

# Effects of a trophic cascade on a multi-level facilitation cascade

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## Abstract

1. The role of cascades in natural communities has been extensively studied, but interactions between trophic and facilitation cascades are unexplored. In the White Sea (65°N) shallow subtidal, bivalve primary facilitators provide hard substrate for secondary facilitator barnacles, that, in turn, provide substrate for conspecifics, ascidians, red algae and multiple associated organisms, composing a multi-level facilitation cascade. Previous research revealed that predation by the whelk *Boreotrophon clathratus* accounts for ~7% of adult barnacle mortality. Low whelk abundance limits their effect, with barnacles living on conspecifics several times more vulnerable to predation than those living on primary substrate.
2. Trophic cascades can selectively shield foundation species from consumers, and hence may affect the structure and length of facilitation cascades. We tested the hypothesis that low abundance of the whelks results from mesopredator predation on their juveniles. Depending on the magnitude of the effect, this would mean that a trophic cascade controls the abundance of barnacles on all substrates or only barnacles living on conspecifics. We also suggested that barnacles on primary substrates and conspecifics facilitate different dependent assemblages.
3. We manipulated the presence of crab and shrimp mesopredators in field caging experiments to assess their effect on whelk recruitment. In a field survey, we compared the assemblages of sessile macrobenthic organisms associated with barnacles living on different substrates.
4. Caging experiments evidenced that crab and shrimp mesopredators reduce whelk recruitment by 4.6 times. Field data showed that barnacles on primary substrate and on conspecifics promote different dependent assemblages including secondary facilitator ascidians.
5. Although mesopredators do not shield barnacles from elimination, their absence would restrict them from living on conspecifics. Barnacles on conspecifics are functionally different from barnacles on primary substrate, and can be considered a separate level of the facilitation cascade. Trophic cascades thus can generate community-wide effects on facilitation cascades by affecting their structure and possibly length.

## KEYWORDS

crabs, facilitation cascade, foundation species, gastropod, predation, shrimp, top-down control, trophic cascade

## 1 | INTRODUCTION

Interspecific interactions that drive community structure and functioning are embedded in ecological networks (Segar et al., 2020). Networks of negative interactions, such as predation and competition, have long attracted attention of ecologists (Elton, 1927; Watt, 1964). For nearly a century, trophic chain length has been a central characteristic of community structure and has been studied extensively (Post, 2002). Facilitation cascades, of hierarchical positive interactions, were described much later (Altieri et al., 2007), following recent wide recognition of facilitation as one of the principal processes shaping natural communities (Bruno et al., 2003). Most facilitation cascades examined to date have two levels of foundation species (principal facilitators; Gribben et al., 2019), but multi-level systems with up to six levels also occur, and factors influencing the number of levels are unknown (Thomsen et al., 2016; Yakovis & Artemieva, 2017). Facilitation cascades are assumed to function within specific food webs, but how the structure and complexity of the food webs impacts the functioning, stability and length of facilitation cascades is unclear (Gribben et al., 2019).

We hypothesized that foundation species in facilitation cascades can be controlled by trophic cascades releasing them from consumer pressure, affecting facilitation cascade structure. Keystone predators frequently shape communities by controlling the abundance of dominant competitors (Paine, 1969) or foundation species (Chesher, 1969), thus determining community-level competition or facilitation. The mechanisms that regulate keystone predation on foundation species are important drivers of species composition and community structure (Sanford, 1999). Predators are also known to affect the composition and diversity of dependent assemblages promoted by secondary foundation species in facilitation cascades (Gribben et al., 2017; Yakovis & Artemieva, 2019). Trophic cascades arise in multi-level food webs when top predators control the abundance or behaviour of their prey which is, in turn, a predator or grazer, so that the next trophic level is shielded from predation or grazing (Paine, 1980). Trophic cascades commonly release single foundation species from consumer pressure causing indirect effects on dependent assemblages (Bridgeland et al., 2010; Estes & Palmisano, 1974; Polis, 1999). How facilitation cascades are affected by trophic cascades, however, is unexplored. Here we evaluate the presence and strength of a trophic cascade targeting a secondary facilitator in a multi-level facilitation cascade and estimate trophic cascade impacts on the structure of the facilitation cascade.

Within a multi-level facilitation cascade in the White Sea shallow subtidal (65°N), barnacles *Balanus crenatus* monopolize small hard substrate (principally Greenland cockle, *Serripes groenlandicus* shells, a primary facilitator) scattered across the soft sediment, and facilitate a suite of dependent species, including next-level secondary facilitators: solitary ascidians, mussels and red algae (Yakovis & Artemieva, 2017; Yakovis et al., 2008). Barnacles attached to cockle shells face severe spatial limitation (Yakovis et al., 2013) and minimize self-thinning by settling on conspecifics leading to multi-tier clustering. 'First-layer' barnacles attached to primary substrate are

typically more crowded than 'second-layer' barnacles attached to conspecifics, and often coalesce as they grow, partially covered by soft sediment. Second-layer barnacles are generally located higher relative to the sediment surface (Figure S1). This may result in differences between epibenthic assemblages promoted by first- and second-layer barnacles.

