A trophic cascade facilitates native habitat providers within assemblages of multiple invasive marine species

K. Liversage,1,† J. Kotta,1 I. Kuprijanov,2 M. Rätsel,1 and K. Nöömaa1

1Estonian Marine Institute, University of Tartu, Mäeklase 14, Tallinn 12618 Estonia
2Department of Marine Systems, Tallinn University of Technology, Akadeemia tee 15a, Tallinn 12618 Estonia

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Abstract. Anthropogenically influenced habitats are becoming increasingly impacted by multiple invasive species that can regionally control main ecological processes and functions. Management requires predictions of invasive species’ effects, but multiple invasions may cause unpredictable outcomes, for example, synergistic impacts or interactions among trophic levels causing trophic cascades. The Baltic Sea is prone to species invasions that increasingly occur at multiple trophic levels. We used a laboratory experiment to test whether multiple invasive predators may cause interactive effects in the Baltic Sea. In aquaria, we simulated a coastal community that has developed dominated by invasive species—the decapod predators Palaemon elegans and Rhithropanopeus harrisii, the amphipod grazer Gammarus tigrinus, and the filter-feeder Dreissena polymorpha. The orthogonal experiment determined separate and interactive effects from predators on the lower trophic level invasive species and native algae including the foundation species Fucus radicans. The main result was that while both predators significantly impacted the community, in no cases were their effects interactive. Another important result was that P. elegans appeared to cause a trophic cascade, as in its presence F. radicans and its epiphytes had the greatest biomass while G. tigrinus grazers were heavily reduced. G. tigrinus were negatively correlated with F. radicans biomass, so variable amphipod grazing may be the link allowing an indirect effect of P. elegans on F. radicans. R. harrisii also reduced G. tigrinus abundance but did not affect F. radicans biomass. Both predators significantly affected the lengths of F. radicans plant stems that were comprised of new vegetative growth—P. elegans reduced the lengths of new vegetative tissue while R. harrisii increased it. Thus, the presence of P. elegans induced shorter and denser F. radicans bushes compared to taller and thinner bushes observed in other treatments. Lastly, R. harrisii caused significant declines in D. polymorpha numbers. Overall, ecological management needs to consider positive effects from predator invasion which may reduce grazing pressure on low trophic level foundation species. A trophic cascade involving two invasive species highlights the importance of multi-species approaches to management of Baltic Sea invasive species and in other regions prone to biological invasions.

Key words: Baltic Sea; facilitation; Fucus radicans; Gammarus tigrinus; grazing; indirect effects; non-indigenous species; Palaemon elegans; predation; Rhithropanopeus harrisii; zebra mussel.

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†E-mail: kiran.liversage@ut.ee

INTRODUCTION

Myriad anthropogenic influences increasingly contribute to invasive species being a dominant structuring component of ecological systems, ranging from single species that spread through and impact otherwise pristine habitats (e.g., Taylor 1977) to multiple species which may have
additive or synergistic impacts (e.g., Didham et al. 2005, Crego et al. 2016). When invasive species occupy positions at multiple levels of ecological structure (e.g., trophic levels and primary/secondary facilitation), they may marginalize almost all native species and constitute most significant biotic aspects of ecological function (Hobbs et al. 2006). Research emphasizing potential effects from invasive species combinations is important because their synergistic interactions may cause sufficiently large impacts to drive ecological systems to tipping points with wide-ranging ecological and economic consequences (Boudouresque et al. 2005, Havel et al. 2015). Multiple invasive species may also be involved in causing novel trophic cascades when ≥3 trophic levels are occupied by strongly interacting species (Borer et al. 2005). Trophic cascades have often been studied that include at least one invasive species, for example, invasive water fleas in the North American Great Lakes reduce native Daphnia spp. populations and effects from their grazing, causing algal blooms and decreased water quality (Walsh et al. 2016). Likewise, introduced cane toads in Australia reduce abundances of large reptile predators, producing high abundances of small reptile prey species (Feit et al. 2020). Novel predators can also counteract the influence of other invasive consumers with results for native species that may be beneficial but not easily predicted based on previous knowledge of the invaders’ separate impacts (Johnson et al. 2009, Preston et al. 2012, Hervás et al. 2013, Doherty et al. 2015). Any beneficial effects of invaders may also be direct, such as facilitation of native species (Rodriguez 2006) or use of the invader as a food source by native species (Beckmann and Shine 2011). An understanding of direct and indirect effects involving especially multiple invasive species is becoming increasingly necessary for effective ecological management (Bergström et al. 2009).

