Growth parameter *k* and location affect body size responses to spatial protection by exploited rockfishes

Madeleine McGreer*[1], Alejandro Frid*[1,2], Tristan Blaine[1], Sandie Hankewich[3], Ernest Mason[3], Mike Reid[4], Hannah Kobluk[1]

*Equal contributions

[1] Central Coast Indigenous Resource Alliance, Campbell River, BC, Canada
[2] School of Environmental Studies, University of Victoria, Victoria, BC
[3] Kitasoo/Xai'xais Fisheries, Klemtu, BC, Canada
[4] Heiltsuk Integrated Resource Management Department, Bella Bella, BC, Canada

Corresponding Author:
Alejandro Frid[1,2]
Central Coast Indigenous Resource Alliance, 2790 Vargo Rd, Campbell River, BC, V9W 4X1, Canada
Email address: alejfrid@gmail.com

Abstract

For many fish taxa, trophic position and relative fecundity increase with body size, yet fisheries remove the largest individuals, altering food webs and reducing population productivity. Marine reserves and other forms of spatial protection can help mitigate this problem, but the effectiveness of these management tools may vary interspecifically and spatially. Using visual survey data collected on the Central Coast of British Columbia, for 12 species of exploited rockfish we found that body size responses to spatial fishery closures depended on interspecific variation in growth parameter *k* (the rate at which the asymptotic body size is approached) and on location. For two closures, relative body sizes were larger at protected than at adjacent fished sites, and these differences were greater for species with lower *k* values. Reduced fishery mortality likely drove these results, as an unfished species did not respond to spatial protection. For three closures, however, body sizes did not differ between protected and adjacent fished sites, and for another closure species with higher *k* values were larger at fished than at protected sites while species with lower *k* values had similar sizes in both treatments. Variation in the age of closures is unlikely to have influenced results, as most data were collected when closures were 13 to15-years-old. Rather, the lack of larger fish inside four of six spatial fishery closures potentially reflects a combination of smaller size of the area protected, poor fisher compliance,

40 and lower oceanographic productivity. Interspecific differences in movement behavior did not
41 affect body size responses to spatial protection. To improve understanding, additional research
42 should be conducted at deeper depths encompassing the distribution of older, larger fish. Our
43 study—which was conceptualized and executed by an alliance of Indigenous peoples seeking to
44 restore rockfishes—illustrates how life history and behavioral theory provide a useful lens for
45 framing and interpreting species differences in responses to spatial protection.
46

Introduction

47

48 For centuries, many Indigenous cultures have recognized that protecting parts of the ocean from
49 exploitation mitigates human impacts on biodiversity and contributes to fishery sustainability
50 (Johannes, 1978; Jones, Rigg & Lee, 2010; Ban et al., 2018). Consistent with the knowledge and
51 practices of these cultures, there is growing evidence that marine reserves or other forms of
52 spatial protection promote recovery from exploitation (Baskett & Barnett, 2015), and that
53 spillover of adults and larvae from protected areas can enhance adjacent fisheries (Di Lorenzo,
54 Claudet & Guidetti, 2016; Baetscher et al., 2019).
55   The benefits of spatial protection often are quantified as increases in the density, biomass,
56 and body sizes of exploited species (Baskett & Barnett, 2015). Understanding factors affecting
57 body size distributions is particularly important because fisheries remove the largest individuals,
58 often at great ecological cost (Strong & Frank, 2010; Hixon, Johnson & Sogard, 2014). Larger
59 individuals tend to occupy higher trophic positions (e.g. Trebilco et al., 2016; Olson et al., 2020),
60 and their removal may alter food web structure (Shackell et al., 2010; Zgliczynski & Sandin,
61 2017). Further, for many fish taxa the relationship between fecundity and body size is
62 hyperallometric (a power function with exponents >1), such that larger females contribute
63 disproportionately more offspring (per unit of body size) than smaller females (Dick et al.,
64 2017a; Barneche et al., 2018). Size differences between protected and fished areas, therefore, can
65 signal the extent to which spatial protection promotes species recoveries and restores food webs.
66   The benefits of spatial protection, however, can differ across species, and understanding this
67 variation may help predict reserve performance (Jennings, 2000; Claudet et al., 2010; Kaplan et
68 al., 2019). Species with longer lifespans often have slower growth rates, later maturity, and other
69 traits which increase their vulnerability to exploitation and reduce their recovery rates during
70 fishery reprieves (Jennings, 2000). Consequently, the benefits of spatial protection may require
71 more time to manifest in longer-lived species (Starr et al., 2015; Kaplan et al., 2019).
72   Variation in parameter k of the von Bertalanffy growth function, which depicts the rate at
73 which the asymptotic body size is approached, should influence the time required by different
74 species to restore a larger size structure after the implementation of spatial protection (Jennings,
75 2000; Kaplan et al., 2019). Additionally, species characterized by smaller movements and greater
76 site fidelity are more likely to remain within a protected area (Hannah & Rankin, 2011) and may
77 benefit more from spatial protection than more mobile species (Kramer & Chapman, 1999;
78 Moffitt et al., 2009). These predictions, however, do not apply to unfished species, for which

