

Trophic position scales positively with body size within but not among four species of rocky reef predators

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ABSTRACT: Intra- and interspecifically, larger-bodied predators generally occupy higher trophic positions (TPs). With widespread declines in large predators, there is a need to understand their size-based trophic roles to predict ecosystem-level responses. In British Columbia, Canada, we examined size-based trophic interactions between predatory fishes—3 rockfish species (genus *Sebastes*) and lingcod *Ophiodon elongatus*—and their prey, converting predator $\delta^{15}\text{N}$ signatures to TP and analyzing stomach contents. Intraspecifically, TP scaled positively with predator length and gape width, but the rates of change varied by species. Interspecifically, TP did not scale positively with the observed mean sizes or known maximum sizes of species. Lingcod TP was lower than that of yelloweye and quillback rockfishes, which were 51 and 37%, respectively, smaller than lingcod. Yellowtail rockfish had the smallest average size, yet their mean TP did not differ significantly from that of lingcod. Neither species differences in some morphometric traits known to influence body size–TP relationships nor phylogenetic history explained these results. Most prey consumed were <20% of the predator's size, which might partially explain the lack of a size-based trophic hierarchy among species. Currently, large size classes of rockfishes are being lost due to fisheries and perhaps climate-driven changes. Our findings on intraspecific size–TP relationships indicate that fishery removals of large individuals may diminish trophic structures. Interspecific comparisons of TP suggest that, along with size, species remain an important factor in understanding trophic dynamics. In addition, smaller-bodied predator species may have significant ecological roles to be considered in ecosystem-based fisheries management.

KEY WORDS: Food webs · Stable isotopes · Size-based predator–prey interactions · Diet · Rockfish · Lingcod · Allometric scaling

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1. INTRODUCTION

The relative sizes of predators and prey influence the structure, stability, and resilience of food webs (Barnes et al. 2010, Trebilco et al. 2013). Yet fishery removals, combined with changes in climate, have led to declines in large size classes of predators and degradation of food webs (Harvey et al. 2006, Petchey & Belgrano 2010, Shackell et al. 2010, Strong & Frank

2010). To better predict how marine communities might respond to the loss of large size classes of predators and to implement ecosystem-based fisheries management (Pikitch et al. 2004), there is an urgent need to identify and better understand size-based trophic interactions (Petchey & Belgrano 2010, Strong & Frank 2010).

Predatory fishes can exert top-down control on the structure of marine ecosystems via prey removal or

by inducing behavioral shifts of prey (Baum & Worm 2009, Madin et al. 2016), yet body size may modulate the strength of these ecological interactions (McCauley et al. 2010, Strong & Frank 2010, Heupel et al. 2014). Most predatory fishes swallow prey whole, and their maximum prey size is constrained by the size of their oral gape, which scales allometrically with body size such that larger individuals can consume larger prey (Scharf et al. 2000, Karpouzi & Stergiou 2003, Barnes et al. 2010). Consequently, trophic level of fishes may scale positively with maximum body size interspecifically, reflecting size variation among predator species (Jennings et al. 2001, Romanuk et al. 2011). Intraspecifically, ontogenetic growth of individual predators may also result in trophic level increases with larger body size (Werner & Gilliam 1984, Karpouzi & Stergiou 2003, Marsh et al. 2017). Not all studies, however, have found positive slopes for body size–trophic level relationships, and some of this variation has been attributed to species-specific morphological traits (Ríos et al. 2019), phylogenetic differences at the level of taxonomic order (Romanuk et al. 2011), or foraging strategies (Ou et al. 2017).

The extent to which individual predators consume small prey items throughout their ontogenetic size range might influence the extent to which body size scales positively with trophic level. Prey items that are much smaller than the maximum expected size (based on gape limitation) require less time and energy to capture and may yield higher net energy gain than larger prey items (Werner et al. 1983, Gill 2003). Consistent with this notion, maximum prey size generally increases with predator body size while minimum prey size remains relatively constant as individuals grow (Scharf et al. 2000, Juanes 2016). A wider spectrum of prey sizes may lead to a greater diversity of taxa consumed by larger predators. For instance, off the Washington (USA) coast, lingcod *Ophiodon elongatus*—a predatory fish—fed almost exclusively on Pacific sand lance *Ammodytes hexapterus* when at small size (total length ≤ 30 cm), but its diet encompassed 9 fish families and 3 invertebrate families when at larger sizes (Beaudreau & Essington 2007).

Little is known about the status of size-dependent trophic interactions on temperate rocky reef fishes of the Northeast Pacific, where 2 genera of predatory fishes—rockfishes (*Sebastes* spp.) and lingcod—potentially exert top-down control on prey communities (Beaudreau & Essington 2007, Frid & Marliave 2010,

Frid et al. 2012). Rockfish species diversity is large; it encompasses wide variation in maximum size, morphological and life history traits, prey preferences, and relative use of benthic and pelagic habitats (Love et al. 2002). Many rockfishes are long-lived and slow-growing, and some reach maximum lengths of nearly 1 m (e.g. yelloweye rockfish *S. ruberrimus*, max. age = 118 yr and max. total length = 91 cm; Love et al. 2002), which potentially makes them upper-level predators. Lingcod are the only extant member of their genus. Their lifespan is relatively short, but their maximum total length exceeds that of any rockfish (max. age = 25 yr; max. total length = 152 cm; Froese & Pauly 2019), potentially making adult lingcod a top predator in the system.