One highly invaded marine system is the Baltic Sea (Leppäkoski and Olenin 2000, Reusch et al. 2018). High volumes of ship movement (Kotta et al. 2016) and intermediate salinity levels (Paa- vola et al. 2005) have contributed to large-scale fish (Ojaveer 2006) and invertebrate (Kotta et al. 2006a) invasions, which become more severe yearly. In the Baltic Sea, many ecological functions that typically occur in most marine systems may be missing, and each function that is present may be represented by only a single or few native species; so overall, the main components of entire systems can be realistically experimentally assessed (Elmgren and Hill 1997). Testing for indirect effects among trophic levels in the Baltic Sea is aided by our relatively extensive understanding of the sea’s general ecology. This understanding has been gained due to the richness of accumulated regional data and the long history and experience of marine management there. Overall, the Baltic Sea a good model system from which the lessons learnt will likely be applied to other seas in coming decades (Reusch et al. 2018).

The Baltic Sea has a strong salinity gradient leading from >30 psu waters near the only connection to the North Sea at the Kattegat to <5 psu in eastern basins and lagoons influenced mostly by riverine input. Each salinity zone has different combinations of native and invasive species typical of fully marine, brackish, and/or fully freshwater environments. The NE Baltic Sea has been particularly affected by species invasion. An invasive predatory crab (Rhithropanopeus harrisii) now occupies a functional predatory guild never occupied by native species in the food web. The crab consumes large numbers of ecologically important shellfish and other smaller invertebrates that previously had no major invertebrate predators in this area (Hegele-Drywa and Normant-Saremba 2009, Kotta et al. 2018). It is native to eastern America, was reported as having invaded western European waters by 1874, was reported in the Baltic Sea as early as 1936, and has become established in NE Baltic Sea regions in recent years (Kotta and Ojaveer 2012). Another invasive decapod predator is the shrimp Palaemon elegans, which was found in regions of the Baltic Sea such as the Gulf of Gdansk soon after the year 2000 (Janas et al. 2004) and was widely distributed in NE regions by 2011 (Kotta and Kuprijanov 2012). It has an ecological role similar to a native shrimp Palaemon adspersus (Kuprijanov et al. 2015) but is able to occupy a wider range of habitats (Kuprijanov et al. 2017). The invasive crab and shrimp are omnivorous meaning possible direct consumption impacts on
multiple trophic levels. These introductions add to a list that includes invasive species long established in the Baltic Sea; included in this study is the zebra mussel *Dreissena polymorpha*, which greatly altered benthic–pelagic trophic coupling in invaded areas (Kotta et al. 2002, Orlova et al. 2004, Lauringson et al. 2007). This mussel became invasive in the Baltic Sea in the early nineteenth century (Mordukhay-Boltovskoy 1964). A more recent arrival is the amphipod grazer *Gammarus tigrinus* that was first recorded in European waters in England in 1931 and reached the Baltic Sea by 1975 (Rewicz et al. 2019).