79 environmental variation is a primary driver of population characteristics (Claudet et al., 2010;
80 Caselle et al., 2015).
81   Rockfish (*Sebastes* spp.), a genus of marine fish with diverse life history traits, allow tests of
82 these ideas. In the northeast Pacific, maximum lifespans range across rockfish species from two
83 decades to two centuries, and interspecific variation in body size and growth parameters are
84 similarly wide (Love, Yoklavich & Thorsteinson, 2002). While most rockfishes associate with
85 rocky reefs, their behavior ranges from sedentary to very mobile and from demersal to
86 benthopelagic. Most rockfishes are exploited yet some small planktivores are unfished (Love,
87 Yoklavich & Thorsteinson, 2002).
88   In British Columbia, Canada, commercial and recreational sectors overfished rockfishes
89 during the latter part of the 20th century, diminishing their abundance and body sizes (Yamanaka
90 & Logan, 2010; Eckert et al., 2017). During the 2000s federal legislators implemented more
91 conservative management and established a network of spatial fishery closures known as
92 Rockfish Conservation Areas (RCAs) where commercial and recreational fishers cannot use
93 bottom trawls, groundlines, or hook-and-line gear (Yamanaka & Logan, 2010; Appendix S1).
94 For some species, however, declines in size and age structure have continued and their biomass
95 remains depressed (McGreer & Frid, 2017 and references within). RCAs can help reverse these
96 trends, yet prior studies in British Columbia, conducted only 5-7 years after RCA
97 implementation, found no evidence of larger or more abundant rockfishes inside protected sites
98 (Haggarty, Shurin & Yamanaka, 2016; Olson, Trebilco & Salomon, 2019). As time since RCA
99 implementation progresses, size and biomass increases are more likely to be detected (Starr et
100 al., 2015; Keller et al., 2019), particularly for shorter-lived species with greater k values (Kaplan
101 et al., 2019).
102   Analyses of RCA benefits must account for variation in habitat characteristics which,
103 independently of exploitation, affect the distribution and sizes of rockfish. For some demersal
104 species, relative abundance may increase with topographic structural complexity and larger or
105 older individuals tend to use greater depths than smaller or younger individuals (Love, Yoklavich
106 & Thorsteinson, 2002). Benthopelagic species, however, have a wider range of vertical
107 movements into the water column (Love, Yoklavich & Thorsteinson, 2002; Hannah & Rankin,
108 2011) and their relationships to depth or topographic structural complexity might be more
109 variable.
110   Canada is among the countries where Indigenous people are using their traditional
111 knowledge and science to improve marine conservation (Jones, Rigg & Lee, 2010; Ban et al.,
112 2018; Ban, Wilson & Neasloss, 2020). Since 2013, the Central Coast Indigenous Resource
113 Alliance (CCIRA)—comprised of the Wuikinuxv, Nuxalk, Heiltsuk and Kitasoo/Xai'xais First
114 Nations—has been surveying rockfish populations and their habitats (Frid et al., 2018) inside and
115 outside RCAs of British Columbia's Central Coast (Fig. 1; Appendix S2). Data collected to date
116 represent RCAs that were 8 to 15-years-old and encompass the earliest stage expected for the
117 benefits of spatial protection to manifest for rockfishes (Keller et al., 2019; Kaplan et al., 2019).

118   Within this temporal context, we used CCIRA's visual survey data to test the hypothesis that
119 body size responses to spatial protection vary according to species life history traits, movement
120 behavior, and susceptibility to fishing, while controlling for depth and topographic structural
121 complexity. We predicted that the body sizes of exploited species would be larger inside RCAs
122 than in adjacent fished areas, but the strength of this effect would decrease for species which
123 require more time to reach their asymptotic body size (i.e. have lower k values) (Jennings, 2000;
124 Kaplan et al., 2019) or that are more mobile (Kramer & Chapman, 1999; Moffitt et al., 2009).
125 We also predicted that the body sizes of Puget Sound rockfish (*S. emphaeus*), a small planktivore
126 unlikely to be caught by fishing gear (Love, Yoklavich & Thorsteinson, 2002), would not differ
127 between protected and fished sites (Claudet et al., 2010; Caselle et al., 2015).
128   In addition to testing *a priori* predictions, we examined differences in conservation
129 effectiveness between RCA locations. Though exploratory, this aspect of our research was
130 motivated by the need to understand whether some RCAs are performing poorly and the
131 potential ways to improve their management or design (Haggarty, Martell & Shurin, 2016; DFO,
132 2019a,b).
133 .

