering, Adler, Taylor, & Peterson, 2017).

Habitat structural complexity—the variation in vertical relief, overall size and abundance of structures and interstices at a specified scale—is a form of habitat heterogeneity. It can be topographic, as determined by different-sized rock particles and other geologic features (Paxton et al., 2017; Stein, Gerstner, & Kreft, 2014). It can also be biogenic, as determined by marine sessile invertebrates (Luckhurst & Luckhurst 1978), macroalgae (Bodkin, 1988), or terrestrial vegetation (Stein et al., 2014).

In marine ecosystems, variation in slope—from plateaus to cliffs—is another form of habitat heterogeneity; it influences upwelling, downwelling, and currents that affect particle transport (Thomson, 1981) and energetic costs incurred by fish (Webb, 1989). Also, depth range in the ocean is equivalent to elevation range on land; both forms of heterogeneity may affect community composition (Allouche et al., 2012; Yoklavich et al., 2000).

Understanding the contexts in which richness–heterogeneity relationships are positive or unimodal is important for the design of protected areas. If species richness responds to an area–heterogeneity tradeoff, then it may be priority to protect habitats with intermediate heterogeneity (Allouche et al., 2012). Alternatively, if heterogeneity effects are positive, then protecting the most heterogeneous habitats may be priority.

We applied the area–heterogeneity tradeoff to investigate drivers of spatial variation in the area-corrected richness, or species density, of rockfishes (*Sebastes* spp.) in the central coast of British Columbia (BC), Canada (Appendix S1). We focus on this marine genus of primarily benthic species because it is diverse (≥ 37 species in BC). Some rockfishes are long-lived (maximum age >80 years: Love, Yoklavich, & Thorsteinson, 2002), vulnerable to overexploitation, evolutionarily isolated (Magnuson-Ford, Ingram, Redding, & Mooers, 2009), culturally significant to Indigenous people, and undergoing declines in BC (McGreer & Frid, 2017).

The relationship between habitat heterogeneity and local species density is potentially nonlinear in rockfishes because species vary in the range of depths and habitats they occupy (Love et al., 2002). Species with wider preferences may overlap spatially with species that have narrower preferences only at a subset of depths, slopes and levels of structural complexity. Further, some rockfishes confine their adult lives to small areas (≤ 100 m²) of specialized habitat and move longer distances infrequently (Freiwald, 2012; Love et al., 2002), potentially contributing to an area–heterogeneity tradeoff. Additionally, some rockfishes associate with structure-forming benthic invertebrates—such as glass sponges and corals—which might provide a flow refuge against strong currents (Du Preez & Tunnicliffe, 2011); biogenic structures might also have unimodal effects on species density.

Understanding species density–heterogeneity relationships for rockfishes is important to ongoing processes for spatial protection. The central coast of BC is part of the Northern Shelf Bioregion, which Canada intends to partially protect in a network of marine protected areas (MPAs) by 2020 (<https://mpanetwork.ca/bcnorthernshelf/>). Data available to inform MPA network design in nearshore areas, however, are limited. To fill data gaps, since 2013 the Wuikinuxv, Nuxalk, Heiltsuk and Kitasoo/Xai'xais First Nations—coordinated by the Central Coast Indigenous Resource Alliance (CCIRA)—have surveyed rockfishes and their habitats over a wide depth range (hereafter “CCIRA surveys”). These surveys also have filled some data gaps in the nearshore distribution of corals (Alcyonacea and *Styaster* spp.) and glass sponges (Hexactinellida), which have rigid structures and (except for *Styaster*) reach heights ≥ 1.5 m (Lamb & Hanby, 2005).

We applied the framework of the area–heterogeneity tradeoff to generate predictions relevant to marine spatial planning, which we tested with data from CCIRA surveys. Specifically, we predicted unimodal effects on rockfish species density of habitat structural complexity (biogenic and topographic), slope range, and depth range. Tests of these predictions are important for determining whether habitats with intermediate or high heterogeneity should be priority for spatial protection.