This study aimed to test separate and interactive effects of two recent NE Baltic Sea invasive predators on multiple trophic levels involving a foundation alga associated with epiphytes and mesoherbivores. Unpredictably large impacts may result from synergistic effects among invaders—our experiment tested the hypothesis that effects from *R. harrisii* (Kotta et al. 2018) will exacerbate effects from *P. elegans* (Kuprijanov et al. 2017) and vice versa. The experiment included three trophic levels, the highest two being invasive species. This tested the hypothesis that one or both invasive predators reduce grazing impacts, caused by the invasive prey species *G. tigrinus* (Jänes et al. 2015) on the important native habitat-providing *Fucus* algae. *Fucus vesiculosus* in particular has been widely studied as a Baltic Sea foundation species (Borg et al. 1997, Korpinen et al. 2010, Dijkstra et al. 2012, Westerbom et al. 2019). Our study used *Fucus radicans* which has similar physical structure and foundation species role (Schagerström et al. 2014) and is the perennial alga typical of invasive species-rich coastal areas in the NE Baltic Sea. Besides *G. tigrinus*, the other invasive prey species tested in this study was the non-native mussel *D. polymorpha*, an important filter-feeder that influences benthic–pelagic coupling (Bagdanaviciute et al. 2018). It was hypothesized that *R. harrisii* crabs would reduce mussel abundances, but it was unknown how any predation effect may be altered by the presence of the second predator, the shrimp *P. elegans*. These hypotheses were tested in experiments that included an overall assemblage of invasive and native species representing the invaded coastal habitats (Table 1).

**Methods**

A laboratory experiment was done at the Kõiguste field base of the Estonian Marine Institute (58°22′22.7″ N 22°58′55.2″ E) using organisms captured from the nearby coast. Within one or two days of capture, the experiment was started by placing organisms in aerated aquaria of dimensions 38 h × 48 w × 36 d cm filled close to capacity, kept indoors under exposure to natural sunlight through windows. The water used in aquaria was collected from Kõiguste Bay which has salinity of 5.0–6.5 psu (Kotta et al. 2009). The water was aerated but not exchanged during the experimental duration. The room temperature provided conditions simulating Baltic Sea coastal summer conditions with 20°C water temperature. Each experimental treatment had 0, 2, or 4 adult *Rhithropanopeus harrisi*, and 25 *Dreissena polymorpha* placed on another cobble, resting on a clean natural sand substratum. The densities used of *D. polymorpha* and *G. tigrinus* were means calculated from the Estonian Marine Institute monitoring database and were similar to densities from previous studies on these species (e.g., Kotta et al. 1998, Jänes et al. 2015). The different densities used of *R. harrisi* and *P. elegans* were also within commonly recorded ranges from the database. *Fucus radicans* wet weight was measured after being blotted dry before and after the experiment along with percentage cover of *F. radicans* epiphytes and the average length per plant of vegetative growth, providing a measure of recent active growth.

The experiment ran from 29 August to 30 September 2017. After completion, all animals were collected and stored at −20°C. Percentage changes in species abundances and *F. radicans* biomass change and vegetative tissue length from the beginning to end of the experiment were compared among treatments using ANOVA on GMAV v5 (The University of Sydney). The assumption of homogeneity of variances was tested using Cochran’s test; this assumption was met in all analyses. Assessment
of Q-Q plots showed no severe deviations of observations from a normal distribution model to prevent the robustness of the ANOVA (Underwood 1997). The factors were *R. harrisii* density and *P. elegans* density with the interactions being tested to determine whether additive or synergistic effects occur. Effects were tested on percentage changes from the beginning to end of the experiment of the consumed prey *D. polymorpha* (density), *G. tigrinus* (density), and *F. radicans* (biomass). Extensive reproduction of *G. tigrinus* occurred in the treatments, and it was not possible to accurately count all the smallest juvenile individuals so the *G. tigrinus* measurements included mostly only adult populations and late-stage juveniles. In addition, effects were tested on the two predators themselves (i.e., percentage changes in densities of the crab and shrimp were also response variables). These tests used the same levels within each factor as other tests except the zero density treatments were excluded for either predator when the test was of that predator’s effect. The significance of differences among levels of factors was tested using Student-Newman-Keuls (SNK) tests on GMAV. *G. tigrinus* is known to exert a strong grazing effect (Orav-Kotta et al. 2009). In our experiments, an indication of grazing was tested by correlating *G. tigrinus* abundance with change in *F. radicans* biomass, epiphytes, and vegetative