Materials & Methods

135 *Ethics statement*
136 Data collection was observational and did not require permits from federal agencies. The
137 Wuikinuxv, Kitasoo/Xai'xais, Heiltsuk and Nuxalk First Nations hold Indigenous rights to their
138 own territories, where all data were collected. Scientific staff conducting field research—who are
139 members of these Nations or work directly for them—had the approvals required by Indigenous
140 rights holders.
141
142 *Surveys by SCUBA divers*
143 During March-April or July-October of 2013 and 2015-2019, we sampled rocky reefs, which
144 were located through local Indigenous knowledge or a bathymetric model (Haggarty &
145 Yamanaka, 2018). Within the constraints of weather, we attempted to balance sample sizes
146 between paired sites inside RCAs (protected treatment) or outside the same RCA but ≤10 km
147 from its nearest boundary (control treatment) (Fig. 1).
148   SCUBA divers collected visual data on rockfish and their habitats along depth contours
149 within transects that were 30 m-long by 4 m-wide by 4 m-high (480 m^3). Dives generally
150 included three transects stratified by depth: 25-35 m, 15-18 m, and ≤6 m. Observations included
151 estimates of topographic structural complexity (variation in vertical relief, size, and abundance of
152 rocky structures: Appendix S3), relative density by species (count/480 m^3), and total lengths of
153 individual fish. Video was taken during most transects to corroborate habitat descriptions and
154 species identifications.
155   Total lengths were estimated visually with the aid of a 1-metre-long ruler attached to a pole.
156 Early in their training, the 3 divers who collected these data tested their accuracy measuring fish
157 models attached to a line suspended in the water column. Comparisons of estimated and actual

158   sizes showed low measurement errors that did not vary with model size, and relatively low
159   variation between divers (Appendix S4).
160   Most fish were encountered alone or in small groups (<20 fish) and sized individually.
161   Benthopelagic species, however, sometimes formed larger schools. In these cases, divers sized
162   fish in clusters, recording a length and a multiplier for the corresponding fish count. This
163   approach allowed divers to avoid long pauses, reducing their influence on attraction or avoidance
164   behaviors that bias counts (Emslie et al., 2018). A tradeoff is that size estimates that may have
165   spanned 2-3 cm (had fish been sized individually) were collapsed into a single measurement
166   inflating peaks in the frequency of that measurement (see *Analyses*). For further details on dive
167   surveys, see Frid *et al.* (2018).
168
169   *Species characteristics*
170   We obtained literature values for maximum lifespan, maximum total length, total length at 50%
171   maturity, and von Bertalanffy growth parameter *k* (Table 1). The latter two parameters vary with
172   latitude (Love, Yoklavich & Thorsteinson, 2002), so we prioritized estimates from British
173   Columbia (Anderson, Keppel & Edwards, 2019); if unavailable, we used estimates from Oregon
174   and Washington. Species lacking sufficient observations or key information were not analyzed
175   (Appendix S5). The exception was Tiger rockfish (*S. nigrocinctus*), a long-lived species for
176   which we had a large sample size but which lacked data on growth rates; *k* for this species was
177   estimated as a function of maximum lifespan (Appendices S6, S7).
178   We used the literature or consulted three experts to class species behaviors according to a
179   combination of relative mobility (high or low) and habitat preference (benthopelagic or
180   demersal) (Table 1; Appendix S8). No species qualified as high mobility-demersal and the one
181   species classed as low mobility-benthopelagic had insufficient observations (Appendix S5).
182   Analyses, therefore, included only 2 behavioral categories: high mobility-benthopelagic and low
183   mobility-demersal (Table 1).
184   Species were classed as "exploited" or "unfished" based on fishery data compiled by
185   Anderson *et al.* (2019) or descriptions by Love *et al.* (2002). Only Puget Sound rockfish
186   qualified as unfished. With the caveat that Puget Sound rockfish have the smallest maximum size
187   in our sample, and therefore shows less body size variation than other rockfishes, we assumed
188   that size distributions for this species are driven primarily by environmental variability, and
189   therefore are an adequate control for the effects of exploitation and protection. Should this
190   assumption be wrong, body size increases under spatial protection are likely to be detected, as
191   Puget Sound rockfish have the highest *k* value in our sample (Table 1).
192
193   *Analyses*
194   We limited analyses to individuals with total lengths of ≥10 cm. Smaller individuals are unlikely
195   to be caught by fishing gear and their abundance is influenced by environmental variability
196   (Markel, Lotterhos & Robinson, 2017) outside the scope of analyses.

197   Total lengths were standardized as length anomalies (LA) which, pooling data from all
198   locations and all years, were calculated for each species as:

199
$$LA_s = \frac{Ls_i - Ls_{\bar{x}}}{Ls_{std}}$$

200   where Ls_i is the observed length for individual i belonging to species s and $Ls_{\bar{x}}$ and Ls_{std} are,
201   respectively, the mean and standard deviations of all lengths observed for species s. The use of
202   length anomalies, rather than actual lengths, allowed us to include multiple species that differ in
203   maximum body size into a single comprehensive analysis that tested for the effects of species
204   traits on responses to spatial protection. This approach also increased sample sizes, allowing us
205   to include all predictors of interest without overfitting the model.
206   Length anomaly was the response variable in two generalized least squares models (GLSMs)
207   implemented in R (Pinheiro et al., 2020). The first included all exploited species. The predictors
208   were RCA treatment (protected or control) and its two-way interaction with location (i.e., name
209   of RCA associated with protected and control treatments), k and its interaction with RCA
210   treatment, behavioral class and its interaction with RCA treatment, topographic structural
211   complexity and its interaction with behavioral class, and depth and its interaction with behavioral
212   class. Parameter k values (Table 1) were averaged for males and females, which divers cannot
213   distinguish visually. Because each site contained multiple transects, a Gaussian correlation
214   structure derived from the latitude and longitude of each sampling site (projected into the Albers
215   coordinate system) accounted for the spatial autocorrelation of residuals (Pinheiro & Bates,
216   2000). The second GLSM was specific to the unfished Puget Sound rockfish; its predictors were
217   depth, topographic structural complexity, and RCA treatment and its interaction with location.
218   This analysis also included the Gaussian correlation structure derived from the coordinates of
219   each sampling site.
220   Although surveys spanned 6 years, sampling across RCA age-location-treatment
221   combinations was unbalanced (Appendix S9), precluding GLSMs from testing RCA age by
222   treatment interactions. Consequently, analyses pooled data for RCA ages of 8-15 years, with
223   ages 13-15 being best represented (Appendices S9, S10).
224   To reduce skew in size frequency distributions, multipliers assigned to similarly sized
225   schooling fish were truncated to the 95th percentile of their distribution and incorporated into
226   GLSMs as weights. Competing models were compared with AICc model selection procedures
227   (Burnham & Anderson 2002). We expected the independent effects of topographic structural
228   complexity and depth to affect responses (Love, Yoklavich & Thorsteinson, 2002); these
229   predictors did not undergo model selection, reducing the number of competing models. Results
230   are presented in terms of the best GLSMs. Quantile-quantile plots, residuals vs fitted plots, and
231   correlation values between variables were examined to verify model assumptions.
232
233 **Results**

234   Of 13224 observations for exploited species (Appendix S11), 73% were from high mobility-
235   benthopelagic species, and 27% from low mobility-demersal species. The proportion of
236   individuals that had reached or exceeded length at 50% maturity was 47% for low mobility-
237   demersal species and 5% for high mobility-benthopelagic species (Appendix S12).
238   The effects of spatial protection on the body sizes of exploited species depended on growth
239   parameter k and RCA location, but not on behavioral class (Fig. 2; Appendices S13a, S14a). At
240   two RCAs (West Aristazabal, Goose Island), body sizes were larger at protected than control
241   sites, but these differences were greater for slower- than for faster-growing species (Fig. 3). At
242   three RCAs (Fish Egg Inlet, McMullin Group, Smith Sound), body sizes did not differ between
243   protected and control sites, regardless of k values. At the remaining RCA (Kitasu Bay), species
244   with greater k values were larger at control than at protected sites while species with lower k
245   values had similar sizes in both treatments (Fig. 3). Independently of RCA treatment, the body
246   sizes of high mobility-benthopelagic species increased with depth and decreased with greater
247   topographic structural complexity. In contrast, the body sizes of low mobility-demersal species
248   increased with both depth and topographic structural complexity (Fig. 4).
249   For the unfished Puget sound rockfish, body sizes increased with depth and topographic
250   structural complexity but did not differ between RCA treatments or locations (Fig. 2b,
251   Appendices S13b, S14b, S15).
252
253   Discussion
254   We predicted that the body sizes of exploited species would be larger inside RCAs than in
255   adjacent fished areas, but the strength of this effect would decrease for species which require
256   more time to reach their asymptotic body size (i.e. have lower values for growth parameter k) or
257   that are more mobile. Our results were inconsistent with these predictions. At two RCAs (Goose
258   Island, West Aristazabal) the body sizes of exploited rockfishes were larger at protected than at
259   adjacent fished sites, but these differences *increased* with lower k values. One potential
260   explanation for this result is that body size differences between protected and exploited sites
261   could be influenced by an interaction between parameter k and the intensity of exploitation (see
262   Jennings, 2000; Kaplan et al., 2019); exploitation rates at control sites may have not been high
263   enough to generate strong RCA effects for species with high k values. Also, most rockfishes shift
264   ontogenetically to deeper depths (Love, Yoklavich & Thorsteinson, 2002), and the depths that
265   we sampled (≤35 m) encompassed primarily immature fish. Data collected at deeper depths via
266   remotely operated vehicles (e.g. Haggarty, Shurin & Yamanaka, 2016) are required to more fully
267   understand how variation in growth parameters affect responses to spatial protection.
268   Also contrary to our predictions, interspecific differences in movement behavior did not
269   affect responses to spatial protection by exploited species. One potential explanation is that the
270   proportion of immature fish was greater for high mobility-benthopelagic species (95%) than for
271   low mobility-demersal species (53%). Most mature individuals from high mobility-
272   benthopelagic species may have already undergone ontogenetic depth shifts below the reach of
273   our dive surveys (Love, Yoklavich & Thorsteinson, 2002), reinforcing the need to collect data at