Despite their strong effect on community structure, causes of barnacle mortality in this system are unclear (Varfolomeeva et al., 2008). Previous experiments revealed that adult (8–28 mm shell height) boring muricid whelks *Boreotrophon clathratus* prey on adult (6–17 mm aperture length, 4–10 years old) barnacles. In the field, however, drilling evidence suggests that whelks only account for 7% of adult *Balanus* mortality due to low whelk abundance (Yakovis & Artemieva, 2015). In temperate and tropical habitats, in contrast, predation on barnacles is commonly the primary source of mortality (Castilla et al., 1994; Harley & O'Riley, 2011; Menge, 1976). Importantly, second-layer barnacles are several times more vulnerable to *Boreotrophon* predation than first-layer barnacles (Yakovis & Artemieva, 2015), which may indirectly affect the structure of the facilitation cascade.

It is unclear whether physical or biotic factors maintain the low abundance of *Boreotrophon*. We suggested that juvenile whelks experience strong predation pressure. Spider crabs *Hyas araneus* and shrimp *Spirontocaris phippis* are common omnivorous mesopredators in this system (Yakovis & Artemieva, 2019). We hypothesized that juvenile whelk abundance is controlled by these mesopredators. By predator exclusion and manipulation of the presence of *Hyas* and *Spirontocaris* in field caging experiments, we tested this hypothesis to assess the role of trophic cascade in regulation of the multi-level facilitation cascade where barnacles are secondary facilitators. Negative effects of mesopredators on whelk recruitment would explain the low abundance of adults resulting in their low consumer pressure on barnacles. Since the vulnerability of second-layer barnacles to predation is higher, depending on the magnitude of the effect potentially revealed in our experiments, without mesopredators, *Boreotrophon* could control the abundance of all the barnacles or only second-layer barnacles. We used a field survey to evaluate the difference of assemblages promoted by first- and second-layer barnacles and estimate community-wide effects of their possible elimination in the absence of trophic cascade.

## 2 | MATERIALS AND METHODS

We tested mesopredator effects on whelk recruitment to barnacle clusters in a series of year-long field experiments conducted at a 12 m deep subtidal site in the Solovetsky Islands (65°01.180'N, 35°39.721'E, see Yakovis & Artemieva, 2015). In July 2009–2012 and 2015, we collected empty shells with live *B. crenatus* and similar shells with empty barnacle tests (the latter are almost equally abundant in the field). We defaunated these shells except of adult barnacles (4 or more annual growth rings) and their empty tests and attached them in alternating order to the bottom of 300 × 375 × 70 mm plastic

cages covered with 2.5 mm nylon mesh (2–3 shells with live barnacles and 2–3 shells with empty tests per cage). *Boreotrophon* is a direct developer with crawl-away recruits, attaching egg masses to hard substrates, with a life span of several years. The mesh is permeable for juvenile whelks with shell height within 7 mm (Yakovis & Artemieva, 2015).

Each year we deployed a new set of cages (which were collected next year) randomly distributed between the following treatments: (a) full cages (predator exclusions) and (b) open cages (unmanipulated controls, no mesh, subject to normal predation) in all years; (c) partial cages to control for caging effects, similar to full cages but with two side windows 175 × 50 mm each, in all years except 2012; (d) cages with predatory spider crabs *Hyas araneus* (crab enclosures) in 2015 only and (e) cages with predatory shrimp *S. phippsi* (shrimp enclosures) in 2015 only. The set of cages deployed in 2015 was also used to assess the effect of crustacean predators on other mobile fauna associated with barnacles (Yakovis & Artemieva, 2019). There were 2 cages/treatment/year in 2009–2010, 2010–2011, 2011–2012 and 2012–2013. In 2015–2016, there were 6 cages/treatment, except for predator exclusions, which were 8, and open cages, which were 5. We exposed all the cages anchored to the bottom in a haphazard pattern ( $\geq 0.5$  m apart) for 1 year, collected them, counted, weighed and individually measured (since 2011) crabs and shrimp with carapace length  $\geq 2.5$  mm and whelks with shell height  $\geq 0.5$  mm found inside (except for crustaceans in open cages, which were too mobile to be sampled in absence of mesh). For details of the 2015–2016 predator enclosures experiment, see Yakovis and Artemieva (2019).

In the field whelks, crabs and shrimps concentrate in patches formed by barnacles and their empty tests rather than on unstructured sediment. Thus, the abundance of predators is more related to that of adult barnacles rather than bottom area. To account for that, barnacle weight in each cage was estimated in the end of the experiments from aperture length measurements using allometric relationships (Yakovis & Artemieva, 2015). Empty barnacle tests were also measured and their equivalent weight was calculated using the same allometric relationships. The sum of calculated weights of live and dead barnacles is hereafter called equivalent barnacle weight, EBW,  $151 \pm 6$  g per cage ( $n = 53$ ). Here we did not expect any substantial effect of year-long mesopredator manipulations on EBW or adult barnacle mortality, since *Boreotrophon* juveniles potentially preyed upon by crabs and shrimp need several years to grow large enough to attack adult barnacles. The effect of adult whelks on adult barnacles was extensively quantified separately (Yakovis & Artemieva, 2015). Consistently, in the end of the 2015–2016 experiments, EBW and mortality of adult barnacles were similar across treatments (one-way ANOVA,  $F_{4,26} = 0.90$ ,  $p = 0.480$  and  $F_{4,26} = 2.49$ ,  $p = 0.068$ , respectively), though the latter was insignificantly higher (9%–12%) in partial and open cages than in mesopredator enclosures and exclusions (3%–6%) likely due to consumption by ambient adult *Boreotrophon* or other predators. Crab and shrimp densities in the enclosures matched their per EBW field abundances (Yakovis & Artemieva, 2019).