| Species                                      | Phylum   | Class     | Order  | Family         | Main functional group | Place of origin | Hypothesized effect                                                                 |
|----------------------------------------------|----------|-----------|--------|----------------|-----------------------|-----------------|-----------------------------------------------------------------------------------|
| *Rhithropanopeus harrisii* (Gould, 1841)     | Arthropoda | Malacostraca | Decapoda | Panopoidae      | Predator, grazer       | NW Atlantic     | 1) Predation reducing *G. tigrinus* and *D. polymorpha* abundance. 2) Grazing reducing macroalgal growth. 1) Trophic cascade involving *G. tigrinus* increasing algal growth. 2) Synergistic interaction with effects from *P. elegans*.                 |
| *Palaemon elegans* (Rathke, 1837) Rockpool shrimp | Arthropoda | Malacostraca | Decapoda | Palaemonidae    | Predator, grazer       | Atlantic and Mediterranean Seas | 1) Predation reducing *G. tigrinus* abundance. 2) Grazing reducing macroalgal growth. 1) Trophic cascade involving *G. tigrinus* increasing algal growth. 2) Synergistic interaction with effects from *R. harrisii*. |
| *Gammarus tigrinus* (Sexton, 1939) Tiger scud | Arthropoda | Malacostraca | Amphipoda | Gammaridae      | Grazer                 | NW Atlantic     | 1) Grazing reducing macroalgal growth                                              |
| *Dreissena polymorpha* (Pallas) Zebra mussel | Mollusca  | Bivalvia   | Myida   | Dreissenidae    | Filter-feeder          | Black, Caspian and Aral Seas | –                                                   | –                                          |
| *Fucus radicans* (Linnaeus, 1753) Narrow wrack | Ochrophyta | Phaeophyceae | Fucales  | Fucaceae        | Primary producer, foundation species | –              | –                                                                                   | –                                          |
| Epiphytes (*Elachista fucicola, Pylaiella littoralis, Cladophora glomerata, Vertebrata fucoides*) | –        | –         | –       | –              | Primary producers, secondary facilitators | –              | –                                                                                   | –                                          |

**Note:** Responses in the form of abundance and/or biomass changes were measured for all species. It was hypothesized that the two predators would reduce abundances of the grazer and filter-feeder, with potential implications such as reduced grazing impact on the primary producers. It was also tested whether either predator exacerbates any impacts caused by the other (i.e., synergist interaction).
tissue growth using linear regression including aquaria from all treatments as independent replicates.

**Results**

ANOVA showed that both predators exerted significant influence on the communities but the effects from the predators were separate (Table 2). The lack of interaction indicates that no synergistic or even additive effects occurred (i.e., if *Palaemon elegans* are added to treatments with *Rhithropanopeus harrisii* within the densities used in this experiment, there are no significantly greater (or lesser) impacts compared to treatments with only *R. harrisii*). The density of *P. elegans* affected *Fucus radicans* biomass, *F. radicans* vegetative tissue length, epiphyte cover, and *Gammarus tigrinus* abundance (Table 2). *R. harrisii* also affected *F. radicans* vegetative tissue length and *G. tigrinus* abundance, and an additional effect occurred on *Dreissena polymorpha* abundance (Table 2). There was no evidence that the predators influenced each other’s survivorship (Table 2).

In all treatments, the mean biomass of *F. radicans* declined throughout the experiment while the length of vegetative tissue increased. Both these changes occurred most strongly in treatments without *P. elegans* (Fig. 1A, C). There was a mean increase in epiphyte cover in the highest *P. elegans* density treatment and decreases in other treatments (Fig. 1E). Mean *G. tigrinus* population size increased by 145% in the absence of *P. elegans* while populations were stable or decreasing when *P. elegans* was present (Fig. 1G). *P. elegans* did not significantly affect *D. polymorpha* (Fig. 1I).

