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Size-structured abundance relationships between upper- and mid-trophic level predators on temperate rocky reefs

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Top-down control of community structure can manifest as inverse relationships between the abundances of organisms at adjacent trophic levels. Due to the time costs of handling very large prey it may be optimal for gape-limited predatory fishes to select prey with body depths that are $\leq 60\%$ of predator gape width. We tested for inverse relationships between the abundances of different sized rockfish (prey) and of lingcod (predator) large enough to be expected to select that rockfish size. We predicted that these relationships would be stronger when assuming that body depth of selected prey is $\leq 60\%$, rather than $\leq 100\%$, of lingcod gape width. Results were consistent with this prediction for small and medium size classes of rockfish. Regardless of prey selection assumptions there were no negative relationships between lingcod and large size classes of rockfish, possibly because only 2.3% of observed lingcod were large enough to select large rockfish when assuming prey body depth selection of $\leq 60\%$ of predator gape width. Large rockfish, therefore, may have occupied a size refuge from lingcod risk. Our results, however, are characterized by large statistical uncertainty. We suggest that prey antipredator behaviour, which has the cost of reducing access to resources and the benefit of lowering mortality rates, might explain much of this uncertainty. Quillback and copper rockfish are long-lived species with late maturity. As such, they are expected to maximize fitness by investing heavily in antipredator behaviour, and this investment may have weakened numerical relationships between lingcod and small and medium size classes.

KEY WORDS: body size, gape limitation, lingcod, marine predators, predator-prey body size relationships, rockfish, top-down control.

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INTRODUCTION

Top-down control of community structure occurs when predators limit the numbers of their prey and manifests as inverse relationships between the abundances of organisms at adjacent trophic levels (HAIRSTON et al. 1960). Evidence for such relationships includes both small-scale experiments (e.g. PAINE 1966) and observational data in large ecosystems (STENECK 2005). The fishery removal of large predatory fishes, for instance, has led to increases in prey populations, providing widespread evidence for top-down control in marine systems (BAUM & WORM 2009). The strength of top-down control exerted by a species of predator, however, may be modulated by body size (NILSSON & BRÖNMARK 2000; SHACKELL et al. 2010) and other factors.

Body size effects are particularly important in aquatic systems, where many predators swallow prey whole and therefore are gape-limited (e.g. WERNER 1974; NILSSON & BRÖNMARK 2000; GILL 2003). Both the gape size and the prey size spectrum of aquatic predators generally increase with body size, such that small predators eat only small prey while large predators eat both small and large prey (e.g. SCHARF et al. 2000; BEAUDREAU & ESSINGTON 2007). The time costs of prey handling, however, increase with prey body size, and gape-limited predators might optimize net energy gain by selecting prey with body depths that are $\leq 60\%$ of predator gape width (WERNER 1974; GILL 2003). For instance, sunfishes (*Lepomis* spp.) and threespine sticklebacks (*Gasterosteus aculeatus*) most frequently fed on items that had a prey body depth to predator gape size ratio of 0.6 (WERNER 1974; GILL & HART 1994). Consumption of larger prey is less frequent (e.g. NILSSON & BRÖNMARK 2000) and may be optimal only when the predator's food deficit is large or smaller prey are unavailable (WERNER 1974; GILL 2003). The size structure of predator and prey populations, therefore, may influence the proportion of vulnerable prey individuals (WERNER & GILLIAM 1984; NILSSON & BRÖNMARK 2000) and the strength of top-down control (SHACKELL et al. 2010).

Predator-prey body size relationships are important for understanding the ecology of temperate reefs of the northeast Pacific, where lingcod (*Ophiodon elongatus*) and rockfish (*Sebastes* spp.) are upper- and mid-trophic level predatory fishes, respectively (LOVE et al. 2002; BEAUDREAU & ESSINGTON 2007) (Fig. 1). A study in Washington state, USA, found that rockfish were absent from the stomachs of lingcod with total lengths of < 30 cm, yet comprised 13% and $\approx 18\%$ by mass of the diet of lingcod with total lengths of 30–50 cm and 51–90 cm (BEAUDREAU 2009), respectively. A size spectrum calculated for all prey suggested that lingcod > 90 cm long would be capable of consuming even larger rockfishes (BEAUDREAU & ESSINGTON 2007), and bioenergetic modeling suggested that consumption rates increase with lingcod size. Lingcod > 90 cm long, therefore, may have a stronger top-down effect on rockfish populations than smaller lingcod (BEAUDREAU & ESSINGTON 2009).