TABLE 1 Characteristics of each survey method for details, see Appendix S2

Method	Years sampled	Mean depth and range (m)	Sample size	Data collected	Caveats
Towed video	2015–2017	73 (2–230)	578 subtransects nested within 119 transects. Transects covered 100–1200 m ² . Subtransects averaged 120 m ² (range 100–130 m ²), covered a range of depths, and were contiguous within transects.	Habitat characteristics, % cover of glass sponges, presence/absence of corals (Table 2) and counts of each rockfish species.	Avoidance/attraction responses by fish to lights and camera could bias counts for some species. Camera field of view is narrow (median = 1.95 m), likely leading to much lower fish counts than dive surveys.
Dive surveys	2013, 2015–2017	23 (13–35)	249 transects nested within 135 sites. Transects covered 120 m ² (480 m ³) at fixed depths.	Habitat characteristics (Table 2) and counts of each rockfish species.	Restricted to shallower depths where some rockfishes, corals, and concentrations of glass sponges are unlikely to occur.

2 | METHODS

2.1 | Field surveys

CCIRA surveys used two fishery-independent visual methods to document rockfishes and their habitats in nearshore areas of BC's central coast: dive transects and towed video transects. Dive transects covered 120 m² at fixed depths between 13 m and 35 m. Towed video transects covered areas of 100–1200 m² to a maximum depth of 230 m. For analyses, towed video transects were divided into contiguous subtransects that averaged 120 m² (range 100–130 m²) and encompassed a range of depths (Table 1; Appendices S1, S2)

Surveys targeted rocky reefs embedded in a matrix of soft substrates and varying in depth and structural complexity, thereby sampling a wide range of habitat attributes expected to be used by a diversity of rockfish species (Appendix S3). Analyses exclude cases with uncertain species identifications due to the brevity of an encounter (dive survey) or image blurriness (towed video). For fieldwork details, see Appendices S1 and S2.

2.2 | Testing predictions based on the area–heterogeneity trade-off

We tested predictions with generalized linear mixed models (GLMMs: Zuur, Ieno, Walker, Saveliev, & Smith, 2009) implemented in R and applied separately to towed video and dive data. We used topographic structural complexity as a predictor and excluded the percent covers of the geologic substrates that provide its building blocks (for correlations between these variables, see Appendix S4). This approach allowed for parsimonious analyses consistent with prior studies that found structural complexity, rather than the identity of

its individual components, to be the stronger driver of diversity (Luckhurst & Luckhurst 1978; Tews et al., 2004).

Species density—estimated as number of rockfish species per 120 m², stratified by dive transect or towed video subtransect—was the response variable. Species density is a useful metric for understanding the value of spatial protection because it indicates the potential number of species protected per unit area.

For the dive data we used a mixed effect Poisson model (R package lme4, version 1.1–14: Pinheiro & Bates, 2000). Towed video data, however, had a larger proportion of zero values for species density (46%, vs. 2.4% for dive data) and were analyzed with a zero-inflated mixed effect Poisson model (glmmTMB, version 3.4.2: Magnusson et al., 2017). Because tow video transects ranged from 100 to 130 m², area was used as an offset (Crawley, 2013) in the model for towed video data.

Random effects identified individual sites (dive data) or transects (towed video data). These accounted for the spatial autocorrelation of 2–3 transects per dive site, and of 2–12 subtransects per towed video transect. An observation-level random effect corrected for overdispersion in both models.

Fixed effects lacking explanatory power were eliminated via AIC model selection (Burnham & Anderson, 2002). When competing models did not differ (i.e., $\Delta\text{AIC} < 2$), we selected the most parsimonious one. For dive data models, all combinations of predictors were considered. For towed video, which included a greater number of predictors, variables were eliminated stepwise.

For the towed video data, fixed effects included polynomial and linear terms for topographic structural complexity, percent cover category of glass sponges, and the ranges (maximum minus minimum values) of slope category and depth. A given range may occupy deeper or shallower portions of the water column (depth), or steeper or flatter bathymetry (slope),