In Pacific Canada, size-dependent trophic relationships involving lingcod or rockfish may be changing. Although lingcod stocks were last assessed as ‘healthy’ (King et al. 2012), several rockfish species have a tenuous conservation status. For example, yelloweye rockfish are listed as a species of ‘special concern’ under the Species at Risk Act (Fisheries and Oceans Canada 2018), and quillback rockfish *S. maliger* are listed as ‘threatened’ by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2009). On the central coast of British Columbia, both rockfish species have been declining in average body size, which suggests that fishery exploitation might be affecting the strength of top-down control in rocky reef communities (McGreer & Frid 2017, Eckert et al. 2018).

To better understand these potential changes to rocky reefs, we used field data collected on British Columbia’s central coast to examine size-based trophic structure and diets of 4 species of predatory fish: lingcod, yelloweye rockfish, quillback rockfish, and yellowtail rockfish *S. flavidus*. Importantly, these species differ in maximum known body sizes (Table 1), yet all 4 are Scorpaeniformes (i.e. their

Table 1. The 4 fish species examined and their key biological characteristics as determined from the literature (Love et al. 2002, Beaudreau & Essington 2007, Froese & Pauly 2019). BPMP: benthic predator of mobile prey (e.g. crabs, fish); Pelagic: planktivore or piscivore of pelagic prey; Mixed: both pelagic and benthic mobile prey consumed frequently

Common name	Scientific name	Max. total length (cm)	Max. lifespan (yr)	Primary feeding mode
Lingcod	<i>Ophiodon elongatus</i>	152	25	Mixed
Yelloweye rockfish	<i>Sebastes ruberrimus</i>	91	118	BPMP
Yellowtail rockfish	<i>Sebastes flavidus</i>	66	64	Pelagic
Quillback rockfish	<i>Sebastes maliger</i>	50	95	BPMP

phylogenetic history is shared at the level of order) and have similar morphometric traits (i.e. thoracic pelvic fin, maxillary extends to center or posterior end of eye, notched dorsal fin; Hart 1973) associated with positive slopes in body size–trophic level relationships (Ríos et al. 2019). Morphology and phylogeny, therefore, are unlikely to confound size effects on trophic position (TP) for these species, and we expected TPs to scale positively with body size within and among species (Romanuk et al. 2011, Ríos et al. 2019).

2. MATERIALS AND METHODS

2.1. Specimen collections

Fish specimens were collected from rocky reefs on the central coast of British Columbia, Canada, in Heiltsuk, Kitasoo/Xai'xais, Nuxalk, and Wuikinuxv First Nations territories (Fig. 1) in 2015 and 2016. These collections occurred during a study on population trends using methods detailed by Frid et al. (2016). From spring to fall, fish sampling occurred at rocky reefs with varying depth, exposure, and regional oceanographic processes. Two methods were used: (1) fishery-independent sampling with hook-

and-line jigging gear and standardized lures targeting depths of 10–200 m (mean = 47 m), and (2) opportunistic sampling in association with local indigenous fisheries for food, social, and ceremonial purposes that targeted depths of 5–120 m with hook-and-line gear (unbaited hooks, various jigging lures) or depths of ~50–100 m with 550–1100 m long ground lines equipped with 100–200 baited circle hooks.

In the field and shortly after specimen collection, fish morphometrics were measured, including total length (TL, cm), weight (kg), and gape width (cm). Gape width was measured with a ruler across the horizontal plane of the mouth from one side of the inner jaw to the other (i.e. oral gape: Mihalitsis & Bellwood 2017). Entire stomachs and dorsal muscle tissue samples were immediately frozen for stomach content analysis and stable isotopes, respectively. Some stomachs, particularly those of yelloweye rockfish, were everted due to decompression (i.e. barotrauma) and therefore empty. Rockfish otoliths and lingcod dorsal fins (48th ray) were also collected for age analysis at the DFO Pacific Biological Station Sclerochronology Laboratory (Frid et al. 2016). Although a diversity of reef species was collected, only yelloweye rockfish, quillback rockfish, yellow-tail rockfish, and lingcod had sufficient sample sizes for analyses.

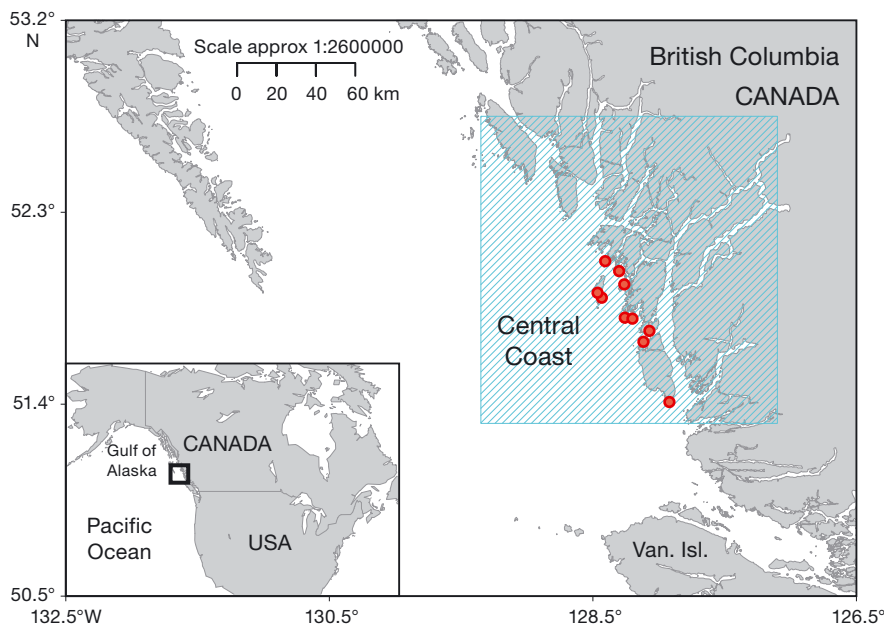


Fig. 1. Central coast of British Columbia, Canada. Fish were sampled at 48 rocky reef sites from Aristazabal Island in the north to Smith Sound in the south and encompassed protected inside and exposed outside waters (blue box). Individual sampling locations are not displayed in order to protect First Nations fishing areas (see Frid et al. 2016 for site details). Red sea urchins were collected at sites across the same spatial gradient (red circles)