Prior studies, however, have not examined size-structured abundance relationships between lingcod and rockfish. This is a major gap in our understanding of temperate reef communities because both lingcod and rockfish have been overexploited throughout much of their range (CASS et al. 1990; KING & SURRY 2000; LOVE et al. 2002) and, consistent with general trends in overfished populations (PAULY et al. 2002; SHACKELL et al. 2010), fishing skews their size structure towards smaller fish (PALSSON & PACUNSKI 1995; HARVEY et al. 2006). The strength of top-down control in reef communities of the northeast Pacific, therefore, could potentially vary according to the local exploitation history and size-structure of lingcod and rockfish populations.

We examined size-structured relationships between the abundances of lingcod and quillback rockfish (*S. maliger*) and copper rockfish (*S. caurinus*). We first estimated



Fig. 1. — Lingcod consuming a copper rockfish, southern British Columbia (Photo credit: Conor McCracken|CDM Images).

the relationship between total length and gape width for lingcod, and used it to estimate the minimum lengths of lingcod expected to select different sizes of rockfish under the assumptions that body depth of selected prey is $\leq 60\%$ or $\leq 100\%$ of lingcod gape width. We then used field survey data to test for negative relationships between the abundances of different sized rockfish and of lingcod large enough to be expected to select that rockfish size range. We predicted that these negative relationships would be stronger when assuming that body depth of selected prey is $\leq 60\%$, rather than $\leq 100\%$, of lingcod gape width (WERNER 1974; GILL 2003). Size frequency data were then used to estimate the proportion of observed lingcod expected to select different sized rockfish under the two assumptions.

METHODS

Estimating the sizes of lingcod expected to select different sized rockfish

We estimated for lingcod the relationship between total length and gape width from 40 specimens which, to avoid further damage to the recovering fish community of Howe Sound (see below), were collected outside the study area. Thirty-two lingcod were collected along the west coast of Vancouver Island during 2009 (Department of Fisheries and Oceans permit XR 99 2010 to S.J. Dick and R.W. Markel). The remainder were collected along the southeast coast of Haida Gwaii during 2010 (two specimens, Department of Fisheries and Oceans permit XR_58_2010_Salomon and Parks Canada permit 5980 to R. Trebilco) and 2011 (six specimens under sports fishing licenses). Following the framework of GILL (2003), we assumed that lingcod position deep-bodied large prey, such as rockfish, on their side while swallowing (see Fig. 1) and, therefore, gape width constrains their maximum prey size. Thus, we measured gape width along the lateral plane of specimens. From these data (Fig. 2) we estimated the relationships between total gape width, G , and total length, TL , and between 60% of gape width, $0.6 G$, and TL as:

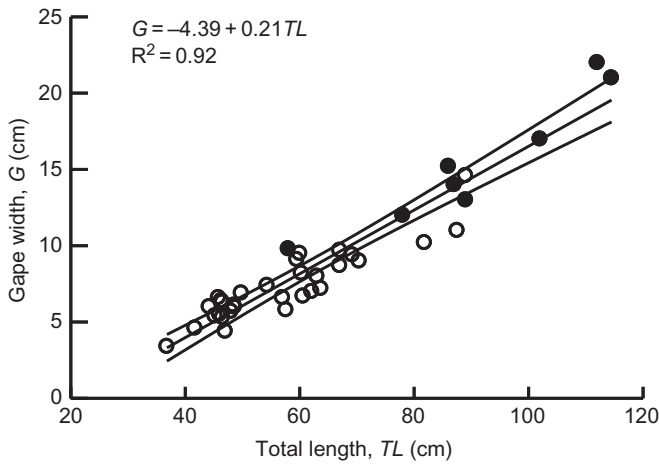


Fig. 2. — Relationship between total length and gape width of lingcod based on fish collected on the west coast of Vancouver Island (open symbols) and southeastern Haida Gwaii (filled symbols). The regression line pools data for both regions and includes 95% confidence intervals.

$$G = -4.39 + 0.21 TL \quad (1)$$

and

$$0.6G = -2.63 + 0.13 TL \quad (2)$$

During field surveys (see next section) we assigned rockfish to size categories based on total length (Table 1), which is a more practical field measurement than body depth. The midpoint of each length category was converted to body depth based on a 0.33 depth to total length ratio (FROESE & PAULY 2013). This ratio excludes the height of dorsal spines from body depth. The midpoint values for body depth and Equations (1) and (2) were used to estimate the minimum lengths of lingcod expected to select a given set of size categories (small only, small plus medium, all) of rockfish under the assumptions that body depth of selected prey is $\leq 60\%$ or $\leq 100\%$ of lingcod gape width (Table 1).

Natural history and field surveys

We conducted field surveys of lingcod and rockfish in a study area spanning $\approx 500 \text{ km}^2$ in Howe Sound, British Columbia, Canada (Fig. 3). Lingcod and rockfish were overexploited in Howe Sound and vicinity during the twentieth century but spatial protection and other measures have been implemented recently to promote their recovery (KING & SURRY 2000; MARTELL et al. 2000; MARLIAVE & CHALLENGER 2009).

