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# Predatory fishes affect trophic cascades and apparent competition in temperate reefs

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**We provide evidence for a trophic cascade involving apex predators and mesopredators of marine temperate reefs, lingcod and rockfish, respectively. We measured spatio-temporal variation in the relative abundance of lingcod, subadult rockfish and two shrimp groups eaten by rockfish (*Pandalus* sp. and three smaller-bodied genera aggregated). Lingcod had an indirect positive effect on shrimps, as mediated by the direct negative effects of lingcod on rockfish and of rockfish on shrimps. These top-down effects on shrimps, however, were stronger for *Pandalus* than for small-bodied shrimps. Further, abundances of *Pandalus* and small-bodied shrimps were negatively correlated and the latter had a stronger positive effect on rockfish, suggesting that rockfish mediated asymmetrical apparent competition between shrimps. Our results indicate mechanisms by which predatory fishes may influence the structure of marine communities.**

**Keywords:** asymmetric apparent competition; marine predators; rockfish; trophic cascade

## 1. INTRODUCTION

Trophic cascades occur when the direct effects of predators on mesoconsumers indirectly alter the direct effects of mesoconsumers on their resources (Heithaus *et al.* 2008). Other indirect interactions involving predators include apparent competition, a negative relationship between the abundances of two species occupying the same trophic level that is mediated by symmetrical or asymmetrical effects of a shared predator (Chapin & Bonsall 2000).

Many marine fishes with the potential to influence community structure over vast areas are declining (Heithaus *et al.* 2008). Lingcod (*Ophiodon elongatus*) and rockfish (*Sebastes* sp.), for instance, are commercially exploited top predators and mesopredators in temperate reefs. Understanding the ecological role of these and other predatory fishes may inform conservation strategies (Heithaus *et al.* 2008). We used spatio-temporal variability in the relative abundance of species at different trophic levels to infer two aspects of community dynamics mediated by subadult copper (*Sebastes caurinus*) and quillback rockfish (*Sebastes maliger*): a trophic cascade from lingcod to

demersal shrimps, and asymmetrical apparent competition between shrimp groups. Our results suggest that the alteration of multispecies interactions driven by predatory fishes can be an ecological cost of overfishing.

## 2. MATERIAL AND METHODS

The study area covers Howe Sound and eastern Georgia Strait in southern British Columbia, Canada. From mid-July 2008 to September 2009, we conducted SCUBA-based timed counts along permanently marked line transects; one diver counted lingcod and rockfish and a second diver counted demersal crustaceans. Transects were spread over nine reefs at depths of 15–27 m below chart datum. Four reefs were within 1–2 km from each other and five were 5–15 km from other sampled reefs. Five reefs had two distinct sections differing in structural complexity where separate transects were established (i.e. 14 transects total). Individual transects were treated as independent spatial units and were sampled 12–22 times during the study (see the electronic supplementary material, table S1). Structural habitat complexity, which affects rockfish positively (Marliave & Challenger 2009), was indexed with rugosity measurements (see the electronic supplementary material, Supplemental Methods).

Analyses aggregated quillback and copper rockfish and focused on subadults (total length 8–19 cm) because their size-specific vulnerability to lingcod is greater than for larger rockfish (Beaudreau & Essington 2007). Also, demersal crustaceans are more important diet items for subadult than for adult rockfish (Murie 1995), and our methods tallied demersal crustaceans accurately. Demersal shrimps—namely *Pandalus danae* and smaller-bodied genera unidentifiable from stomach contents—are major prey items year round (Murie 1995). At our sites, small-bodied genera of shrimp consisted primarily of *Eualus*, *Heptacarpus* and *Lebbeus*, which we aggregated into one group named EUHEL. Although rockfish use the inside of rocky crevices year round, during winter this habitat preference increases and activity levels decrease (Carlson & Barr 1977; see the electronic supplementary material, figure S1).

We partitioned data into four periods. Period 1 covered mid-July to early December 2008 (summer and autumn). Period 2 covered late December 2008 to early April 2009 (winter). Period 3 covered mid April to late June 2009 (spring). Period 4 replicated summer (early July to early September 2009).