274   deeper depths to strengthen inferences. Additionally, high mobility-benthopelagic species tended
275   to have higher k values (Table 1), which might have confounded mobility effects.
276   The relative body sizes of high mobility-benthopelagic species increased with depth and
277   decreased with greater topographic structural complexity, while the body sizes of low mobility-
278   demersal species had the opposite relationship to these habitat variables. Perhaps the different
279   responses reflect the distribution of resources being tracked (high mobility-benthopelagic species
280   feeding more on pelagic prey near the surface: Love *et al*. 2002) and different antipredator
281   strategies (low mobility-demersal species relying more on crypsis and refuges in complex reefs).
282   The larger body sizes for exploited species within the Goose Island and West Aristazabal
283   RCAs likely reflect reduced fishery mortality rather than environmental variation, as body sizes
284   for the unfished Puget Sound rockfish did not differ between protected and fished sites. Given
285   that fecundity increases disproportionately with body size (Dick et al., 2017b) and that larvae
286   exports can occur from protected to fished areas (Baetscher et al., 2019), these RCAs may
287   already be contributing to fishery sustainability; such benefits should increase over time (Starr et
288   al., 2015; Kaplan et al., 2019).
289   At four of six RCAs that we examined, however, rockfish body sizes at protected sites were
290   similar to or smaller than those at adjacent fished sites. There are at least three potential, non-
291   mutually exclusive explanations that might explain this result. First, the effectiveness of a
292   protected area generally increases with its size and age (Molloy, McLean & Côté, 2009). In our
293   sample, RCA age varied little, but RCA size ranged widely. The two RCAs that included larger
294   fish within their boundaries (relative to adjacent areas) also were the two largest RCAs that we
295   examined (Appendix S2). While more RCAs of varying sizes need to be examined, it is plausible
296   that RCA size influenced our results.
297   Second, despite analyses controlling for depth and topographic structural complexity , some
298   of the variation in RCA performance might reflect oceanographic differences between control
299   and protected sites (see Caselle et al., 2015). Within a rockfish species, growth rates are faster in
300   oceanic areas—which have lower temperatures and higher salinity—than in inland coastal waters
301   (West, Helser & O'neill, 2014). Oceanographic context, therefore, may partly explain why we
302   found no protection benefits at the Fish Egg Inlet RCA; this RCA encompasses inland coastal
303   waters but local geography constrained control sites to more oceanic conditions (Fig. 2), where
304   growth rates likely are faster (West, Helser & O'neill, 2014). Perhaps also reflecting
305   oceanographic factors, at the Kitasu Bay RCA a control site just outside its boundary
306   encompassed a reef with outstanding rockfish productivity, which might explain why individuals
307   from faster-growing species were larger outside this RCA. Similarly, the Goose Island and
308   McMullin Group RCAs share a boundary, yet only the former had larger fish in protected than in
309   control sites; the control sites for the McMullin Group include several locations where conditions
310   are more oceanic than at the control sites for Goose Island, which may have influenced this result
311   (Fig. 2).
312   Third, while analyses are lacking for the extent to which legal and illegal fisheries occur
313   within RCAs of the Central Coast, the intensity of these activities might have varied between

314   locations. Studies in southern British Columbia documented a high incidence of illegal
315   recreational fisheries within RCAs (Lancaster, Dearden & Ban, 2015; Haggarty, Martell &
316   Shurin, 2016). Fisher compliance tended to decline with fishing effort adjacent to the RCA and
317   with the RCA's proximity to fishing lodges. Further, lower compliance was associated with
318   fewer resources for enforcement and smaller RCA sizes (Haggarty, Martell & Shurin, 2016).
319   Importantly, RCAs were created to protect rockfish from the highest-risk commercial and
320   recreational fisheries, yet trap fisheries for invertebrates and mid-water trawls for groundfish
321   remain legal within them (Appendix S1), likely causing rockfish mortalities (DFO, 2019b). The
322   extent to which illegal and legal fisheries may have contributed to the lack of larger fish sizes at
323   two thirds of the RCAs that we examined requires further investigation. Further, responses to
324   spatial protection might be more likely to be detected if areas adjacent to reserves are fished
325   more intensely (see Jennings, 2000; Kaplan et al., 2019), and future analyses should consider
326   these effects.
327   Indigenous fisheries for traditional foods are allowed in RCAs, yet these fisheries are
328   regulated by traditional laws derived from the long-term knowledge and stewardship principles
329   that have allowed sustainable harvests over centuries (Jones, Rigg & Lee, 2010; Ban et al., 2018;
330   Ban, Wilson & Neasloss, 2020). Hereditary chiefs remain the traditional stewards of their
331   territories who, with technical staff, develop food fishing policies consistent with traditional
332   laws. Such policies are operationalized via Coastal Guardian Watchmen who communicate with
333   food fishers and patrol the waters for compliance, mitigating impacts from traditional fisheries in
334   protected areas. Additionally, Central Coast First Nations run their own catch-monitoring
335   programs, which they use to inform the governance and management of their traditional fisheries
336   (Ban et al., 2018; Ban, Wilson & Neasloss, 2020). Thus, it is unlikely that Indigenous traditional
337   fisheries contributed to the lower performance of some RCAs. Consistent with this notion, other
338   studies in British Columbia found that the relative abundance of Dungeness crab (*Cancer
339   magister*) increased over time after spatial fishery closures for commercial and recreational
340   fishers where implemented, despite traditional Indigenous fisheries continuing within these
341   closures (Frid, McGreer & Stevenson, 2016; Burns et al., 2020).
342

Conclusions

344   At two spatial fishery closures that were only 13 to 15 years-old when most data were collected,
345   we found that the body sizes of 12 species of exploited rockfishes were larger at protected than at
346   fished sites. Differences between protected and fished sites were greater for species with lower
347   values for growth parameter k, which was the opposite of what we expected. Also contrary to
348   expectation, interspecific differences in movement behavior did not affect body size responses to
349   spatial protection. Nonetheless, life history and behavioral frameworks guided the prediction and
350   interpretation of species differences in responses to spatial protection, which is essential for the
351   adaptive management of protected areas (Jennings, 2000; Claudet et al., 2010; Kaplan et al.,
352   2019).