Lingcod are the top predator in the food web segment that we studied (BEAUDREAU & ESSINGTON 2007), but both lingcod and rockfish may be prey to harbour seals (*Phoca vitulina*) (LANCE & JEFFRIES 2006). Although lingcod in some areas are relatively sedentary (TOLIMIERI et al. 2009; BEAUDREAU & ESSINGTON 2011), lingcod in Howe Sound and southeast Alaska use specific reefs preferentially but also move large distances, travelling for days or weeks away from preferred reefs (MARTELL et al. 2000; STARR et al. 2004).

Table 1.

Rockfish size categories and minimum lengths of lingcod expected to select different sizes of rockfish when assuming prey body depth selection of $\leq 100\%$ or $\leq 60\%$ of predator gape width. Values for rockfish sizes are the mid-point of size ranges; the latter were estimated empirically (see text) and are given in parentheses. Percents of predator gape width are relative to the midpoint of body depth.

Rockfish size	Minimum total length (cm) of lingcod expected to select different sizes of rockfish when assuming prey body depth selection of:			
	Category	Total length (cm)	Body depth (cm)	$\leq 100\%$ of predator gape width
small	10 (8–12)	3.3 (2.6–4.0)	37	47
medium	16 (13–19)	5.3 (4.3–6.3)	46	63
large	25 (20–30)	8.3 (6.6–9.9)	60	87

Copper rockfish and quillback rockfish dominate the rockfish assemblage in the study area (MARLIAVE & CHALLENGER 2009). These species generally prefer structurally complex reefs over simpler substrates (MARLIAVE & CHALLENGER 2009), possibly because rocky interstices (crevices or spaces between boulders) provide refuge from predators and turbulence (CARLSON & BARR 1977). In contrast to the wider-ranging movements of lingcod, both copper and quillback rockfish have very small home ranges ($< 10 \text{ m}^2$ in structurally complex reefs) and strong fidelity to small areas within a reef (MATTHEWS 1990).

During daylight hours from mid-July 2008 to December 2009, we conducted scuba-based timed counts of lingcod and rockfish on permanently marked transects on 10 reefs at depths of 5.5 to 23 m below mean low tide. Four reefs were within 1 km of each other and six were > 5 km from other sampled reefs (Fig. 3). Seven of the reefs contained two to three distinct sections of habitat where separate transects were established for a total of 19 transect locations. Transects were stratified by depth, and their length varied between approximately 20 m in the narrowest reef to 150 m in larger reefs. Sampling occurred year-round for a total of 338 transect counts (Supplementary Table S1).

Data consisted of counts per unit effort (CPUE) of each species and size class combination (fish counted per minute). As much as possible, swimming speed by observers was standardized across transects. All fish were counted, regardless of their distance from the line transect. There were no significant correlations between visibility, estimated as the maximum horizontal distance at which divers could count fish, and the CPUE of rockfish (Supplementary Table S2), suggesting that variable visibility did not bias the data.

Total lengths of fish were estimated with rulers attached to poles or drawn on data slates. Lingcod total lengths were estimated to the nearest cm, while rockfish were recorded into three classes of total length: 8–12 cm (small), 13–19 cm (mid-sized), and 20–30 cm (large). Rockfish larger than 30 cm were encountered infrequently and included in the large size category.

The structural complexity of sites was indexed with rugosity measurements at points separated by restricted random distances (i.e. one to four standardized fin kicks). Depending on transect length, three to 16 points were sampled per site. At each point, we measured a 2-m straight-line distance above the substrate, and then measured the distance that contoured over the underlying substrate. Rugosity was estimated as the ratio of contoured over straight distances (LUCKHURST & LUCKHURST 1978) and averaged for each transect site (Table S1).

Data were divided into four sampling seasons. Season 1, late July to early December 2008, represented summer-fall, when most observed rockfish are outside crevices (FRID & MARLIAVE