2.2. Stable isotope preparation

Stable isotope analysis is an established method of estimating long-term diets of consumers in ecological systems. The $\delta^{13}\text{C}$ isotope of a consumer can represent the mixture of its prey sources because little fractionation occurs in $\delta^{13}\text{C}$ during the trophic transfer of energy from prey to predator (Peterson & Fry 1987). In contrast, enrichment in the $\delta^{15}\text{N}$ isotope occurs with each trophic transfer (e.g. predator–prey interaction) in consumer tissue by ~3.4‰ (Minagawa & Wada 1984), but can vary due to numerous factors (see McCutchan et al. 2003). Expected enrichments in $\delta^{15}\text{N}$ among trophic interactions can be used as a proxy for increasing TP, whereby one can infer consumer TP by assessing its $\delta^{15}\text{N}$ signature relative to the $\delta^{15}\text{N}$ from the base of the food web (Post 2002).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values of rockfish and lingcod were used to determine long-term dietary assimilation and TP. Fish dorsal muscle tissue was thawed, visually inspected and cleared of debris, and then rinsed in 2 baths of deionized water. Tissue samples were oven-dried for 48 h at 60°C, ground to a fine powder with a Wig-L-Bug, and packaged in tin capsules. Fish isotope signatures were analyzed at the University of Victoria's Mazumder Lab using a Delta IV Isotope Ratio Mass Spectrometer and calculated as:

$$\delta^{13}\text{C} / \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (1)$$

where R is the ratio of heavy to light isotope ($^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$).

Red sea urchins *Mesocentrotus franciscanus* are slow-growing and are estimated to reach 200 yr of age (Ebert & Southon 2003). Given these life history attributes, and their direct consumption of primary producers in nearshore rocky reef systems (see Post 2002), red sea urchins likely represent a long-term trophic baseline in rocky reef ecosystems. In 2013, 2–5 red sea urchins were collected by scuba at 10 sites on the central coast (Pang 2018) (Fig. 1). Connective tissue around the Aristotle's lantern was dissected and frozen until thawed for laboratory processing. Tissue samples were rinsed with 10% HCl baths followed by deionized water baths, and oven dried at 60°C for 48 h. Samples were ground with a mortar and pestle, packaged in tin capsules, and sent to the University of California Davis for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic analysis (and calculated with Eq. 1) using a PDZ Europa 20-20 Isotope Ratio Mass Spectrometer (Pang 2018). All fish and red urchin isotopes are reported in permil (‰), relative to the international standards Vienna PeeDee Belemnite and air for carbon and nitrogen, respectively. Average stable isotope values are reported with standard deviation (SD), unless otherwise stated.

Differences in tissue preparation techniques (e.g. rinse methods) and laboratories (Pestle et al. 2014), and differences in collection year, may influence isotopic comparisons. However, sea urchin isotopic values in this study were similar to elsewhere (i.e. Newsome et al. 2009, Szpak et al. 2013). Local environmental conditions are also likely contributors to variation in isotope values. By using the average values of sea urchins across the same spatial gradient as fish were collected (Fig. 1), we attempted to capture similar spatial variability (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m640p189_supp.pdf). Moreover, $\delta^{15}\text{N}$ values showed no regional patterns in site-level differences in fish (i.e. no

groupings by ocean subregion: Fig. S2) and thus, we assessed trophic trends for the study area as a whole.

2.3. Trophic level estimations

We estimated the TP of rockfish species and lingcod using predicted $\delta^{15}\text{N}$ enrichments relative to red urchins (i.e. basal source). Calculating consumer TP with $\delta^{15}\text{N}$ may be conducted using an additive framework, assuming that the change in $\delta^{15}\text{N}$ is constant and typically 3.4‰ (Minagawa & Wada 1984) between predator and prey trophic transfers (see Post 2002). However, recent evidence (e.g. Caut et al. 2009) shows that $\delta^{15}\text{N}$ generally decreases, or 'scales,' with TP which has been seen across many types of fauna, including fishes (Hussey et al. 2014a). Here, we estimated fish TP with a scaled approach using Eqs. (2) to (4) from Hussey et al. (2014a,b):

$$\text{TP} = \log(\delta^{15}\text{N}_{\text{lim}} - \delta^{15}\text{N}_{\text{base}}) - \log(\delta^{15}\text{N}_{\text{lim}} - \delta^{15}\text{N}_{\text{consumer}})/k + \text{TP}_{\text{base}} \quad (2)$$

where:

$$k = \left(\frac{\beta_0 - \delta^{15}\text{N}_{\text{lim}}}{-\delta^{15}\text{N}_{\text{lim}}} \right) \quad (3)$$

$$\delta^{15}\text{N}_{\text{lim}} = \frac{-\beta_0}{\beta_1} \quad (4)$$

Values for β_0 and β_1 were taken from Hussey et al. (2014a). TP_{base} was assigned a value of 2 (second trophic level) because sea urchins are herbivorous grazers in reef ecosystems that feed on primary producers. $\delta^{15}\text{N}_{\text{base}}$ was set as the mean value of sea urchins in the study region (8.75‰).