353   Canada's federal fishery management agency is reviewing the effectiveness of RCAs (DFO,
354   2019a,b) and our results can inform this process. For four of six RCAs we found no evidence
355   that fish were larger in protected than in adjacent fished sites. Perhaps these deficiencies in
356   conservation effectiveness could be mitigated by increasing resources for compliance monitoring
357   and enforcement, and potentially by modifying some RCA boundaries to increase the proportion
358   of more productive, oceanic habitats within such boundaries.
359   Critically, the trophic position of rockfishes increases with their individual body sizes
360   (Trebilco et al., 2016; Olson et al., 2020). Larger size classes of yelloweye rockfish (*S.*
361   *ruberrimus*)—a long-lived demersal species inherent to Indigenous diets and undergoing size
362   declines (Eckert et al., 2017; McGreer & Frid, 2017)—occupy a particularly high trophic
363   position in rocky reefs (Olson et al., 2020). Ensuring that RCAs effectively restore large size
364   structures for exploited species, therefore, is essential for ecosystem-based fishery management.
365

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377

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Rockfish species analysed, and their biological characteristics.

Data are from Love et al. (2002), unless noted by superscripts. TL = Total Length. Relative mobility classes are: low = strong site fidelity to small reefs, high = species may or may not exhibit periods of site fidelity to small reefs but also conducts large movements (Appendix S8). For growth parameter k and length at maturity, estimates are for females (F), males (M), and unspecified sex (U). Areas where estimates were obtained are British Columbia (BC), Oregon (OR), Washington (WA).

Sebastes species	Common Name	Max. lifespan (yrs)	Max. TL (cm)	Growth parameter *k*	TL at 50% maturity (cm)	Habitat preference	Movement class
S emphaeus	Puget Sound rockfish	22	18.3	*F=0.535, WA *M=0.704, WA	*F=12.2, WA	Benthopelagic	*
S. melanops	Black rockfish	50	60	[1]F=0.171, WA [1]M=0.201, WA	[2]F=41.0, BC [2]M=42.0, BC	Benthopelagic	High
S. paucispinis	Bocaccio	50	98	[2]F=0.170, BC [2]M=0.210, BC	[2]F=52.0, BC [2]M=48.5, BC	Benthopelagic	High
S. caurinus	Copper rockfish	50	66	[2]F=0.090, BC [2]M=0.110, BC	[2]F=25.8, BC [2]M=26.9, BC	Demersal	Low
S. miniatus	Vermilion rockfish	60	76	[3]F=0.075, OR [3]M=0.114, OR	[3]F=39.4, OR	Demersal	Low
S. entomelas	Widow rockfish	60	53	[2]F=0.160, BC [2]M=0.180, BC	[2]F=41.3, BC [2]M=39.9, BC	Benthopelagic	High
S. flavidus	Yellowtail rockfish	64	66	[2]F=0.140, BC [2]M=0.200, BC	[2]F=40.9, BC [2]M=37.6, BC	Benthopelagic	High
S. nebulosus	China rockfish	79	41	[4]U=0.147, WA	[2]F=23.5, BC [2]M=21.4, BC	Demersal	Low
S. brevispinis	Silvergray rockfish	82	71	[2]F=0.100, BC [2]M=0.130, BC	[1]F=43.1, BC [1]M=42.7, BC	Benthopelagic	High

S. pinniger	Canary rockfish	84	76	[2]F=0.130, BC [2]M=0.130, BC	[2]F=42.9, BC [2]M=40.2, BC	Benthopelagic	High
S. maliger	Quillback rockfish	95	50	[2]F=0.100, BC [2]M=0.120, BC	[2]F=27.9, BC [2]M=29.1, BC	Demersal	Low
S. nigrocinctus	Tiger rockfish	116	61	**	[1]M=20.9, BC	Demersal	Low
S. ruberrimus	Yelloweye rockfish	121	91	[2]F=0.040, BC [2]M=0.050, BC	[1]F=41.3, BC [1]M=47.2, BC	Demersal	Low

1   *Puget Sound rockfish, a small planktivore, is the only "unfished" species analyzed (Love *et al.* 2002); growth and maturity are from
2   Beckmann *et al.* (1998); movement data were unavailable but no required. [1]Post-2000 estimate of Cope *et al* (2016). [2]Anderson et al.
3   (2019). [3]Hannah & Kautzi (2012). [4]Northern assessment model of Dick *et al.* (2016).
4   **For tiger rockfish, *k* was derived from regression analyses for the remainder of species (Appendices S6, S7).

Figure 1

Map of the study area.