TABLE 2 Habitat variables recorded

Variable	Definition	^a Metric
Fines	Particles with diameter <6 cm (sand, pebbles, mud, shell hash).	Percent cover category
Cobbles	Rock fragment with diameter 6–25 cm	Percent cover category
Boulder	Rock fragment with diameter ≥26 cm	Percent cover category
Bedrock	Unbroken, solid rock	Percent cover category
Topographic structural complexity	Variation in vertical relief, overall size and abundance of structures and interstices—as determined by the relative abundance of different-sized rock particles and corrugations in bedrock—at the scale of 120 m ² sampling units.	Visual ranking based on primary substrate, with larger numbers indicating greater complexity: 0: fines 1: cobbles and/or cracks in bedrock are small and few. 2: boulders <50 cm diameter, large cracks in bedrock often present 3: boulders 50–100 cm diameter and a combination of smaller boulders or abundant large cracks in bedrock. 4: boulders with >100 cm diameter, and a combination of smaller boulders or large cracks in bedrock.
Slope	Steepness category.	1: <10 degrees 2: 11–40 degrees 3: 41–60 degrees 4: >60 degrees
Depth	Depth of habitat	Metres (continuous variable).
^b Coral	Alcyonacea: mainly <i>Paragorgia arborea</i> and <i>Calcigorgia spiculifera</i> . Stylasteridae: <i>Stylaster</i> spp. was abundant at a single site.	Presence/absence (binomial variable)
^b Glass sponges	Hexactinellida: mainly <i>Aphrocallistes vastus</i> , <i>Farrea occa</i> , <i>Heterochone calyx</i> , <i>Rhabdocalyptus dawsoni</i> , and <i>Staurocalyptus dowlingi</i> .	Percent cover category

^aPercent cover categories are 0%, 1–25%. 26–50%. 51–75%, 76–100%.

^bDuring dive surveys (which are restricted to shallower depths), corals were absent and glass sponges sparse.

which may influence encounter rates with different species (Love et al., 2002). Thus, we included linear terms for mean depth and mean slope as predictors. Additionally, we included a linear term for the presence/absence of corals, but this was limited to Alcyonacea. (*Stylaster* were excluded because they are ≤15 cm tall and unlikely to provide sufficient structure for rockfishes.) We removed one outlier subtransect with a 130 m depth range and a species density of 4.74 (other species densities at similar depth ranges were much lower).

During dive surveys, depths did not vary within transects and were restricted to ≤35 m, where corals were absent and glass sponges sparse. Predictors tested with dive data, therefore, were polynomial and linear terms for topographic structural complexity and slope range, and linear terms for depth and mean slope. We removed one outlier transect with 5 m depth (others were 13–35 m).

For visual displays of the dive model, 95% confidence intervals were calculated via bootstrapping with 500 simulations (using lme4 package function bootMer). For the towed video model, we calculated standard errors with the R function predict.GLMMTMB. Appendix S5 describes model diagnostics.

3 | RESULTS

We recorded a total of 22 rockfish species (Appendix S3). Seventeen species had a wide depth range, which included shallow habitats (≤35 m deep) observable by both survey methods, while five species were recorded only at relatively deep depths (≈50–130 m) observable only by towed video (Appendix S8).

In the dive data, topographic structural complexity and depth had positive effects on species density (Table 3). The GLMM estimated that, on average, species density increased 3.2-fold between complexity categories 1 and 4, and by nearly 60% between 10 m and 30 m depths (Figures 1a,b). Slope range and mean slope did not affect species density (Appendix S6).

In the towed video data, overall values for species density were much lower than in the dive data (Figure 1), possibly due to the more limited field of view of the camera relative to that of divers (Appendix S2). In these data, topographic structural complexity and glass sponge cover had positive effects on species density, although uncertainty around these estimates

TABLE 3 Best generalized linear mixed models (as determined by AIC model selection) describing variation in species density of rockfishes, by survey type. “Complexity” refers to topographic structural complexity

Survey type	Predictor	Coefficient	SE	z	Pr(> z)
Dive	Intercept	1.32282	0.03374	39.2	<2E-16
	Depth	0.14075	0.03172	4.44	9.11E-06
	Complexity	0.35162	0.03344	10.52	<2E-16
Towed video	Intercept	-0.37146	0.07861	-4.725	2.30E-06
	Depth (mean)	-0.16182	0.07332	-2.207	0.0273
	Glass sponge cover	0.12138	0.05569	2.180	0.0293
	Slope range	0.09972	0.04592	2.171	0.0299
	Complexity	0.41256	0.05627	7.332	2.27E-13
	Depth range	1.06917	1.52892	0.699	0.4844
	(Depth range) ²	-3.13803	1.66301	-1.887	0.0592