To assess the overall effect of predation on *Boreotrophon* recruitment, the number of *Boreotrophon* juveniles ( $\leq 7$  mm) per cage in the experiments from 2009–2010, 2010–2011 and 2011–2012 was analysed with ANCOVA (Type III) with factors Treatment (3 levels, fixed), Year (3 levels, random), and EBW as a covariate. The means were compared between Treatment levels with planned linear orthogonal contrasts: (a) open versus partial cages to check for the artefacts of the caging procedure, (b) open and partial cages versus predator exclusions to test for the effect of predation. The data were square root transformed to achieve homogeneity of variances (Cochran's test).

The effects of crustacean predators were tested by the ANCOVAs (Type III) on the numbers of juvenile whelks per cage from the 2015–2016 experiment, with Treatment as a fixed factor (5 levels), and EBW as a covariate. The means were compared between Treatment levels (where this effect was significant) using the following sequence of planned linear non-orthogonal contrasts: (a) open cages versus partial cages to check for the artefacts of the caging procedure, (b) open and partial cages versus predator exclusions to test for the effect of predation, (c) open and partial cages versus crab cages and (d) predator exclusions versus crab cages to assess the effect of *Hyas*, (e) open and partial cages versus shrimp cages and (f) predator exclusions versus shrimp cages to assess the effect of *Spirontocaris*. Significance level was adjusted for multiple comparisons using the single-step procedure (Hothorn et al., 2008). The variances were homogeneous (Cochran's test).

Homogeneity of slopes was checked by first fitting the models with Treatment × EBW interaction (which was non-significant in all the analyses), and then dropping that term and running the reduced models (Neter et al., 1996). Fitted values were screened against the standardized residuals and no noticeable asymmetry around zero or wedge-shaped patterns were found.

To compare the associated assemblages of sessile organisms between barnacles attached to primary and secondary hard substrates (which are differently affected by predators), we used eight samples obtained by SCUBA divers at the experimental site (65°01.180'N, 35°39.721'E) in July 2012–2014. Each sample contained all the hard substrates visible on the sediment surface collected from a 0.25 m<sup>2</sup> square frame haphazardly placed on the bottom (10–26 such primary substrates per frame). We counted and identified all the sessile macrobenthic organisms larger than 0.3 mm by substrate type; the individuals attached to first- and second-layer barnacles were recorded separately. Average standardized abundances of epibionts found on barnacles were compared pairwise between barnacle layers for each high-level taxa using Wilcoxon's matched pairs test. Multivariate variation of the epibenthic assemblages associated with first- and second-layer barnacles was visualized using principal coordinate analysis (PCoA) based on Bray–Curtis dissimilarities.

Tests were performed in StatSoft STATISTICA (v.8.0) and R software (v.3.2.3). Means are shown  $\pm$ SE, and significance level was 0.05 for all the tests.

### 3 | RESULTS

Treatment significantly affected the abundance of *Boreotrophon* recruits in 2009–2010, 2010–2011 and 2011–2012 experiments, while Year, the Year  $\times$  Treatment interaction and EBW did not. Within any year, the abundance of whelk recruits was similarly low in partial and open cages and higher in predator exclusions (Table 1). The magnitude of the effect of predators was comparable to interannual fluctuations of juvenile whelk abundance. The abundance was highest in 2011–2012 (Figure S2), the warmest of the 5 years studied.

In the experiments with shrimp and crab enclosures, Treatment also significantly affected the abundance of whelk juveniles, while EBW did not (Table 2). The number of the whelks was highest in predator exclusions ( $3.63 \pm 0.60$ ) and much lower in any other cages (Figure 1). There was no significant difference between partial ( $1.17 \pm 0.83$ ) and open ( $0.60 \pm 0.40$ ) cages while both had significantly less whelks than predator exclusions. Shrimp ( $1.50 \pm 0.22$ ) and crab ( $0.50 \pm 0.34$ ) enclosures both demonstrated no significant difference from partial and open cages, and also contained significantly fewer whelks than predator exclusions (Table 2).

In the field,  $29 \pm 6\%$  of adult barnacles (with 4 or more annual growth rings) were attached to conspecifics or their empty tests (occupied the second layer) and the rest resided on primary substrate (first layer). Sessile assemblages associated with second-layer barnacles had significantly less ascidians (*Molgula* spp. and *Styela* spp.) and more cirripedians (mostly barnacles) than those associated with first-layer barnacles (Table S1). In terms of supported epibiotic structure, second-layer barnacles were intermediate between first-layer barnacles and primary substrate (mostly shells of primary facilitator, *S. groenlandicus*, strongly dominated by barnacles; Figure 2). Loss of second-layer barnacles would result in estimated 19%–48% drop of total community abundance depending on taxon, with highest reduction in cirripeds, red algae and sponges (Figure S2; Table S2).

### 4 | DISCUSSION

Our results show that trophic cascades can impact facilitation cascades by controlling the abundance of facilitators. The experiments

revealed that mesopredators strongly restricted the recruitment of *Boreotrophon* which should, in turn, determine the abundance of adult whelks. In the absence of this trophic cascade, estimated predation pressure on barnacles would be several times stronger. The magnitude of the mesopredator effect predicts severe reduction in abundance of first-layer barnacles and complete elimination of second-layer barnacles in the absence of crabs and shrimp. Given the functional difference between barnacles from different layers, this would cause strong community-wide indirect effects.