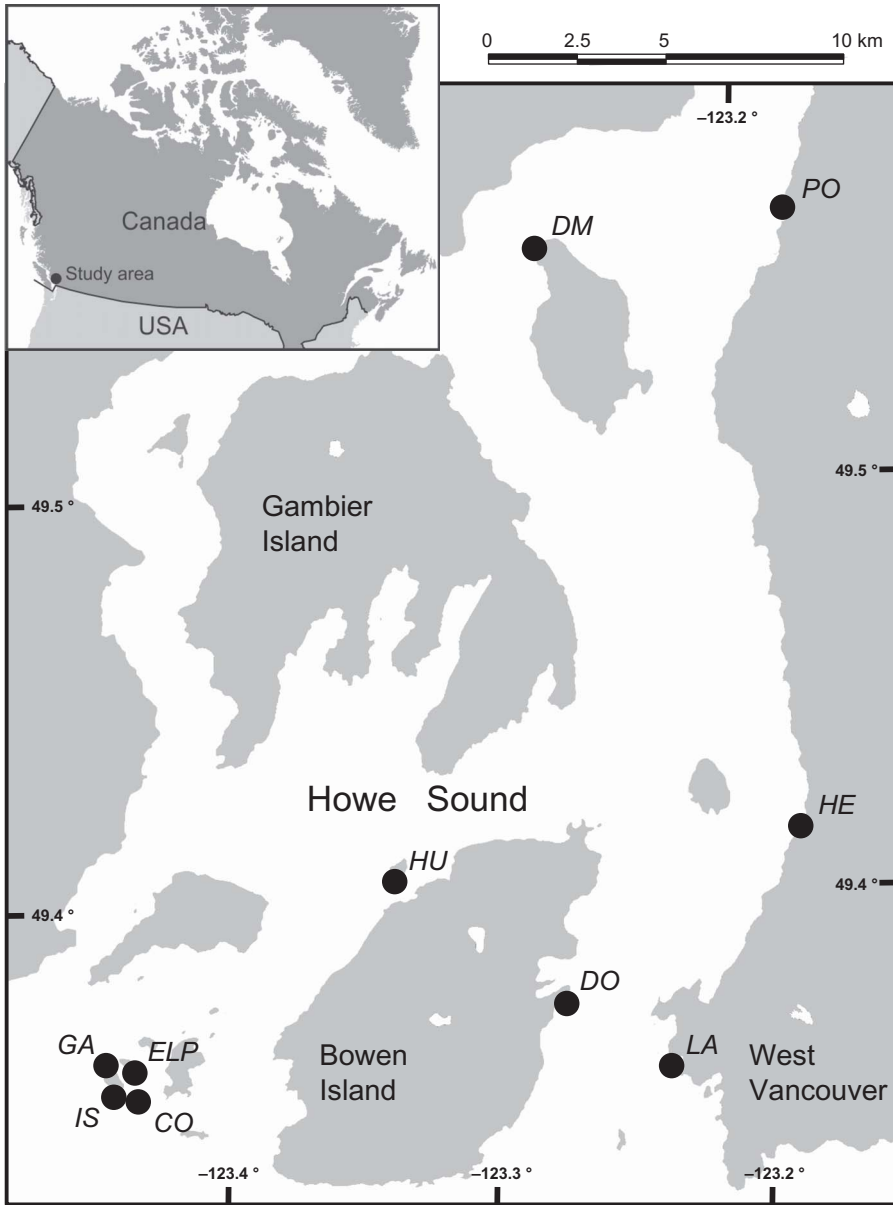


Fig. 3. — Map of the study area. Black circles represent study reefs; uppercase letters in italics are the reef identifier.

2010). Season 2, late December 2008 to early April 2009, represented winter, when most observed rockfish are inside crevices (CARLSON & BARR 1977; FRID & MARLIAVE 2010). Season 3, mid April to late June 2009, represented spring, when the proportion of rockfish outside crevices is rising but has yet to peak. Season 4 replicated summer–fall from early July to early December 2009.

Statistical modelling of field survey data

We related the CPUEs of rockfish to the CPUE of lingcod, season (four-level factor), depth, and rugosity using Generalized Linear Mixed Models (GLMM) with Poisson error and a log link function. This approach allowed us to account for the nested nature of observations (i.e. repeated counts made at transects nested within reefs) and the non-normal error distribution characteristic of count data, and to partition variation attributable to random (transects and reefs) and fixed (lingcod CPUE, season, depth and rugosity) effects while representing the covariance structure of grouped data (BOLKER et al. 2009). Random effects were assumed to be identically and independently normally distributed with a mean of zero and variance that is estimated, and GLMMs included both random intercept and slope terms. Separate analyses were conducted for each rockfish size class and species with the CPUE of lingcod based on the lingcod sizes expected to select that rockfish size under the 60% or 100% gape width assumptions. Models containing all possible variable combinations were fit by Laplace approximation (BOLKER et al. 2009).

Multi-model inferences were based on Aikake's information criterion corrected for small samples (AICc; BURNHAM & ANDERSON 2002, 2004). In this framework, the smallest AICc value, $AICc_{min}$, identifies the model with the greatest data support given the models considered. Relative support for model i , given the models considered, is determined by first calculating the differences between $AICc_i$ and $AICc_{min}$ ($\Delta AICc_i$) and then scaling these differences into model weights (w_i). The ratio of the weight of one model to another is the evidence ratio which reflects the likelihood of one model over another. For example, a model with a weight of 0.80 is 4 times more likely to be the best model than a model with a weight of 0.20 given the data and the models considered. Based on these model weights we could then generate model-averaged coefficients, their unconditional standard errors and sum of the AICc weights (ΣW_i) for each predictor. Importantly, the largest ΣW_i values represent the most important predictors and vice versa (BURNHAM & ANDERSON 2002, 2004).