From the natural history of the system and the frameworks of trophic cascade and apparent competition, we made the following predictions. First, the abundance of subadult rockfish is negatively affected by the abundance of lingcod but positively affected by the abundances of *Pandalus* and EUHEL (i.e. rockfish prefer sites with more food resources) and by structural habitat complexity. Because rockfish prey on shrimp, however, subadult rockfish negatively affect the abundances of *Pandalus* and EUHEL (i.e. rockfish-shrimp relationships are non-recursive or bidirectional). If the above direct relationships between trophic levels were to be found, we expected rockfish to mediate an indirect positive effect of lingcod on shrimps, indicative of a trophic cascade, and an indirect negative relationship between the abundances of *Pandalus* and EUHEL, indicative of apparent competition. Finally, we expected data to support these predictions year-round, except for winter, when rockfish use of crevices increases and activity levels decrease.

We tested predictions using counts per minute (CPM) for each taxon (transformed as  $\log_{10}(\text{CPM} + 1)$ ) and rugosity measures to build a structural equation model (s.e.m. or path analysis) with the RAMONA procedure of SYSTAT 12 (Browne 2007). The model included direct recursive paths (assuming unidirectional causation) from lingcod to rockfish and rugosity to each of rockfish and both shrimp groups, and non-recursive direct paths between rockfish and each shrimp group. A *Pandalus*-to-EUHEL direct path was included because the former may prey on the latter (Jensen 1995). Stomach content data suggest that lingcod consume rockfish never, rarely and commonly when total lengths are less than 40 cm, 40–49 cm, and more than 50 cm, respectively (Beaudreau & Essington 2007). The s.e.m., therefore, excluded lingcod with total lengths less than 50 cm.

RAMONA cannot include nominal variables (e.g. for transect location) and, consequently, rugosity values controlled for location effects. This approach is justifiable because rugosity values, which were distinct for most locations, are a biologically meaningful representation of location effects (see the electronic supplementary material, figure S2). Relative abundances of each taxon varied temporally within most transect locations (see the electronic supplementary material, figure S3). Consequently, results reflect the combined effects of time and space. (Partitioning these effects would have required greater sample sizes than ours.)

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2010.0034> or via <http://rsbl.royalsocietypublishing.org>.