#### 4.1 | Mesopredators, whelk abundance and predation pressure on barnacles

The highest abundance of juvenile *Boreotrophon* was found in predator exclusion cages. Their consistently lower abundance in all other treatments demonstrates the negative effect of mesopredators, particularly *Hyas* and *Spirontocaris*, on juvenile whelk abundance. Crabs and shrimp do not necessarily eliminate most *Boreotrophon* recruits directly but may also deter whelks from barnacle clusters. Non-consumptive predator effects with spatial distribution of a mobile prey largely determined by its migration to the refugia with lower predator abundance have been observed in many marine and terrestrial habitats (Bertness & Coverdale, 2013). This could explain some of our results, since the current design did not separate consumptive and non-consumptive predator effects.

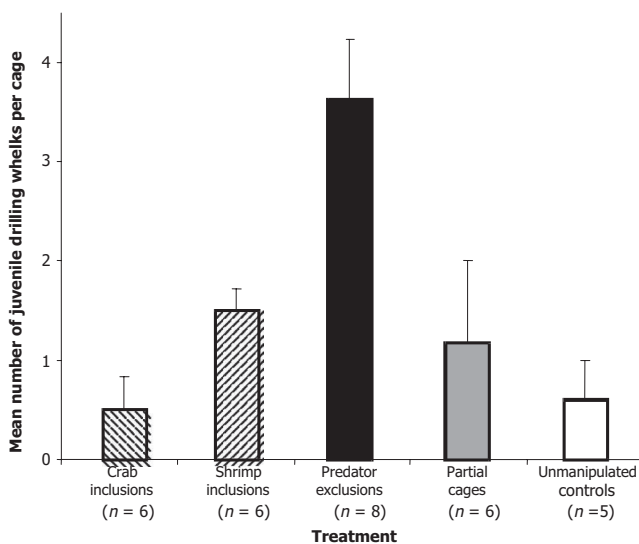
Both *Hyas* and *Spirontocaris* are omnivorous predators (Birkely & Gulliksen, 2003; Nadon & Himmelman, 2010; Quijón & Snelgrove, 2005; Yakovis & Artemieva, 2019). *Boreotrophon* have not been previously identified in their diet, though many other shrimp and crab species control the abundance of adult molluscs by consuming juveniles (Beukema et al., 1998; Eggleston, 1990). While typically crustacean predators directly prey on barnacles (Castilla et al., 1994; Harley & O'Riley, 2011; Menge, 1976), they are also known to release the latter from consumer pressure caused by dogwhelks reducing the mortality by up to 29%, primarily through non-consumptive effects (Matassa & Trussell, 2011; Trussell et al., 2003). Our findings suggest a much stronger impact with crabs and shrimp several times decreasing whelks abundance.

**TABLE 1** ANCOVA contrasting the square root transformed abundance of *Boreotrophon clathratus*  $\leq 7$  mm among treatments sampled in 2010, 2011 and 2012 (open, partial and enclosure cages). dfN: numerator degrees of freedom; dfD: denominator degrees of freedom. Significant effects ( $p < 0.05$ ) are shown in bold

Source of variation	df <sub>N</sub>	df <sub>D</sub>	MS	F	p
Treatment (fixed)	2	7.82	2.918	7.288	<b>0.016</b>
Year (random)	2	10.02	1.709	3.876	0.057
Treatment $\times$ Year (random)	4	8.00	0.328	0.441	0.776
EBW <sup>0.5</sup> (covariate)	1	8.00	0.049	0.066	0.803
Error	8		0.744		
Planned linear contrast	Estimate	SE	t	p	
Partial–open	0.17	0.73	0.24	0.819	
Partial and open–enclosure	-2.72	1.02	-2.66	<b>0.029</b>	

**TABLE 2** ANCOVA contrasting the abundance of *Boreotrophon clathratus*  $\leq 7$  mm among treatments in 2015–2016 (open, partial, predator exclusion, shrimp and crab cages). Significant effects ( $p < 0.05$ ) are shown in bold

Source of variation	df	MS	F	p
Treatment (fixed)	4	45.505	6.110	<b>0.001</b>
EBW (covariate)	1	2.360	1.268	0.271
Error	25	46.548		
Planned linear contrast	Estimate	SE	t	p
Partial–open	0.76	0.84	0.90	0.860
Partial and open–exclosure	–5.62	1.28	–4.40	<b>0.001</b>
Partial and open–crab	0.27	1.46	0.18	1.000
Exclosure–crab	2.94	0.75	3.90	<b>0.003</b>
Partial and open–shrimp	–1.42	1.40	–1.02	0.802
Exclosure–shrimp	2.10	0.74	2.85	<b>0.043</b>

**FIGURE 1** Average per cage abundances of *Boreotrophon clathratus*  $\leq 7$  mm (N) by treatment in the field experiment 2015–2016