Red diagonal lines represent Rockfish Conservation Areas (RCA: protected treatments); dashed boxes encompass control sites paired with each RCA; colored squares depict dive locations aggregated within 16-km^2 grid cells; inset locates the study area in Canada. Individual sites are not identified to protect spatial data considered to be sensitive by First Nations.
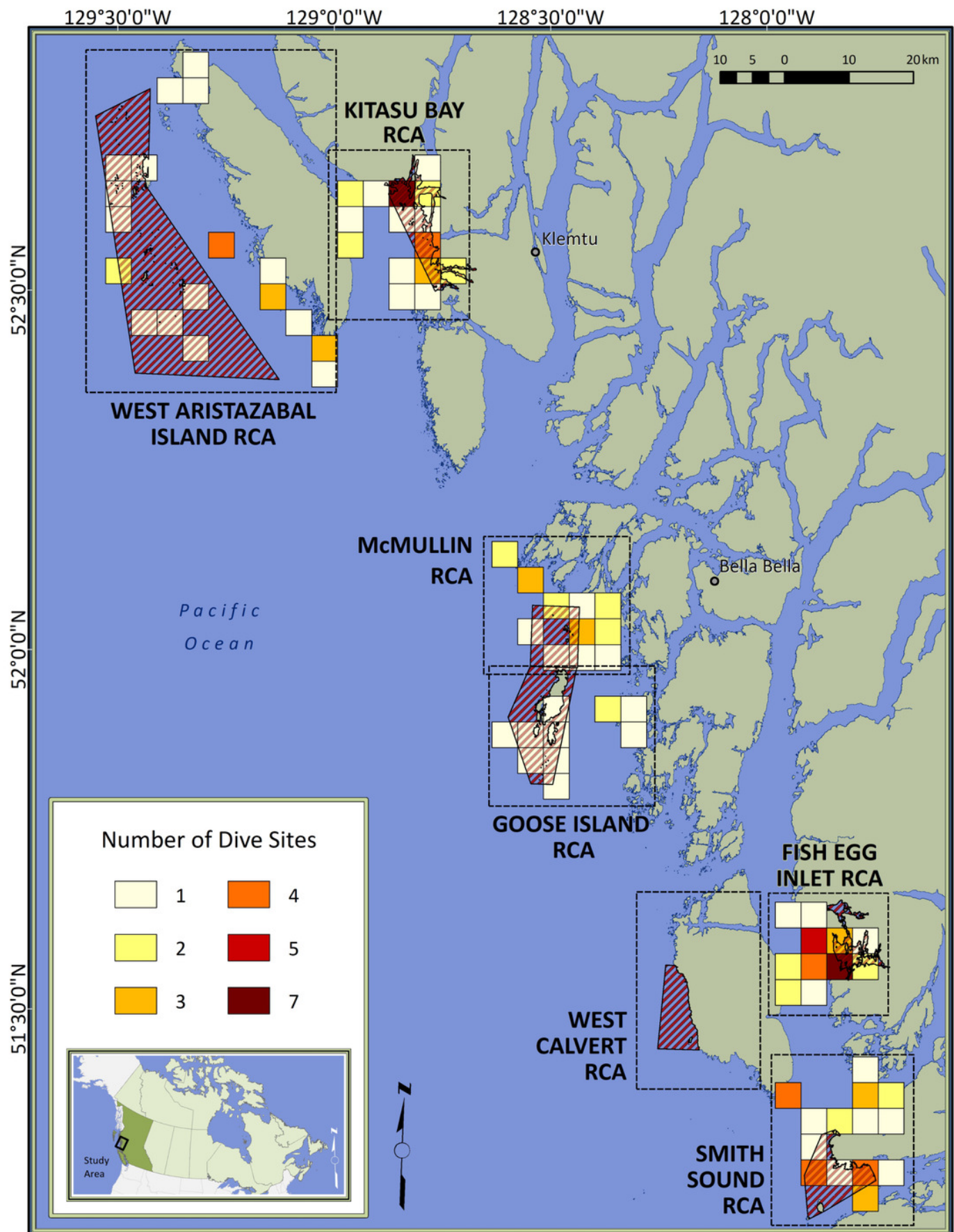
Figure 2

Best generalized least squares models describing body size responses to predictors for (A) exploited species and (B) Puget Sound rockfish.