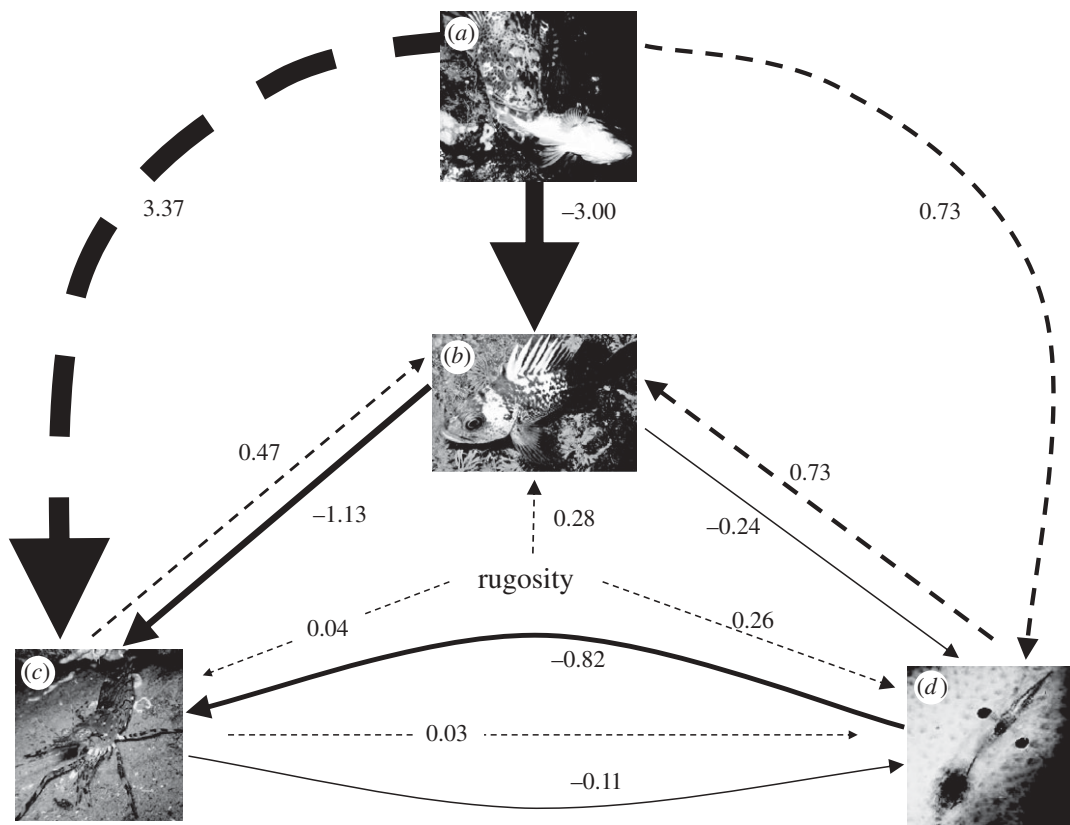


Figure 1. Path model measuring direct (straight arrows) and indirect (curved arrows) interactions between (a) lingcod, (b) subadult rockfish, (c) *Pandalus* and (d) EUHEL during non-winter periods (periods 1, 3, 4 aggregated; table 1). Except for the very weak rugosity-to-*Pandalus* and *Pandalus*-to-EUHEL paths, line thickness is proportional to path coefficients (values beside or on lines); solid and dashed lines indicate negative and positive relationships, respectively. Photo details/credits: (a) lingcod consumes copper rockfish (Conor McCracken), (b) quillback rockfish (Kevin Kaufman), (c) *Pandalus danae* (Conor McCracken) and (d) *Heptacarpus* sp. (Donna Gibbs).

Indirect path coefficients were calculated by multiplying direct path coefficients that involved mediating variables. Variances and 90% CI for indirect path coefficients were calculated, respectively, with eqns (4) and (6) of Mackinnon *et al.* (2007).

We first applied the s.e.m. to non-winter periods aggregated. The robustness of results was confirmed by applying the same s.e.m. to each period separately.

### 3. RESULTS

When non-winter periods were aggregated, lingcod had an indirect positive effect on shrimps, as mediated by the direct negative effects of lingcod on subadult rockfish and of the latter on shrimps (figure 1 and table 1). Direct and indirect top-down effects on shrimps, however, were 4.6 times stronger for *Pandalus* than for EUHEL. Both shrimp groups had a direct positive effect on subadult rockfish, but the effect of EUHEL was 1.5 times stronger than the effect of *Pandalus*, and counts per minute for the two shrimp groups were negatively correlated ( $r = -0.25$ ,  $p = 0.001$ ). Evidence for asymmetrical apparent competition was strong; the rockfish-mediated indirect effect of EUHEL on *Pandalus* was seven times greater than from *Pandalus* to EUHEL (figures 1 and 2). We found no direct negative effect of *Pandalus* on EUHEL. Rugosity had direct positive effects of similar magnitude on rockfish and EUHEL (figures 1 and 2) but minor effects on *Pandalus* (figures 1 and 2). The s.e.m. for non-winter periods fitted data well, despite

Table 1. Fit to data and unexplained variability of path models applied to different sampling periods. (Fit improves with lower sample discrepancy function values; residual variable coefficients measure unexplained variability for dependent variables (Browne 2007).)

period	sample size	sample discrepancy function	residual variable coefficients <sup>a</sup>		
			rockfish	<i>Pandalus</i>	EUHEL
1, 3, 4	180	7.50E-008	-3.15	3.60	2.40
1	56	1.79E-008	-2.83	2.64	2.58
2	44	0.41			
3	69	1.56E-008	3.17	3.36	1.98
4	55	1.39E-009	2.55	2.45	2.42

<sup>a</sup>Excluded for period 2 owing to poor fit of model.

much variability in the abundances of rockfish and shrimps being unexplained (table 1). Unexplained variability was unsurprising because analyses focused on key explanatory variables, while other factors may have also been influential (e.g. resources and predators not considered).