We used hierarchical general linear models to examine interspecific influences on the relationship between TP and fish length or gape width. Species identity was used as a categorical variable. Fish length or gape width, continuous variables, were centered around zero (Gelman 2008, Bolker et al. 2009). To assess intraspecific relationships with TP, an interaction term was used between morphometric characteristics and species identity. Post-hoc Tukey's contrasts were examined in the linear models for a pairwise comparison of species' TP least squares means using the R package 'emmeans' (Lenth et al. 2018). Differences in observed means of species TP (i.e. determined by Eq. 2) were assessed by ANOVA and post hoc Tukey's HSD tests, whereby significance was attained at $\alpha = 0.05$. All analyses were conducted in R (R Core Team 2017).

2.4. Prey size as a function of predator size

Fish stomachs were thawed and emptied for analysis of recently consumed prey items. For each non-empty stomach, prey were identified to the lowest taxonomic level possible using a dissecting scope. Individual prey items within a taxonomic level were enumerated for total abundance and weighed (g) as a group. If individual prey items were intact, TL (mm) was measured. Lengths of partially digested prey (2% of dataset) were recorded and analyzed; these provide minimum estimates of maximum prey lengths. Prey items were grouped in broad functional groups for analysis (Table S1). Prey composition was first calculated for each predator species by taking the mean weight or abundance of each prey item and comparing it proportionally to all other prey items found in species' stomachs for % gravimetric (mass) and % abundance, respectively.

We examined the upper and lower bounds of the prey size spectrum as a function of predator body size using quantile regression analysis. To account for the hierarchical nature of the data, where multiple prey lengths were often recorded from a single predator, we used a mixed-effects quantile regression approach with individual predators categorized as a random effect. Using the R package 'lqmm' (Geraci 2014), we quantified the maximum, median, and minimum prey lengths by predator size using 95th, 50th, and 5th quantiles, respectively (Koenker & Hallock 2001). The regression coefficients were bootstrapped ($r = 10^2$) due to low sample size. To determine the quantity of smaller prey consumed by predators, we examined the relative frequency distributions of the prey size to predator size ratio for each predator (Scharf et al. 2000).

3. RESULTS

A total of 159 specimens, representing 3 rockfish species and lingcod, were analyzed for stable isotopes. We analyzed prey contents from the stomachs of 141 fish, of which 46% were female, 51% were male, and the remainder had undetermined sex. 67% of stomachs analyzed were non-empty (Table 2). Fish were caught at depths ranging from 18 to 110 m (median 65 m). Lingcod were the largest fish caught by mass, length, and gape width, while also being the youngest (3–13 yr). Among rockfish, yelloweye rockfish were on average the largest in size and oldest, while yellowtail rockfish were the smallest in size (Table 2).

Species varied in their mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic positions (Fig. 2). Yelloweye and quillback rockfish, which are primarily benthic predators, demonstrated on average enriched $\delta^{13}\text{C}$ values relative to pelagically associated yellowtail rockfish and lingcod. Yellowtail rockfish and lingcod also showed twice the variability in $\delta^{13}\text{C}$ compared to benthic predators, extending to more depleted $\delta^{13}\text{C}$ signatures. Red sea urchins had an average $\delta^{15}\text{N}$ value of $8.75 \pm 0.85\%$ (SD) and $\delta^{13}\text{C}$ value of $-16.12 \pm 1.44\%$ across sites (Fig. S1).

A hierarchy in mean $\delta^{15}\text{N}$ signatures was apparent, such that yelloweye rockfish exhibited the most $\delta^{15}\text{N}$ enrichment (mean: $16.55 \pm 0.45\%$, range: 15.23–17.37‰). Yelloweye rockfish, lingcod, and quillback rockfish were relatively enriched in mean $\delta^{15}\text{N}$ signatures compared to yellowtail rockfish (mean: $14.63 \pm 0.50\%$). For quillback rockfish, variability in $\delta^{15}\text{N}$ (SD = 0.80‰) was 1.6–1.8× greater than for other species (Figs. 2 & 3).

Table 2. Summary of collection depths (mean), sample sizes, and morphometrics (TL: total length) for fish species sampled. Stomach sample sizes indicate total stomachs followed by the number of which were empty in brackets. Number of prey items in each stomach was based on items thought to be from individual prey. Errors are reported as SD

	— Habitat —	— Sample sizes —			— Species morphometrics —				
	Depth (m)	Stomachs (empty)	Prey	Stable isotopes	Mean mass (kg)	Mean age (yr)	Mean TL (cm)	TL range (cm)	Mean gape (cm)
Yelloweye rockfish	66.5 ± 13.2	35 (19) ^a	47	55	2.2 ± 1.5	22.1 ± 10.2	48.4 ± 10.6	26.6–68.5	8.8 ± 2.4
Quillback rockfish	73.9 ± 21.7	79 (21)	199	69	1.0 ± 0.3	25.0 ± 11.9	37.2 ± 4.3	19.1–44.6	6.7 ± 1.2
Yellowtail rockfish	59.7 ± 13.0	12 (4)	57	16	0.6 ± 0.3	12.3 ± 6.4	35.9 ± 5.2	26.2–47.2	4.2 ± 1.1
Lingcod	49.7 ± 20.4	15 (2)	71	19	4.6 ± 2.6	6.6 ± 3.1	76.4 ± 11.0	59.2–94.3	11.82 ± 2.6