For selecting the subset of candidate models to be used for model averaging, BURNHAM & ANDERSON (2004) state that models with values of $\Delta AICc \leq 2$ have the most support and that 'considerably less support' begins at $\Delta AICc \geq 4$, implying that $\Delta AICc$ values between 2 and 4 represent models with some level of support that should not be dismissed necessarily. Accordingly, we calculated model-averaged parameter estimates errors according to the zero method (BURNHAM & ANDERSON 2002, 2004) based on models with $\Delta AICc < 4$.

Analyses were carried out in R (R DEVELOPMENT CORE TEAM 2007) using the lme4 and MuMin packages for the GLMMs and multi-model inference, respectively. While the Results section reports model averaged coefficients, Supplementary Tables S3 and S4 summarize the top models used in model averaging.

RESULTS

The CPUEs of small and medium rockfish were negatively related to the CPUEs of lingcod large enough to be expected to select that rockfish size when assuming that body depth of selected prey is $\leq 60\%$ of lingcod gape width (Fig. 4A, Table 2). These negative relationships were weaker (small rockfish) or absent (medium rockfish) when assuming that body depth of selected prey is $\leq 100\%$ of lingcod gape width (Fig. 4B, Table 3). Regardless of prey selection assumptions, there was no evidence of negative relationships between the CPUEs of lingcod and large rockfish (Fig. 4, Tables 2–3). The uncertainty in these relationships was high, however, as evidenced by the large standard errors around the parameter estimates (Fig. 4, Tables 2–3).

Season, depth and rugosity tended to have stronger effects than lingcod CPUE on rockfish counts (see coefficient and ΣW_i values in Tables 2–3). Rockfish CPUEs generally were lowest during winter (season 2), when rockfish appear to spend more time inside crevices and therefore are more likely to be missed during transect counts

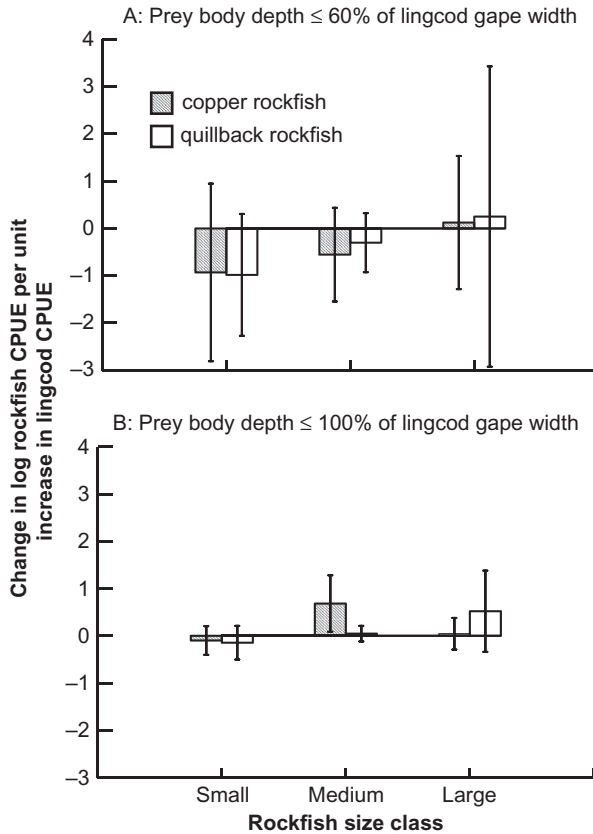


Fig. 4. — Change in log rockfish counts per unit effort (CPUE) per unit increase in the CPUE of lingcod large enough to select small, medium and large rockfish size classes under the assumption that body depth of selected prey is A: $\leq 60\%$ or B: $\leq 100\%$ of lingcod gape width. Values are model-averaged Generalized Linear Mixed Models (GLMM) coefficients (hence they are on the log scale) with unconditional standard errors (also given in Tables 2–3).

(CARLSON & BARR 1977; FRID & MARLIAVE 2010). The effect of depth on rockfish CPUE generally was positive for quillback rockfish and negative for copper rockfish, but the strength of these relationships varied by size class. Except for small quillback rockfish, rugosity had a positive effect on rockfish CPUEs (Tables 2–3).

Small and mid-sized lingcod (TL ≤ 80 cm) were observed frequently but larger lingcod appeared to be rare in the study reefs (Fig. 5A). Given this size frequency distribution, only 2.3% of all observed lingcod ($n = 532$) were large enough (TL ≥ 87 cm) to be expected to select large rockfish (body depth 8.3 cm: Table 1) when assuming prey body depth selection of $\leq 60\%$ of predator gape width (Fig. 5B). When assuming prey body depth selection of $\leq 100\%$, however, 37.7% of observed lingcod were expected to be large enough (TL ≥ 60 cm) to select large rockfish (Fig. 5B), but this assumption might be less plausible (Fig. 4). Due to their less deep bodies, small and medium rockfish were expected to be selected by a much greater proportion of lingcod (Fig. 5B).