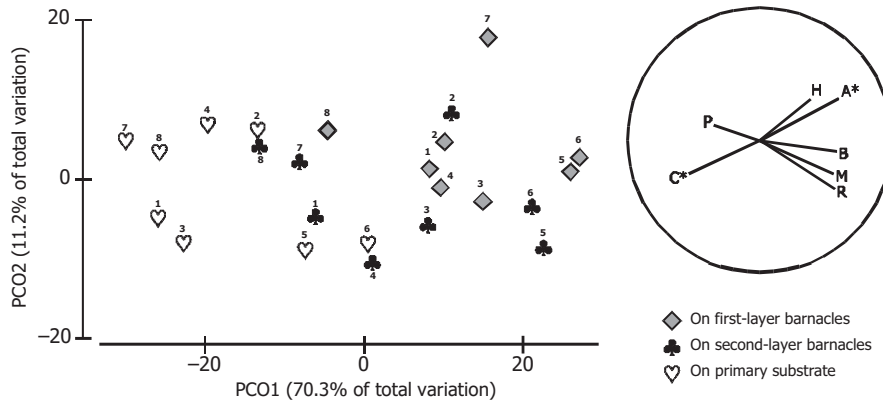
Under natural conditions, *Boreotrophon* contributes ~7% of the adult barnacles' mortality, and adult barnacles are consumed by adult whelks (Yakovis & Artemieva, 2015). We assume that the increase in *Boreotrophon* recruitment rate in the absence of mesopredators would generally translate into similar increase in abundance of adult whelks. Density-dependent mortality can potentially reduce the effect, but seems unlikely given the evident surplus of food (barnacles) and rather low and nearly equal natural abundance of juvenile ( $\leq 7$  mm) and adult (8–33 mm) whelks in the field ( $2.77 \pm 0.93$  and  $2.31 \pm 0.51$  m<sup>-2</sup>, respectively, authors' unpublished data at the study site 2009–2014). Since the abundance of *Boreotrophon* juveniles in predator exclusion cages was 4.6 times higher than an average between partial and open cages, without mesopredators whelks would account for about 32% of total mortality in adult barnacles. Drill marks on empty barnacle tests in the field indicate that adult barnacles attached to conspecifics are 3–4 times more vulnerable to *Boreotrophon* (see Fig. 2 in Yakovis & Artemieva, 2015). In field caging

experiments, second-layer barnacles were killed five times more often than first-layer ones (see Fig. 4 in Yakovis & Artemieva, 2015), and there was a nearly linear relationship between whelk abundance and the barnacles they consumed (see Fig. 5 in Yakovis & Artemieva, 2015). Thus, our results strongly suggest that in the absence of mesopredators, whelks would eliminate second-layer barnacles, and force barnacles to a single tier on primary substrate. Direct assessment of the mesopredator effect on adult barnacles could certainly be more accurate than the above estimates. This, however, would require at least a 4–5 year-long cage exposure due to the long life span of the whelks and their extremely slow predation rates (Yakovis & Artemieva, 2015), which is prohibitively complicated because of cage loss, damage and logistical impracticability.

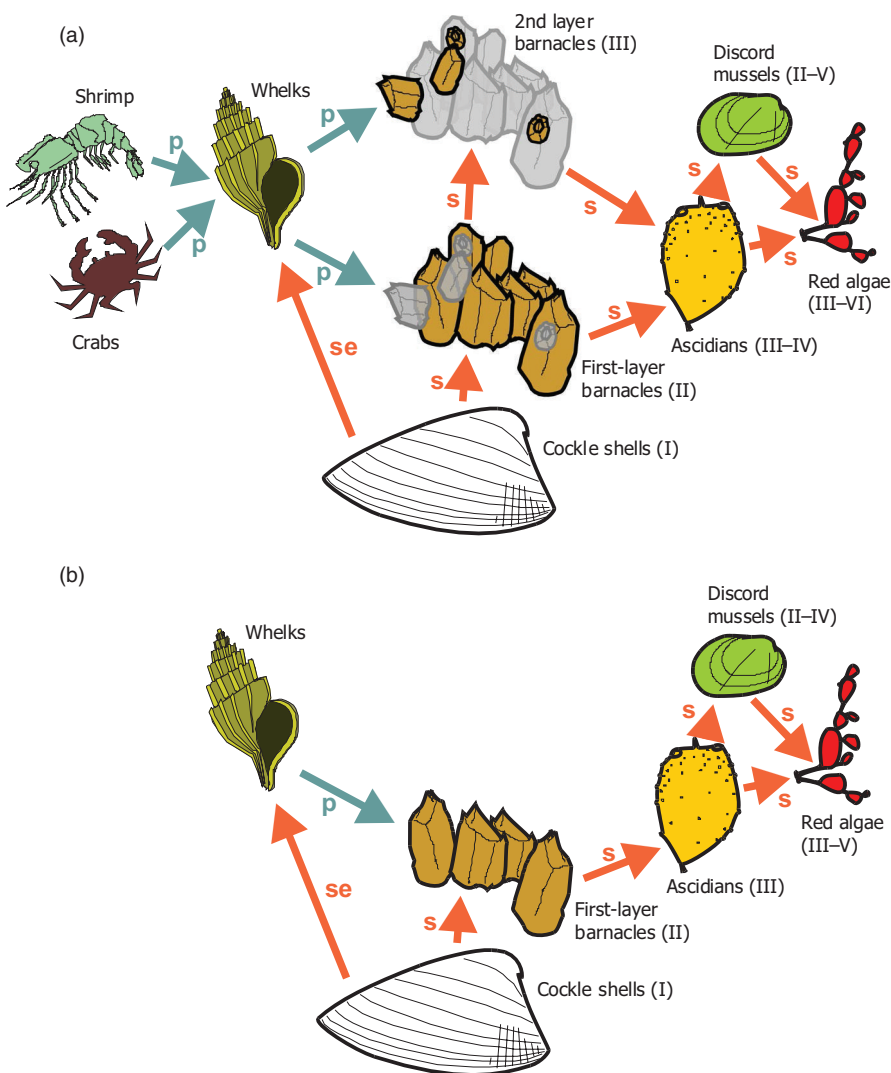
Compared with surrounding unstructured sediment, barnacle clusters provide much more complex, heterogeneous habitat for *Boreotrophon* juveniles to find shelter from predators. Consequently, facilitation of its own predator, as observed in mussels protecting sea stars from environmental stress (Agüera et al., 2015; Silliman et al., 2011), could be expected in barnacles as well. According to our observations, 83% of *Boreotrophon* egg masses are attached to *Serripes* empty shells, suggesting this primary facilitator is not only a habitat provider but also an indirect booster of predation for secondary facilitator barnacles (Figure 3). Finally, shrimp and crabs themselves are potential prey for fish, seals, birds and white whales. The global decline of apex predators (Estes et al., 2011) may thus have additional long-term effects on the trophic cascade.