^aTwo empty yelloweye rockfish stomachs were everted due to barotrauma. A third yelloweye had an everted stomach that we counted as non-empty because this individual had *Pandalus* spp. in its mouth

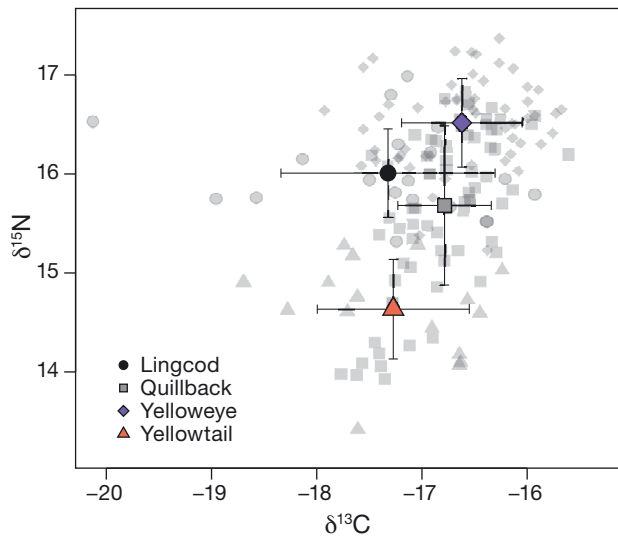


Fig. 2. Mean \pm SD $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope signatures (‰) of lingcod, yelloweye rockfish, quillback rockfish, and yellowtail rockfish. Light grey symbols indicate isotopic signatures of individuals

3.1. Trophic level estimates by predator sizes

Interspecifically, there were significant differences in mean TP from models (Tables 3 & 4, Fig. 3) and observed values (ANOVA: $F_{3,155} = 41.74$, $p < 0.001$). The relative positioning among species did not match expectations based on species' known maximum

sizes (Table 1) or observed mean sizes (Table 2). On average, lingcod specimens were largest in all size metrics measured relative to rockfish. Yet, according to model estimates that account for unbalanced sample sizes (LS means, Table 4), their mean TP was lower than for quillback and yelloweye rockfish which, on average, were 51 and 37% smaller (based on TL) than lingcod, respectively (Table 2). Further, the mean TP of lingcod did not differ significantly from that of yellowtail rockfish, despite yellowtail rockfish being, on average, 66% smaller. Similarly, the mean TP of yelloweye rockfish did not differ significantly from that of quillback rockfish, despite quillback rockfish being, on average, 23% smaller (Tables 2 to 4).

Overall and intraspecifically, however, TP scaled positively with TL (overall: $R^2 = 0.53$, Table 3) and gape width (overall: $R^2 = 0.59$, Table 3). Slopes varied among species (Fig. 3, Table 3). Quillback rockfish length and gape width had a significant interactive relationship with TP (slope $b = 0.66$, $p < 0.05$ and $b = 0.75$, $p < 0.001$, respectively), while this was not significant for other species. Variability was also greatest for quillback (e.g. ~40 cm long quillback varied by up to ~1.0 TP). Given that length and gape width are positively related (Fig. S3), gape–TP slopes generally resembled length–TP slopes across species (Fig. 3B, Table 3). Both TP and size (TL and gape) generally increased with age (Fig. 3).

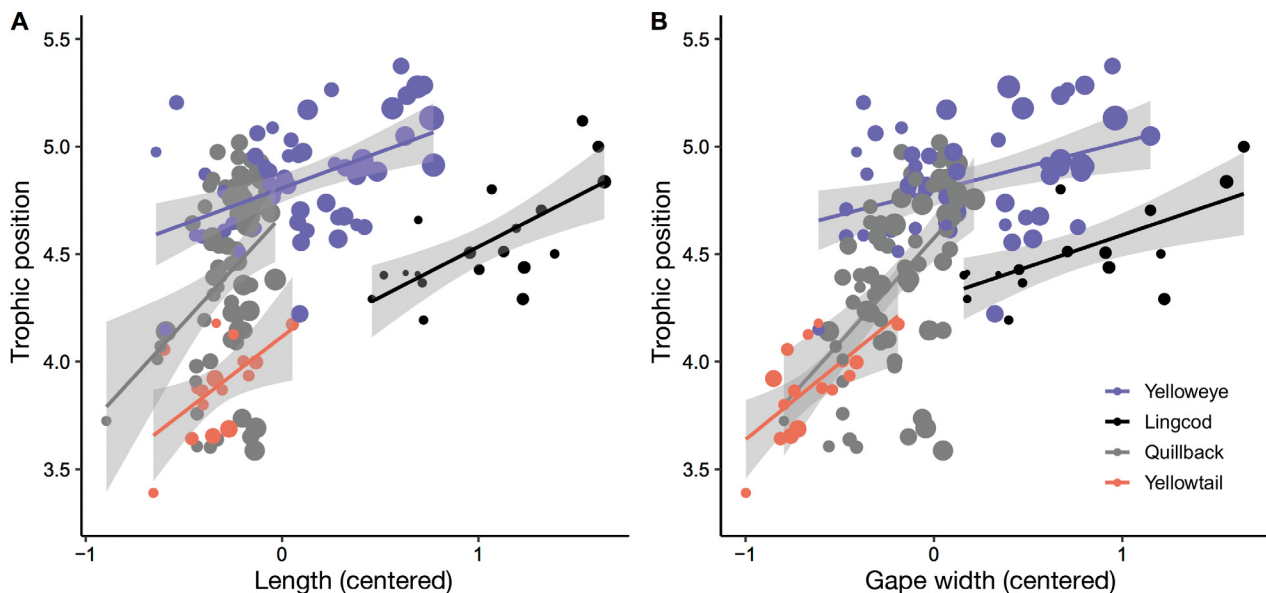


Fig. 3. Relationships between fish trophic position with (A) body length and (B) gape width, for yelloweye rockfish, quillback rockfish, yellowtail rockfish, and lingcod. Grey shading indicates 95% confidence. Larger symbols represent older fish (20 yr bins), ages range from 3–66 yr