Table 2.

Model-averaged coefficients, unconditional standard errors and sum of Aikake's information criterion corrected for small samples (AICc) weights (ΣW_i) for predictors of the counts per unit effort (CPUE) of rockfish when assuming that prey body depth selection is $\leq 60\%$ of predator gape width. Season effects are relative to season 1, the baseline value. Lingcod CPUE is specific to lingcod sizes expected to select the given rockfish size. Variables are ordered according to their weights. Table S3 summarizes the top models used in averaging.

Rockfish size and species	Variable	Coefficient	Unconditional SE	ΣW_i
Small copper	intercept	-3.76	1.42	
	season 2	-1.2	1.13	0.71
	season 3	-0.35	0.50	0.71
	season 4	-1.14	1.02	0.71
	rugosity	0.52	0.81	0.38
	lingcod CPUE	-0.93	1.88	0.30
	depth	0.00	0.03	0.20
Medium copper	intercept	0.45	1.92	
	depth	-0.21	0.07	1.00
	season 2	-1.20	0.27	1.00
	season 3	-0.15	0.16	1.00
	season 4	-0.02	0.16	1.00
	rugosity	1.39	1.02	0.75
Large copper	intercept	-1.53	1.69	
	season 2	-0.81	0.20	1.00
	season 3	0.17	0.13	1.00
	season 4	0.48	0.12	1.00
	rugosity	1.69	0.90	0.86
	depth	-0.06	0.07	0.56
	lingcod CPUE	0.13	1.41	0.22
Small quillback	intercept	-5.69	2.22	
	depth	0.30	0.13	1.00
	season 2	-1.84	0.51	1.00
	season 3	-0.47	0.25	1.00
	season 4	-0.75	0.26	1.00
	lingcod CPUE	-0.98	1.29	0.51
	rugosity	-0.03	0.25	0.26
Medium quillback	intercept	-2.13	1.74	
	season 2	-1.18	0.32	1.00
	season 3	-0.03	0.18	1.00

(Continued)

Table 2.
(Continued)

Rockfish size and species	Variable	Coefficient	Unconditional SE	ΣW_i
	season 4	0.34	0.16	1.00
	depth	0.06	0.08	0.46
	rugosity	0.35	0.58	0.40
	lingcod CPUE	-0.30	0.63	0.32
Large quillback	intercept	-3.10	2.22	
	season 2	-0.75	0.30	1.00
	season 3	0.07	0.20	1.00
	season 4	0.33	0.18	1.00
	depth	0.09	0.10	0.60
	rugosity	0.62	0.82	0.46
	lingcod CPUE	0.25	3.18	0.27

Table 3.

Model-averaged coefficients, unconditional standard errors and sum of Aikake's information criterion corrected for small samples (AICc) weights (ΣW_i) for predictors of the counts per unit effort (CPUE) of rockfish when assuming that prey body depth selection is $\leq 100\%$ of predator gape width. Variables are ordered according to their weights. Table S4 summarizes the top models used in model averaging.

Rockfish size and species	Variable	Coefficient	Unconditional SE	ΣW_i
Small copper	intercept	-3.74	1.46	
	season 2	-1.14	1.13	0.68
	season 3	-0.34	0.49	0.68
	season 4	-1.15	1.06	0.68
	rugosity	0.59	0.88	0.68
	depth	-0.01	0.04	0.23
	lingcod CPUE	-0.10	0.30	0.18
Medium copper	intercept	-0.06	1.97	
	depth	-0.19	0.07	1.00
	season 2	-1.21	0.27	1.00
	season 3	-0.26	0.17	1.00
	season 4	-0.39	0.19	1.00
	rugosity	1.53	1.13	0.72
	lingcod CPUE	0.68	0.60	0.60
Large copper	intercept	-1.68	1.67	

(Continued)

Table 3.
(Continued)