#### 4.2 | Functional difference between first- and second-layer barnacles

Our field survey revealed that first- and second-layer barnacles support notably different epibenthic assemblages. Second-layer barnacles had a lower proportion of ascidians and higher proportion of barnacles than first-layer barnacles. The primary facilitator in this community, cockles, does not directly facilitate ascidians, but facilitates barnacles that facilitate ascidians (Yakovis & Artemieva, 2017).



**FIGURE 2** Multivariate epibenthic community structure in field samples for the subsamples associated with different principal hard substrates: primary (mostly empty shells of *Serripes groenlandicus*), first-layer barnacles *Balanus crenatus* (attached to primary substrate), and second-layer barnacles *B. crenatus* (attached to conspecifics). Principal coordinate analysis on Bray–Curtis dissimilarities calculated from standardized square root transformed abundances of high-order sessile taxa. Labels denote sample numbers. Vectors show the contributions of most abundant taxa (correlation indicated by vector length). C—cirripeds (mostly barnacles), P—polychaetes, H—hydroids, A—ascidians, B—bryozoans, M—molluscs, R—red algae. Stars indicate significant differences in average relative abundance between first- and second-layer barnacles (see Table S1)



**FIGURE 3** Most important interactions between principal consumers and facilitators in the facilitation cascade in the presence (a) and in the absence (b) of the trophic cascade. Facilitator level in the cascade shown in parentheses. P—predation, S—substrate provision, SE—substrate provision for egg masses. The range of levels assigned to red algae and mussels reflects their ability to inhabit also (less frequently) barnacles and cockle shells, respectively (corresponding arrows omitted for clarity). Compiled from present results and Yakovis et al. (2008), Yakovis and Artemieva (2015) and Yakovis and Artemieva (2017)



Both barnacles and ascidians, as secondary facilitators, support diverse epibenthic assemblages of dependent species (Yakovis & Artemieva, 2017; Yakovis et al., 2008). Here we found that second-layer barnacles are functionally more similar to primary facilitator (which hosts almost no ascidians) than first-layer barnacles (Figure 2). The presently unknown mechanism underlying facilitation of ascidians by barnacles is supposedly either selective elimination of ascidian recruits on primary substrate by predators or rugophilic settlement behaviour of ascidian tadpoles (Yakovis & Artemieva, 2017). In contrast to clustered barnacles, cockle shells are smooth and lack refuges. Barnacles living on conspecifics are also loosely spaced and provide much less sheltering structure than tightly packed barnacles on primary substrate, explaining the dissimilarity in associated assemblages of sessile organisms. Formally, the presence of different barnacle layers could be treated as individual trait variation of the secondary facilitator (like body size) which generally adds to habitat heterogeneity for the dependent taxa (Bishop et al., 2013; Gribben et al., 2019). However, all the facilitator traits affecting facilitation cascades studied to date are quantitative, while qualitative ones such as phenotype, gender or attachment layer have not yet been examined. In better studied individual facilitators (particularly alpine avens *Geum rossii*), qualitative traits are known to produce contrasting facilitative effects (Michalet et al., 2011). It is thus important that the observed functional difference between first- and second-layer barnacles is comparable to the difference between them and primary facilitator. This suggests that barnacles from different layers can be considered separate levels of the facilitation cascade. In case we treat barnacles as two levels in a facilitation cascade, the latter shrinks its length in the absence of the trophic cascade (Figure 3).

Our estimates of the community-wide consequences of the elimination of second-layer barnacles in the absence of mesopredators do not account for the space released on the surface of first-layer barnacles. According to our unpublished observations, loosely spaced second-layer barnacles provide at least 5–10 times more substrate surface to other colonizers than they occupy themselves. Given that the abundance of first-layer barnacles would also be reduced by whelks, this should not critically affect the accuracy of our estimates. Moreover, the presence of second-layer barnacles contributes to the provision of sheltered microhabitat for small colonizers attached to first-layer barnacles, which may further boost the indirect effect of the trophic cascade.