When non-winter periods were analysed separately, reduced sample sizes decreased the precision of some path coefficients but the fit of the s.e.m. to each data subset was good and the same relationships that were strong for the aggregated periods remained robust (table 1 and figure 2). Namely, direct negative effects

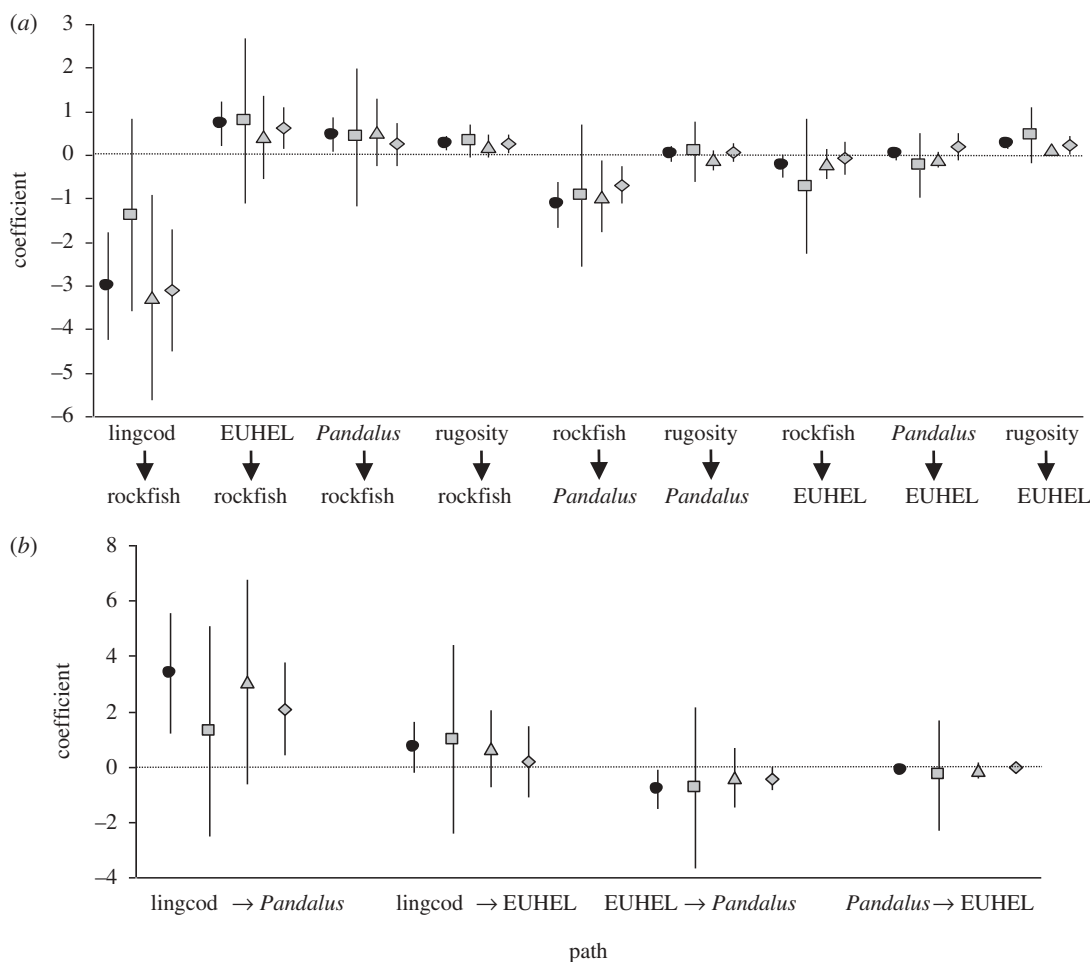


Figure 2. (a) Direct and (b) indirect path coefficients for the path model applied to non-winter periods. Rockfish mediated all indirect paths in (b). Sampling period: filled black ovals, 1,3,4 (grouped); filled grey squares, 1; filled grey triangles, 3; filled grey diamonds, 4. Vertical lines indicate 90% CI.

of lingcod on rockfish remained strong, and indirect positive effects of lingcod (as mediated by rockfish) on *Pandalus* were consistently stronger than for EUHEL. Similarly, rockfish-mediated apparent competition remained consistently asymmetrical with the indirect effect of EUHEL on *Pandalus* being stronger than the reverse (figure 2). The s.e.m., however, fitted the winter period poorly (table 1).