Circles represent standardized coefficients with 95% confidence intervals (horizontal lines). Relative variable importance (RVI) values are provided for predictors that underwent AIC model selection procedures (Appendices S13, S14). Fish Egg Inlet is the baseline for RCA treatment and location. "Complexity" refers to topographic structural complexity. Behaviors are high mobility-benthopelagic (HM-B) or low mobility-demersal (LM-D). Results for exploited species are based on $k = 0.059$ for Tiger rockfish (Appendix S7); results are very similar if the alternative value $k = 0.070$ is used (Appendix S16).
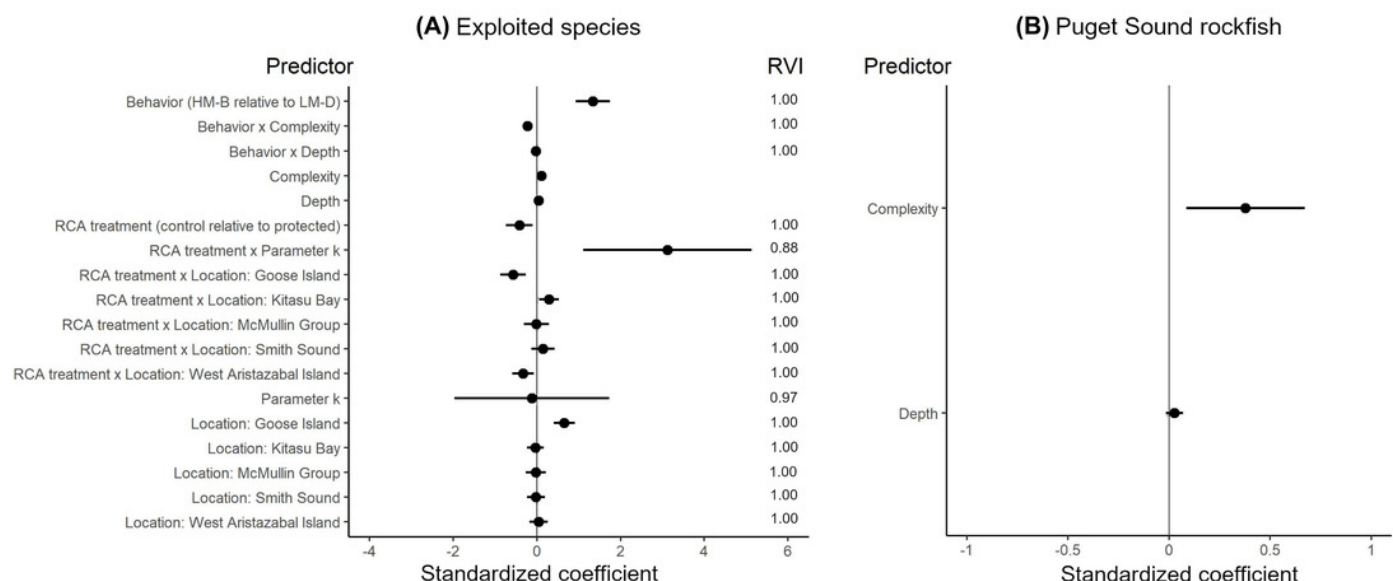
Figure 3

Length anomalies of exploited species in relation to parameter k, location, and RCA treatment, as estimated by the best generalized least squares model (Fig. 2a).

Estimates are for demersal species at 30 m depth and structural complexity = 3 (patterns remain constant under other conditions). Bands represent 95% confidence intervals. Bands are the 95% confidence interval. For descriptive plots of corresponding raw data, see Appendix S17a.
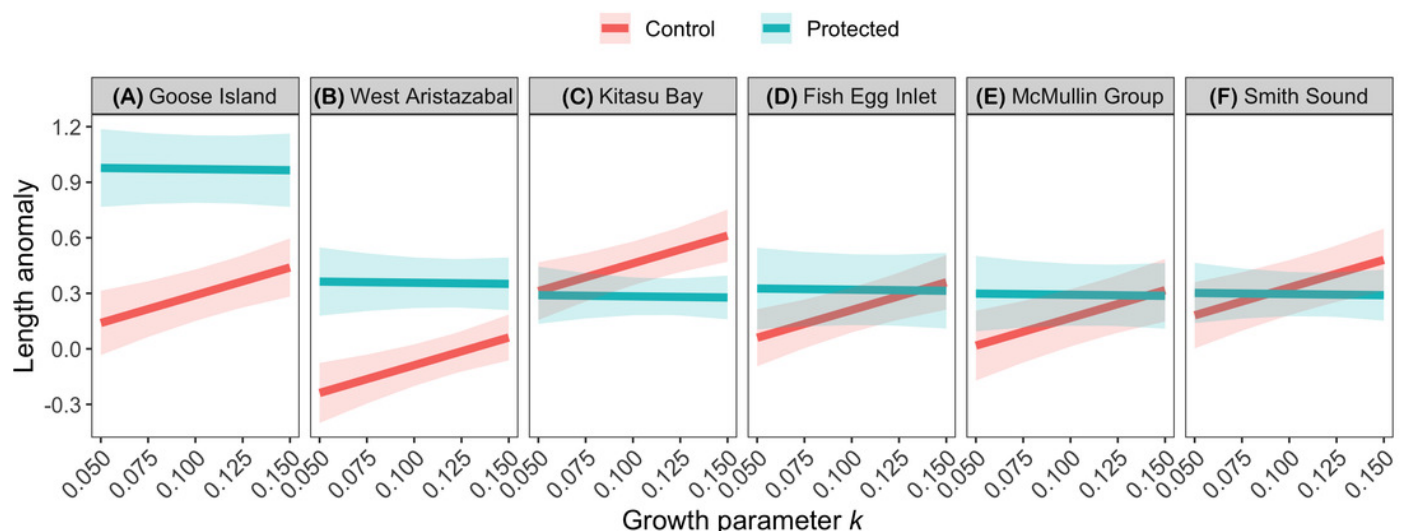
Figure 4

Length anomalies of exploited rockfishes in relation to (A) topographic structural complexity (at a depth of 15 m) and (B) depth (at complexity=2), as estimated by the best generalized least square model (Fig. 2a).

These estimates are for protected sites in the West Aristazabal RCA and k = 0.12 (patterns remain constant under other conditions). Bands are the 95% confidence interval. For descriptive plots of corresponding raw data, see Appendix S17b.