Table 3. Trophic position (TP) relationships with fish total length (Length-TP) and gape width (Gape-TP). The species reference level is set to yelloweye rockfish. **Bold** indicates significant estimates

Model	Parameter	Estimate	SE	p
Length-TP	Intercept	4.81	0.04	<0.001
	Length	0.34	0.11	0.003
	Species(yellowtail)	-0.69	0.17	<0.001
	Species(lingcod)	-0.74	0.21	<0.001
	Species(quillback)	-0.13	0.09	0.158
	Length × Species(yellowtail)	0.37	0.45	0.419
	Length × Species(lingcod)	0.13	0.22	0.547
	Length × Species(quillback)	0.66	0.27	0.018
Gape-TP	Intercept	4.80	0.04	<0.001
	Gape	0.23	0.09	<0.001
	Species(yellowtail)	-0.45	0.25	0.07
	Species(lingcod)	-0.50	0.13	<0.001
	Species(quillback)	-0.22	0.06	<0.001
	Gape × Species(yellowtail)	0.48	0.37	0.188
	Gape × Species(lingcod)	0.07	0.17	0.674
	Gape × Species(quillback)	0.75	0.18	<0.001

Table 4. Mean trophic position (TP) of fish species. TP was assessed by the arithmetic mean (observed mean) and least squares (LS) means from the Length-TP and Gape-TP models (Table 3). Letters indicate significant difference among species TPs. LS estimates account for unbalanced sample sizes and therefore differ from observed means. Errors are reported as SE

Species	LS mean (Length-TP)	LS mean (Gape-TP)	Observed mean
Yelloweye rockfish	4.81 ± 0.04 ^A	4.80 ± 0.04 ^A	4.84 ± 0.26 ^A
Quillback rockfish	4.68 ± 0.08 ^A	4.58 ± 0.04 ^B	4.40 ± 0.40 ^B
Yellowtail rockfish	4.12 ± 0.16 ^B	4.35 ± 0.24 ^{AB}	3.88 ± 0.21 ^C
Lingcod	4.07 ± 0.21 ^B	4.29 ± 0.13 ^B	4.55 ± 0.25 ^B

3.2. Relationships of predator size with prey size and prey composition

We found a wide size range of prey items in the stomachs of quillback rockfish and lingcod specimens. However, using nested quantile regression, we did not find significance in the 5th, median, or 95th quantiles of predator size-prey size relationships of any species examined despite the appearance of wedge-shape patterns (Fig. S4). Although some individuals did consume very large prey items, small prey items dominated the diets of each species, such that the TL of most prey items was <20% of predator length (Fig. 4). Yelloweye rockfish, however, ate a greater proportion of larger prey items (28.6%) than quillback rockfish (9.7%) and lingcod (7.4%) relative to their body size (i.e. prey TL >20% of predator TL, Fig. 4A), and overall (Fig. 4B). Larger sample sizes of predators and prey are needed for a thorough assessment of predator and prey size relationships for these species.

Prey composition was dominated by fish and crustaceans (except for yellowtail rockfish; Fig. S5), yet the proportions of these prey types varied by species and size class (Fig. 5). By mass, fish (e.g. *Sebastes* spp., *Oncorhynchus gorbuscha*) were the primary prey (94%) consumed by lingcod; numerically, however, a variety of small-bodied species characterized lingcod diets, including pelagic (euphausiids) and benthic invertebrates (Fig. 5, Fig. S5). Similarly, yelloweye rockfish diet was composed

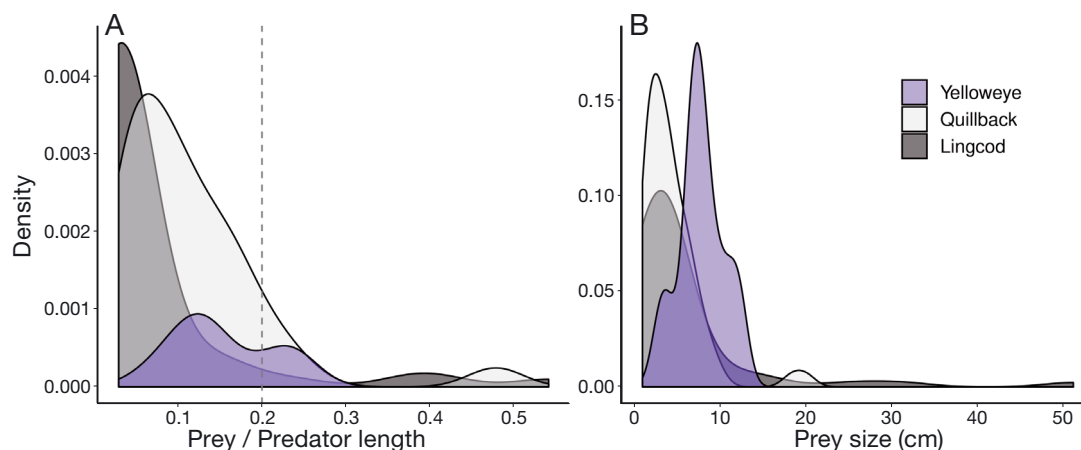


Fig. 4. (A) Density distributions of the ratio of prey length to predator length. Predator fish are yelloweye rockfish, quillback rockfish, and lingcod. Left of the dashed line indicates the frequency of prey that are less than 20% of the predator size. (B) Density distribution of all prey sizes consumed by predator species. Refer to Table 2 for sample sizes and to Fig. S5 for the relative contribution of different individuals to these data