increased at higher predictor values (Figures 1c,e; Table 3). On average, species density increased 5.7-fold between complexity categories 1 and 4 and 66% between glass sponge cover categories 0 and 2; support for the latter effect, however, is weak due to highly variable species densities at low values for sponge cover and scarce data at very high values (Figures 1c,e). Slope range and mean depth had positive and negative effects on species density, respectively. On average, species density declined by 32% between 10 m and 100 m depths and increased by 38% between slope range values of 0 and 3 (Figures 1d,f; Table 3). Depth range showed the only unimodal effect; on average, species density peaked at a ≈ 70 m range, where it was 33% and 81% greater than at depth ranges of 0 m and 150 m, respectively. Support for this unimodal effect, however, is weak due to highly variable species densities at low depth range values and scarce data at intermediate to high values (Figure 1g; Table 3). Mean slope and coral presence had no effect on species density (Appendix S7).

4 | DISCUSSION

Our results were largely inconsistent with unimodal relationships predicted by an area–heterogeneity tradeoff. Of four heterogeneity measures examined, topographic structural complexity was the strongest predictor of variation in species density of rockfishes and its effect was linear. Only depth range had a unimodal effect, which was weak and poorly supported.

In contrast, Paxton et al. (2017) found a unimodal effect of topographic structural complexity on the richness of marine benthic fishes, which suggests that further research is needed to better understand variation in the shape of richness–heterogeneity relationships. For example, the prediction that unimodal relationships should weaken as niche breadth increases has been supported by data from bird com-

munities (Allouche et al., 2012), but not yet tested for marine benthic fishes.

From the standpoint of spatial protection of nearshore areas, the clear implication of our study is that the most topographically complex substrates are likely to have the highest density of rockfish species and therefore should be considered for inclusion in the MPA network being designed for the Northern Shelf Bioregion. Also, our towed video data, which encompassed a maximum depth of 230 m, found a negative effect of mean depth on species density. Though weak, the depth effect is consistent with broader biogeographic patterns (Costello & Chaudhary, 2017), suggesting that species density protection might be maximized in structurally complex habitats that also are relatively shallow. A focus on shallow habitats, however, would result in several tradeoffs. Our findings (Appendix S8) and those of others (Love et al., 2002; Yoklavich et al., 2000) indicate that the species composition of rockfish communities may vary with depth; protection of deeper habitats, therefore, may encompass fewer species, but some of those species may be found only at deeper depths. Further, some culturally significant rockfishes (e.g., *S. maliger*, *S. ruberrimus*) are more abundant, larger or older at depths deeper than 80 m, even in nearshore areas (Frid, McGreer, Haggarty, Beaumont, & Gregr, 2016; McGreer & Frid, 2017). In addition, other benthic fishes of ecological and cultural importance, such as Pacific halibut (*Hippoglossus stenolepis*), often use soft substrates where rockfishes are less common. Optimization analyses for MPA network design are needed to address tradeoffs between protecting different biological values that differ in their depth and substrate distributions (Ball, Possingham, & Watts, 2009).

Although evidence that cover of glass sponges and corals increases the species density of rockfishes was, respectively, weak or absent in our study, these structure-forming invertebrates have their own inherent biological value. Trawl and longline fisheries physically damage corals and sponges (Du Preez & Tunnicliffe 2011). The same fisheries remove