Rockfish size and species	Variable	Coefficient	Unconditional SE	ΣW_i
Small quillback	season 2	-0.81	0.20	1.00
	season 3	0.17	0.13	1.00
	season 4	0.47	0.12	1.00
	rugosity	1.83	0.82	0.92
	depth	-0.06	0.07	0.61
	lingcod CPUE	0.04	0.34	0.24
	intercept	-5.82	2.34	
	depth	0.31	0.13	1.00
	season 2	-1.83	0.50	1.00
	season 3	-0.47	0.25	1.00
Medium quillback	season 4	-0.75	0.26	1.00
	lingcod CPUE	-0.15	0.36	0.29
	rugosity	-0.08	0.32	0.26
	intercept	-2.47	1.97	
	season 2	-1.17	0.32	1.00
	season 3	-0.01	0.18	1.00
	season 4	0.36	0.16	1.00
	depth	0.07	0.09	0.52
	rugosity	0.44	0.67	0.43
	lingcod CPUE	0.05	0.17	0.27
Large quillback	intercept	-2.91	2.13	
	season 2	-0.74	0.30	1.00
	season 3	0.07	0.20	1.00
	season 4	0.33	0.18	1.00
	depth	0.08	0.10	0.58
	rugosity	0.53	0.76	0.45
	lingcod CPUE	0.52	0.86	0.39

DISCUSSION

Model coefficients describing the relationship between lingcod and rockfish abundances had very large standard errors and therefore provided limited support for the predicted size-structured abundance relationships. As elaborated below, these results appear to reflect real variation in a complex biophysical system.

We found inverse numerical relationships between lingcod and small and medium size classes of rockfish, but only when assuming that lingcod select prey with body

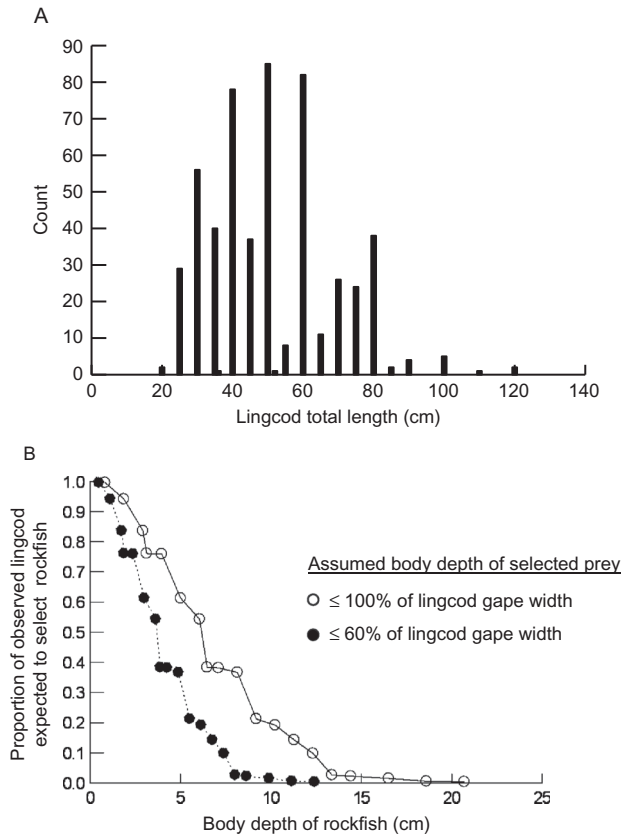


Fig. 5. — A: Frequency distribution of lingcod total lengths recorded during surveys and B: proportions of observed lingcod expected to select different sized rockfish under different prey selection assumptions. Panel B was generated by converting length data in panel A, the field measurement, to gape width (see Fig. 2).

depths that are $\leq 60\%$ of predator gape width, which supports our original hypothesis. To evaluate whether diet studies would be consistent with this result, we compared our estimates of lingcod gape widths (G and $0.6G$) as a function of lingcod length (Equations 1 and 2) against the 95th quantile of prey body depths consumed by different sized lingcod (BEAUDREAU 2009; A. BEAUDREAU pers. comm.). The estimate for $0.6G$ matched the 95th quantile remarkably better than the estimate for G (Fig. 6), which is consistent with our prediction and with studies of prey selectivity by other fishes (GILL 2003).

Regardless of prey selection assumptions, there were no negative relationships between lingcod and large size classes of rockfish, possibly because only 2.3% of observed lingcod were large enough to select large rockfish when assuming prey body depth selection of $\leq 60\%$ of predator gape width. Large rockfish, therefore, may have occupied a size refuge from lingcod risk. These results are consistent with previous studies suggesting that the size frequency distributions of predators and prey,