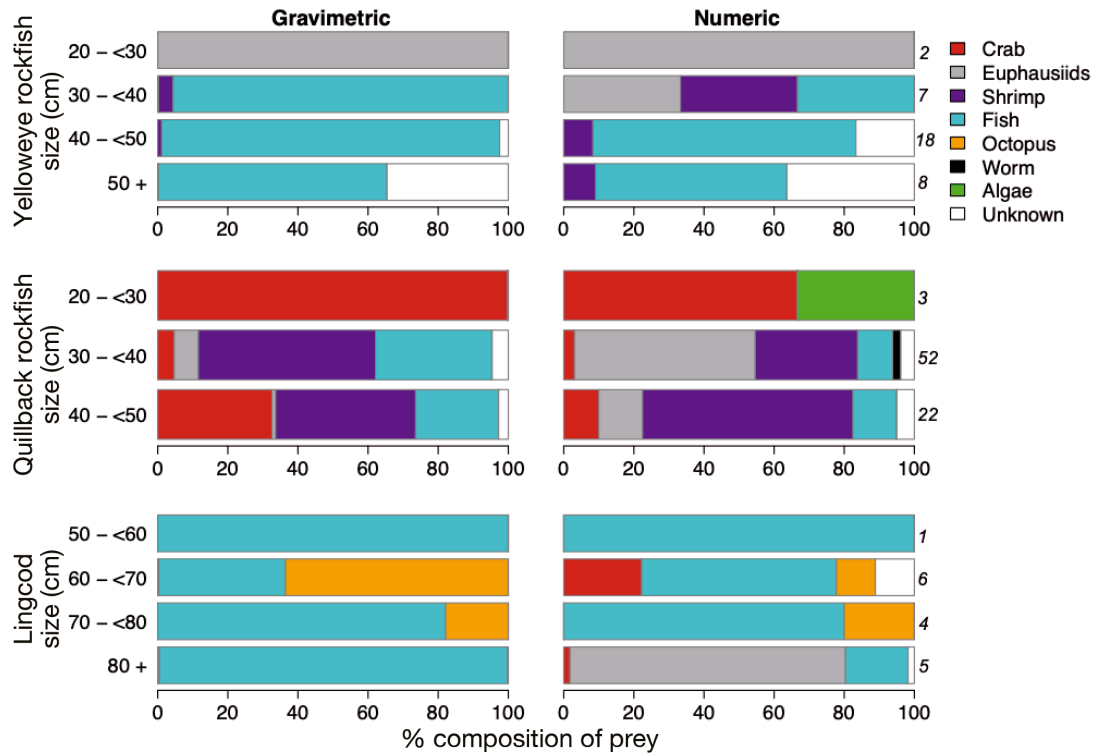


Fig. 5. Percent composition of prey types consumed by different size classes of predators. Numbers on the right in italics indicate sample size of predators in each size class

mainly of fish (e.g. *Clupea pallasii*) by both weight (87%) and abundance (59%), yet also included smaller prey items (Figs. 4 & 5, Fig. S5). Quillback rockfish had the most diverse diet by weight: 48% benthic shrimp (e.g. primarily *Pandalus* spp.), 31% fish, 11% benthic crab (*Pugettia* spp., *Cancer* spp.), and 6% pelagic euphausiids (Fig. 5, Fig. S5).

The data suggested ontogenetic diet shifts in prey type for rockfishes. Invertebrates dominated the stomach content of the smallest size classes (TL 20–30 cm) of quillback rockfish (primarily *Cancer* spp.) and yelloweye rockfish (euphausiids), yet larger sizes of both species consumed shrimp (*Pandalus* spp.) and fish. Yelloweye rockfish, however, consumed more fish than similarly sized quillback rockfish (Fig. 5).

In the size classes of lingcod examined (59.2–94.3 cm), ontogenetic shifts in prey type were less evident (Fig. 5). Fish, alone or in combination with Pacific octopus *Enteroctopus dofleini*, dominated the stomach contents of all size classes of this species, with the notable exception of the numerical dominance of euphausiids (which had a TL of ~3 cm) in the largest lingcod size class. Nevertheless, lingcod consistently consumed larger prey items relative to quillback and yelloweye rockfish (Fig. 4B). Sample

sizes were insufficient to examine the diets of yellowtail rockfish (Table 2); the few stomachs collected contained euphausiids and benthic shrimp (Fig. S5).

4. DISCUSSION

Overall, reef fish TPs were positively associated with body size and gape size, but varied by species. The trophic hierarchy among fish species, however, was unrelated to observed mean body sizes or known maximum sizes, which contradicted our expectation (Romanuk et al. 2011, Ríos et al. 2019). The mean TP of the largest predatory fish, lingcod, was lower than that of quillback and yelloweye rockfishes, which, on average, were 51 and 37% smaller than lingcod. Further, yellowtail rockfish had the smallest average size in our sample, yet in some model estimations their mean TP did not differ significantly from that of lingcod. While the 4 species examined are only a small component of the more diverse fish community inhabiting our study area (Frid et al. 2018), our results suggest that factors other than body size may be influencing TPs in this community.