#### 4. DISCUSSION

The relationships among and within trophic levels inferred from our structural equation model support two general predictions for the ecological role of marine predators. First, predatory fishes occupying high trophic levels may initiate trophic cascades (Heithaus *et al.* 2008); direct and indirect paths initiated by lingcod were consistent with this prediction. Second, predatory fishes may mediate apparent competition (Dill *et al.* 2003); our results suggest that rockfish played that role for apparently competitive shrimps. Trophic cascades initiated by lingcod were previously undocumented, and our study increases the body of evidence for trophic cascades occurring in diverse marine systems (Heithaus *et al.* 2008). More notably, empirical evidence for apparent competition (asymmetric or otherwise) is strong for some invertebrate and terrestrial systems (Chaneton &

Bonsall 2000), but rare for large-scale marine systems. Our data uniquely suggest that rockfish mediated an apparently competitive indirect effect of EUHEL on *Pandalus* that was seven times stronger than the reverse (for aggregated non-winter periods), suggesting a mechanism by which rockfish and other mesopredators could potentially influence the structure of marine communities. This result has conservation implications, because humans can both amplify or diminish the ecological role of mesopredators. Amplification may occur when overexploitation of top predators leads to mesopredator release (Heithaus *et al.* 2008). At the same time, over-exploitation of rockfish could diminish the extent to which these mesopredators mediate apparent competition. We caution, however, that our study's support for trophic cascades and apparent competition is correlational; these processes have yet to be demonstrated experimentally in communities that include rockfish and lingcod.

Asymmetric apparent competition generally arises when the availability of a preferred prey type has a stronger positive effect on the predator's equilibrium density, thereby indirectly increasing predator effects on prey that exert lesser positive effects on the predator, but preferred prey have superior properties (e.g. lower vulnerability) for mitigating predator effects (Chaneton & Bonsall 2000). Currently, we lack the natural history information required to suggest more



explicit mechanisms explaining asymmetric apparent competition between shrimps. An alternative hypothesis to apparent competition is that *Pandalus* prey on EUHEL and rockfish indirectly benefit EUHEL by having a direct negative effect on *Pandalus*. Observations of *Pandalus* predation on smaller shrimps in aquaria (Jensen 1995) suggest that this hypothesis is plausible, yet we found only a weak and seasonally limited direct negative effect of *Pandalus* on EUHEL (see figure 2); by contrast, evidence for apparent competition was strong for all non-winter periods. Indirect amensalism provides another alternative hypothesis, whereby only one prey attracts a shared predator while a second prey does not, but both incur negative effects from the shared predator (Chaneton & Bonsall 2000). Our data, however, do not support indirect amensalism because coefficients were positive for both *Pandalus*-to-rockfish and EUHEL-to-rockfish direct paths.

It is revealing that interactions which were otherwise strong weakened during winter. That season provided a natural experiment in which the role of rockfish as mesopredators may have attenuated owing to low activity levels associated with increased use of rocky interstices (see the electronic supplementary material, figure S1). Although activity shifts by lingcod, which spawn during winter, might have also been operative, *posteriori* analyses suggest that attenuated effects of subadult rockfish on *Pandalus* contributed to the overall weakening of interactions (see the electronic supplementary material, figure S4).

Our study is limited to southern British Columbia, where rockfish and lingcod may be only beginning to recover after a century of overexploitation (Martell *et al.* 2000; Marliave & Challenger 2009). Consequently, our results reflect a shifting baseline whereby current top-down effects are weak remnants from pre-exploitation. For instance, lingcod size structure probably remains skewed towards smaller fish and adult rockfish (total length more than 20 cm) may currently occupy a size refuge from lingcod predation. Future work may infer the extent to which predator effects have been fished down by comparing our results to analyses from under-exploited areas. Also yet to be determined is the relative contributions of direct predation and risk effects (i.e. costs to prey of antipredator behaviour) in structuring communities that include rockfish and lingcod (Heithaus *et al.* 2008).

This study meets the terms of the ethics committee at the institution where the experiment was carried out.

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