### 4.3 | Trophic cascades and stability of multi-level facilitation cascades

Trophic cascades commonly reduce consumer pressure on a single foundation species causing strong indirect community-wide effects (Bridgeland et al., 2010; Estes & Palmisano, 1974; Polis, 1999). While trophic cascades are likely even more powerful drivers of community structure when they affect principal facilitators in a facilitation cascade, the interactions between trophic and facilitation cascades have never been previously addressed (Gribben et al., 2019). To

date, of the dozens of facilitation cascades reported, only a couple are comprised of more than two levels of facilitators (Thomsen et al., 2016; Yakovis & Artemieva, 2017).

This may reflect relative scarcity of multi-level cascades. Longer cascades are considered less resilient as the loss of any intermediate facilitator potentially disrupts all the links at upper levels (Gribben et al., 2019; Yakovis & Artemieva, 2017). This instability apparently can be internally compensated for by redundancy of facilitators at each level of a cascade (Gribben et al., 2019; Hughes et al., 2014). Shielding principal facilitators from predation by trophic cascades provides a mechanism which can externally stabilize long facilitation cascades. While our study system is redundant at higher levels (red algae can grow on barnacles, their empty tests, ascidians and mussel nests), barnacles appear to be the initial colonizer of smooth primary substrates (Yakovis & Artemieva, 2017; Yakovis et al., 2008) indirectly controlling most species diversity. Although the trophic cascade revealed here is nonessential for survival, it is powerful enough to control the important microhabitat associated with barnacles living on conspecifics.

The facilitation cascade under study is functioning at 65°N. Top-down consumer control of community structure is generally thought to decrease with latitude. While average food chain length is similar in polar, temperate and tropical ecosystems (Vander Zanden & Fetzer, 2007), field experiments show lower predation strength in temperate than in tropical regions (Freestone et al., 2011). Predators from higher latitudes are considered relatively ineffective (Bertness et al., 1981). Lower temperatures at higher latitudes can dramatically weaken the effect of consumers on the abundance of foundation species (Birkeland & Lucas, 1990; Jenkins et al., 2001; Sanford, 1999). Predation on barnacles at low latitudes, for instance, is stronger and commonly limited by prey availability (Castilla et al., 1994; Harley & O'Riley, 2011; Menge, 1976). Shielding primary and secondary facilitators from predation by trophic cascades can consequently have much stronger effects on facilitation cascades in temperate and tropical zones.

Our findings show potential for trophic cascades to stabilize multi-level facilitation cascades, a topic that deserves further attention. Trophic/facilitation cascade interactions may commonly be overlooked community structuring processes. Elucidating these interactions, however, will require understanding system natural history and field experimental manipulations that explicitly examine the interdependence of trophic/facilitation cascades.

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**CONFLICT OF INTEREST**

The authors declare no conflict of interest.

**AUTHORS' CONTRIBUTIONS**

E.Y. and A.A. conceived the ideas, designed the methodology and collected the data; E.Y. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

**DATA AVAILABILITY STATEMENT**

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.rv15dv47v> (Yakovis & Artemieva, 2021).

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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## Effects of a trophic cascade on a multi-level facilitation cascade

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### Supporting information

**Table S1.** Average relative abundances of sessile organisms attached to barnacles living on primary substrate (first layer) vs conspecific individuals (second layer) in field samples.

Significant differences ( $p < 0.05$ ) are shown in bold.

High order taxa	Average relative abundance (%) on		Wilcoxon's matched	
	barnacles attached to		pairs test (n = 8)	
	primary substrate (first-layer)	conspecifics (second-layer)	Z	p
Sponges	2.40 ± 0.70	1.97 ± 0.72	0.14	0.889
Hydroids	1.97 ± 1.21	0.82 ± 0.34	1.40	0.161
Polychaetes	0.15 ± 0.09	0.09 ± 0.06	0.73	0.465
Molluscs	9.95 ± 1.87	9.51 ± 2.05	0.14	0.889
Cirripedians	34.69 ± 6.64	<b>49.82</b> ± 8.71	2.24	<b>0.025</b>
Bryozoans	15.53 ± 1.11	13.81 ± 3.03	0.70	0.484
Kamptozoans	0.41 ± 0.20	0.76 ± 0.43	0.94	0.345
Ascidians	<b>20.25</b> ± 2.20	10.02 ± 2.27	2.52	<b>0.012</b>
Red algae	14.66 ± 4.06	13.21 ± 4.80	1.40	0.161