Species differences in morphometric traits suggested by Ríos et al. (2019) and phylogenetic history

(i.e. taxonomic order) (Romanuk et al. 2011) are unlikely to explain our results. The 4 species we examined are Scorpaeniformes with similar fin positions (pelvic and dorsal) and relative mouth size (see Ríos et al. 2019). Moreover, all species demonstrated similar strong positive relationships in gape width and length (Fig. S3).

Rockfish are known for high speciation in their evolutionary history (~70 species in the northeast Pacific, ~36 in British Columbia), where sympatric species display diet (Murie 1995) and habitat (Love et al. 2002) differences that have resulted in niche partitioning (Olson et al. 2019a). In a phylogenetic study of multiple *Sebastes* species, morphological traits associated with foraging, such as number and length of gill rakers, had strong associations with may be an important factor in identifying TP (Ingram & Shurin 2009). The extent to which gill rakers and other morphometric characteristics influence TP in the fish communities of our study area requires further investigation. Among gape metrics, horizontal oral gape may be the best morphological measurement to estimate maximum prey size a fish will consume (Mihalitsis & Bellwood 2017), and thus may be an important factor in identifying TP.

The lack of a size-based trophic hierarchy among species could, potentially, reflect the large proportion of small prey found within predator stomachs. Large numbers of euphausiids, for example, were present in the largest lingcod size class in this study. Consumption of small prey items, which have lower handling times than larger items, is consistent with a theoretical expectation of minimizing costs (Werner 1974, Gill 2003). Alternatively, skill and experience in foraging strategies may be acquired with age (Graeb et al. 2006).

Our field sites included protected inlets and exposed outside waters. Prey availability and oceanographic conditions likely vary within this large area. Spatial heterogeneity might lead to variation in diet and growth rates within species (Love et al. 2002, West et al. 2014, Olson et al. 2019b), potentially affecting size-based TPs. Perhaps consistent with this notion, the TPs of large quillback rockfish and mid-sized yelloweye rockfish ranged across ~1.0 and ~0.5 TPs, respectively. Spatial analyses are still required to understand the underlying mechanisms. Pairing localized samples of prey base to predator isotope signatures with closer temporal sampling may yield clearer results.

In Alaska, demersal yelloweye and quillback rockfishes had similar yet slightly lower TPs (4.4 and 4.0, respectively; Kline 2007) to calculations in this study

(Table 4). Similar to our study, Alaskan yelloweye and quillback rockfish also had higher TPs and more enriched $\delta^{13}\text{C}$ values than yellowtail rockfish (Kline 2007). Depleted $\delta^{13}\text{C}$ signatures in other pelagic rockfish (e.g. black rockfish *Sebastes melanops*) relative to demersal rockfish have also been demonstrated on exposed coastlines of British Columbia (Olson et al. 2019a). Both yellowtail rockfish and lingcod tend to consume a large proportion of pelagic prey in their diet (Love et al. 2002, Beaudreau & Essington 2007). Pelagic prey are likely to be foraging on basal marine-derived energy (Kline 2007), which may explain the relatively depleted, yet variable, $\delta^{13}\text{C}$ signatures for more pelagically associated predators.

Despite the lack of a size-based hierarchy among species, TP scaled positively with body size within species, which is consistent with both metabolic theory (Cohen et al. 1993) and empirical findings of allometric scaling in other temperate fishes (Jennings et al. 2001, Juanes 2016). While species had a significant effect on TP, differences in body size–TP slopes were not found among yelloweye rockfish, lingcod, and yellowtail rockfish. The more rapid increase in TP with size by quillback rockfish may reflect a wider diversity of prey choices relative to other species examined in this study (Fig. 5). Alternatively, variation within fish species, particularly in quillback, could be due to factors unexplored here, such as site or demography (age, sex, etc.) differences.

Our findings demonstrate the importance of both size and species in rocky reef food web structuring. Our inter-specific comparison suggests that some smaller-bodied species of predators can have significant ecological roles, which has potential implications for ecosystem-based fisheries management. At the same time, large size classes of fish are being lost globally due to fishery removals and to the combined effects of ocean warming and deoxygenation, which affect metabolic rates and limit maximum fish sizes (Cheung et al. 2012). Consistent with global trends, recent evidence indicates that large size classes of quillback and yelloweye rockfish are being lost from this coastal British Columbia study area (McGreer & Frid 2017, Eckert et al. 2018). Consequently, the trophic structure of this ecosystem may be in the process of being degraded (Harvey et al. 2006, Strong & Frank 2010). A combination of more conservative fishery management practices and additional marine protected areas may be required to reverse this trend (Berkeley et al. 2004, Baskett & Barnett 2015).

When evaluating the consequences of marine predator declines, it is important to keep in mind that

TP is only one measure of ecological role. Species clearly remains an important factor in understanding food webs; as such, predator diversity should be considered. Moreover, theoretical and empirical evidence suggest that large size classes of predators may influence lower TPs not only through prey consumption, but also via predator–prey behavioral interactions and their cascading effects (Heithaus et al. 2008, Rizzari et al. 2014, Madin et al. 2016). Thus, large predatory fishes that are not necessarily at the top of a trophic hierarchy, as lingcod in this study area appear to be, may still influence the distributions and foraging rates of prey (Frid et al. 2012), potentially influencing community structure and function (Heithaus et al. 2008, Frid et al. 2013).

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