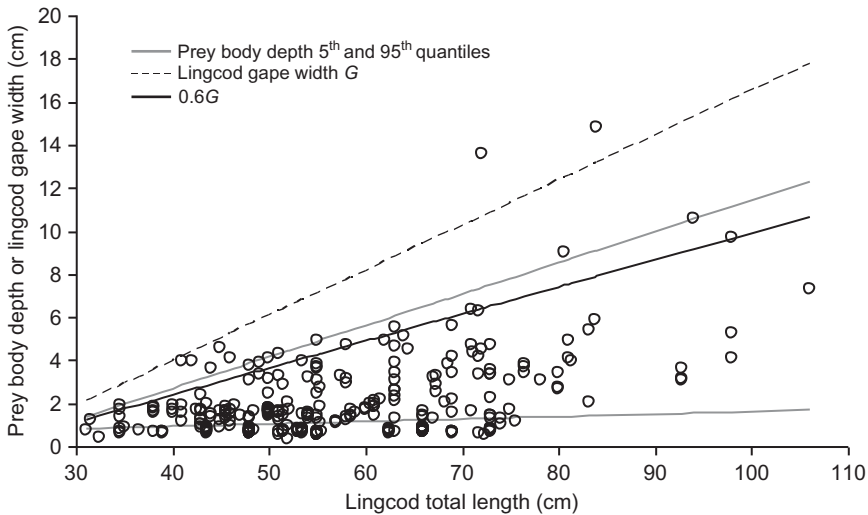


Fig. 6. — Estimates of lingcod gape widths (G and $0.6G$) as a function of length (Equations 1 and 2) overlaid on data on prey body depth PD (all prey species included) in relation to lingcod total length TL , with 5th and 95th quantiles fitted (respectively: $PD = 0.470 + 0.011TL$, $PD = -3.131 + 0.146TL$) (BEAUDREAU 2009; A. BEAUDREAU pers. comm.).

rather than predator abundance alone, influence the strength of top-down control by predatory fishes (e.g. NILSSON & BRÖNMARK 2000; SHACKELL et al. 2010), and that the functional predation capacity of a predatory fish is determined by a fraction, rather than the full width, of its gape (e.g. WERNER 1974; HAMBRIGHT 1991; GILL 2003).

As mentioned, however, coefficients estimating abundance relationships between lingcod and rockfish were characterized by large uncertainty. The multi-model inference approach that we used explicitly accounts for model uncertainty when generating model averaged parameter estimates. This is in contrast to traditional null hypothesis testing, which focuses on whether estimated effects are significantly different from a null effect (i.e. 0). As a result, the large uncertainty in our GLMM coefficients does not invalidate our findings but instead highlights the need for further studies addressing sources of variation not accounted for by our study (BURNHAM & ANDERSON 2002, 2004). Possible sources of variation include the following. First, rockfish size categories were broad and we used length to body depth ratios for rockfish that excluded the height of dorsal spines; some individual rockfish, therefore, may have been misclassified according to their size-specific vulnerability to lingcod. Second, our analysis estimated variation attributable to unmeasured factors (i.e. random effects) among sites, such as histories of rockfish recruitment and fishing pressure, and among seasons, such as temporal shifts in bottom-up processes. However, other factors such as the availability of alternative prey for lingcod (e.g. sculpins and pelagic forage fishes) and seal predation on all fishes may have varied *within* sites, potentially masking relationships between rockfish and lingcod abundance and leading to increased uncertainty in GLMM coefficients. Additionally, our analyses are based on the assumption that lingcod position deep-bodied large prey on their side while swallowing (Fig. 1) and, therefore, gape

width constrains maximum prey size (GILL 2003). Other morphometrics, such as total mouth volume (KARPOUZI & STERGIU 2003) and esophageal width (MANDERSON et al. 1999), may also be important for estimating maximum prey size. Future studies should examine whether accounting for these factors would generate more precise estimates of size-structured abundance relationships between aquatic predators and prey.

More generally, we suggest that prey antipredator behaviour, which has the cost of reducing access to resources and the benefit of lowering mortality rates (LIMA & DILL 1990), might explain much of the uncertainty in our estimates of the relationship between the abundances of rockfish and lingcod. Quillback and copper rockfish are long-lived species with late maturity (LOVE et al. 2002). As such, they are expected to maximize fitness by investing heavily in antipredator behaviour (CLARK 1994; HEITHAUS et al. 2008), more so than other reef fishes with faster life histories (FRID et al. 2012), and this investment may have weakened numerical relationships between lingcod and small and medium size classes of rockfish. Accordingly, recent field experiments found that quillback and copper rockfish were much less likely to feed on tethered prey adjacent to a model adult lingcod than similar-sized mesopredators with faster life histories, such as kelp greenling (*Hexagrammos decagrammus*) and juvenile lingcod (FRID et al. 2012). Also, our current study found that rugosity was positively related to rockfish abundance. This result suggests that rockfish preferentially use structurally complex habitats with refuges, which might facilitate predator avoidance (at a foraging cost) and further reduce direct predation by lingcod. If rockfish invest heavily in antipredator behaviour, more so than other mesopredators of similar size, as current evidence suggests (FRID et al. 2012), then lingcod may affect rockfish populations primarily through lost foraging opportunities that reduce growth and reproductive rates and secondarily through direct consumption (HEITHAUS et al. 2008). Future studies should test these hypotheses, which are consistent with theory and data indicating that numerical relationships between predator and prey may be poor indicators of predation risk in some systems (LIMA & DILL 1990; HEITHAUS et al. 2008).

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