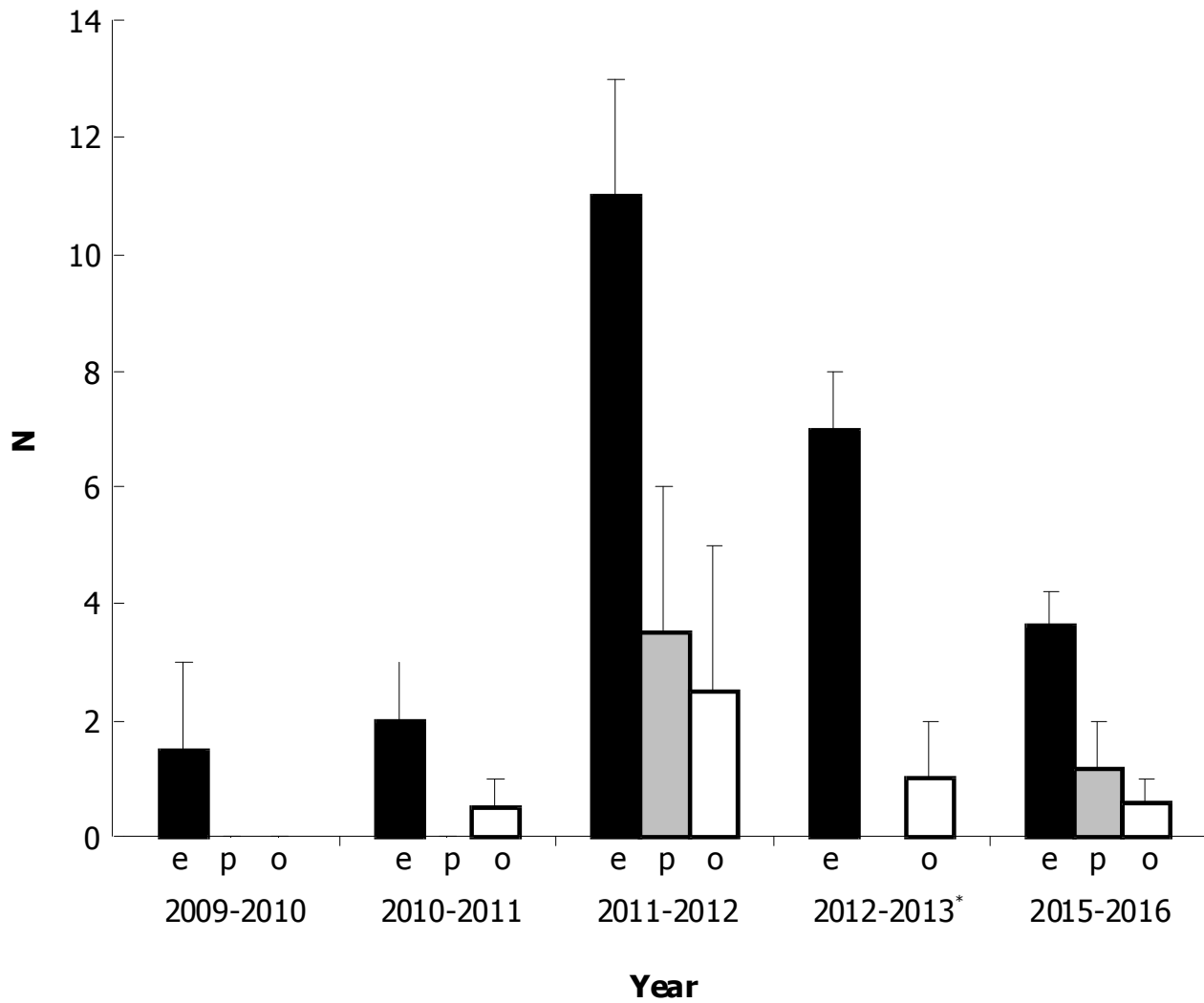
**Table S2.** Average abundances of sessile organisms in field samples and their estimates in case of absence of barnacles living on conspecifics (second layer) and any other organisms they provide substrate to, directly or indirectly (n = 8 samples).

High-order taxa	Average density in the field (m <sup>-2</sup> )		Estimated average difference (%)
	observed in the field	estimated without second-layer barnacles	
Sponges	360 ± 197	214 ± 101	-29 ± 8
Hydroids	89 ± 33	68 ± 25	-22 ± 9
Polychaetes	36 ± 9	25 ± 6	-26 ± 10
Molluscs	1013 ± 144	808 ± 117	-19 ± 6
Cirripedians	3076 ± 837	1562 ± 439	-48 ± 6
Bryozoans	1035 ± 311	730 ± 205	-26 ± 5
Kamptozoans	28 ± 11	23 ± 9	-20 ± 10
Ascidians	840 ± 137	647 ± 118	-23 ± 4
Red algae	1313 ± 404	865 ± 239	-31 ± 8

**Figure S1.** A typical epibenthic patch based on an empty shell of a cockle *Serripes groenlandicus* (primary facilitator, 'P') with secondary facilitators: first-layer barnacles *Balanus crenatus* ('1'), second-layer barnacles *B. crenatus* ('2'), solitary ascidians *Styela rustica* ('S') and *Boltenia echinata* ('B').



**Figure S2.** Average per cage abundance of *Boreotrophon clathratus*  $\leq 7$  mm (N) in predator exclusions (e), partial (p) and open cages (o) by year in the field experiments. \* - there were no partial cages in 2012-2013.





**Figure S3.** Estimated changes to the multivariate epibenthic community structure in absence of second-layer barnacles (i.e. living on conspecifics). Principal coordinate analysis on Bray-Curtis dissimilarities calculated from square root transformed abundances of high-order sessile taxa. Each arrow starts at the point denoting a sample as is and ends at the point denoting the assemblage left in case of absence of the barnacles attached to conspecifics and all other organisms in the epibiosis they provide substrate to, directly or indirectly. Vectors on the right show the contributions of specific taxa (correlation indicated by vector length). C – cirripeds (mostly barnacles), P – polychaetes, H – hydroids, A – ascidians, B – bryozoans, K – kamptozoans (entoprocts), M – molluscs, R – red algae.