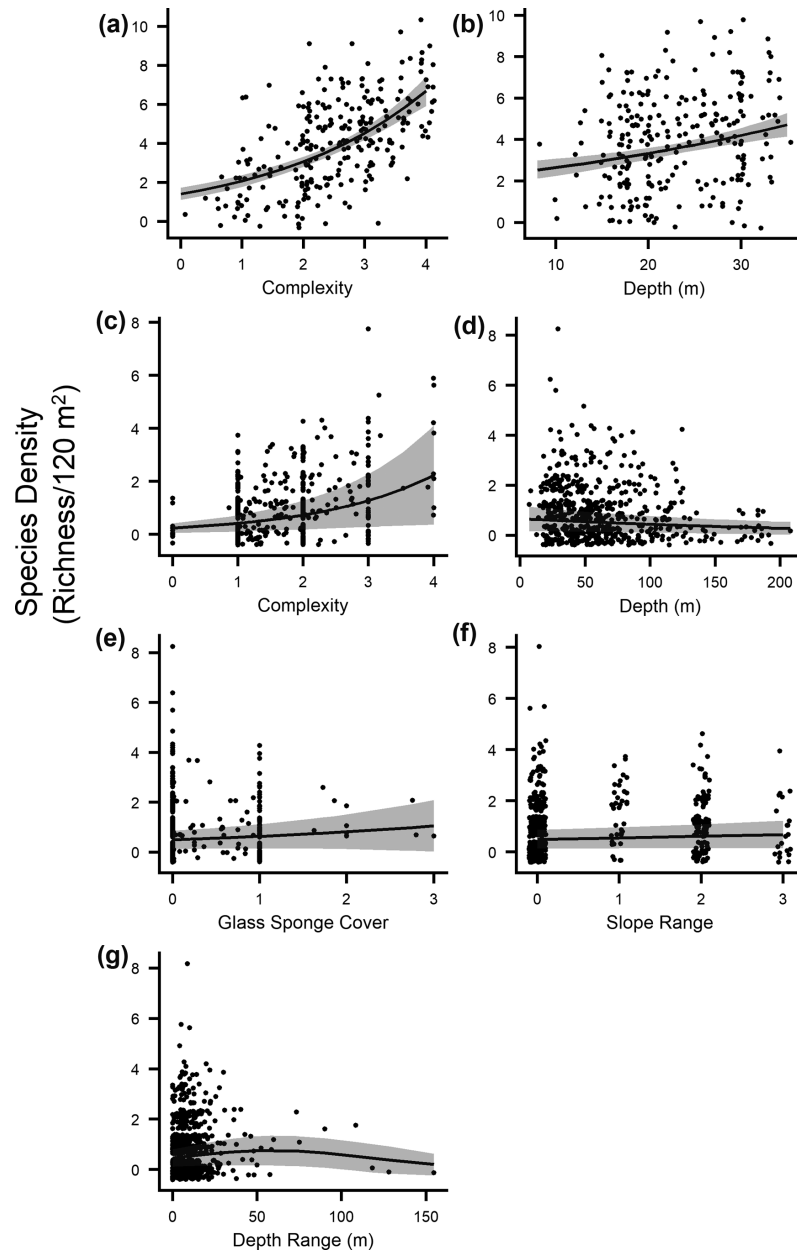


FIGURE 1 Rockfish species density in relation to predictors (fixed effects) tested with (a, b) dive data and (c–g) towed video data. Lines are log-linear estimates from the best GLMMs (Table 3); fixed effects not displayed were held at mean values. Bands are 95% confidence intervals. Circles are bivariate raw data with random jitter

rockfish and other benthic fishes, reducing abundance and truncating size and age structure, which affects per capita fecundity (Hixon, Johnson, & Sogard, 2014). Well-situated MPAs with adequate monitoring and compliance can protect corals and glass sponges (Huvette, Bett, Masson, Le Bas, & Wheeler, 2016) and promote rockfish recovery and persistence, although benefits for species with slow life histories may require decades to manifest (Starr et al., 2016).

Toward these ends, our study makes two contributions. First our surveys identified previously undocumented nearshore areas important to corals, glass sponges and

rockfish species density (Appendix S9); these areas should be considered for inclusion in the developing MPA network. Second, in situ field surveys like ours are expensive and time-consuming; expedient conservation actions, therefore, often rely on environmental data estimated with remote methods, such as bathymetric surveys (e.g., Gregr, Lessard, & Harper, 2013). These data can then be modelled spatially to predict species distributions and inform spatial planning (e.g., Yamanaka & Logan, 2010). The richness–heterogeneity relationships that we uncovered can be used to develop, test, and refine such models, thereby informing MPA network design where in situ surveys are lacking.

More generally, a recent meta-analysis identified the need for “future empirical studies and syntheses focusing on nonlinear effects” to test the “generality of the area–heterogeneity trade-off hypothesis” (Stein et al., 2014). Accordingly, our study adds to the body of evidence suggesting that the area–heterogeneity tradeoff generates useful predictions for conservation planning, yet support for these predictions may be context-dependent (Bar-Massada & Wood, 2014).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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