*Rhithropanopeus harrisii* did not significantly affect *F. radicans* biomass (Fig. 1B), but it did affect its vegetative tissue length, the effect being opposite compared to the effect from *P. elegans* (Fig. 1D). ANOVA showed the crab’s effect was significant (Table 2) with the greatest mean increase occurring with two crab individuals per aquaria and the lowest with zero crabs. However, the SNK test could not determine statistical differences between specific treatments (Fig. 1D). No significant effect was found on epiphytes (Fig. 1F). The effect on *G. tigrinus* was not of sufficient strength to have specific differences determined with SNK tests, but the pattern was similar to the effect from *P. elegans* with greatest mean *G. tigrinus* population increases with zero crabs while with four crabs the population change was negative. (Fig. 1H). A direct

| Source                  | df | MS     | F     |
|-------------------------|----|--------|-------|
| *F. radicans* biomass   |    |        |       |
| Rhithropanopeus density 2 | 7.86 | 0.03   |
| Palaemon density        2 | 1958.41 | 6.41*  |
| Rh × Pa                 4 | 706.23 | 9.23*  |
| Residuals               27 | 305.30 |        |
| *F. radicans* veg. tissue |    |        |       |
| Rhithropanopeus density 2 | 11404.21 | 4.68*  |
| Palaemon density        2 | 107320.79 | 4.40*  |
| Rh × Pa                 4 | 36011.16 | 1.48   |
| Residuals               27 | 24384.24 |        |
| Epiphyte cover          |    |        |       |
| Rhithropanopeus density 2 | 4055.79 | 1.04   |
| Palaemon density        2 | 14528.01 | 3.71*  |
| Rh × Pa                 4 | 3163.66 | 0.81   |
| Residuals               27 | 3912.22 |        |
| *D. polymorpha* abundance |    |        |       |
| Rhithropanopeus density 2 | 3459.11 | 21.60***|
| Palaemon density        2 | 283.11 | 0.77   |
| Rh × Pa                 4 | 118.44 | 0.74   |
| Residuals               27 | 160.15 |        |
| *G. tigrinus* abundance  |    |        |       |
| Rhithropanopeus density 2 | 29565.80 | 3.54*  |
| Palaemon density        2 | 122094.96 | 14.63***|
| Rh × Pa                 4 | 21309.81 | 2.55   |
| Residuals               27 | 8346.59 |        |
| *R. harrisii* abundance  |    |        |       |
| Rhithropanopeus density 1 | 104.17 | 0.13   |
| Palaemon density        2 | 1640.63 | 2.10   |
| Rh × Pa                 2 | 182.29 | 0.23   |
| Residuals               18 | 781.25 |        |
| *P. elegans* abundance   |    |        |       |
| Rhithropanopeus density 2 | 2187.50 | 3.27   |
| Palaemon density        1 | 26.04 | 0.04   |
| Rh × Pa                 2 | 729.17 | 1.09   |
| Residuals               18 | 686.40 |        |

Effects were tested on growth variables of the foundation species *Fucus radicans* algae, including biomass, vegetative tissue growth and % cover of epiphytes. Effects were also tested on the invasive mussel *Dreissena polymorpha* and grazing amphipod *Gammarus tigrinus*, and survivorship of the two predators themselves. All data analyzed were percentage changes of each variable that occurred between the beginning and end of the experiment. In all treatments, n = 4. *P < 0.05, **P < 0.01, ***P < 0.001.
Fig. 1. Mean (± SE) changes in the measured response variables of changes in F. radicans algae biomass (A, B), vegetative tissue length (C, D), and epiphyte cover (E, F), and abundance of G. tigrinus amphipods (G, H) and D. polymorpha mussels (I, J). The experiment tested separate and interactive effects from two invasive predators at densities of 0, 2, or 4 individuals per aquaria of P. elegans shrimp and R. harrisii crabs; no significant interactive effects were found so their separate effects are shown, those of the shrimp in the left hand column of graphs, those of the crab in the right hand column. Letters next to bars show significantly similar treatments determined using SNK tests.
predation effect on *D. polymorpha* was observed. Mortality of *D. polymorpha* was high (mean >50%) in all treatments, but a significant increase in mortality occurred in the treatment with two *R. harrisii*, and higher mortality again with four (Fig. 1J).

An effect was observed of grazing by *G. tigrinus*, with a significant negative correlation between the grazer’s abundance and the change in *F. radicans* biomass ($r = 0.17$, $F = 7.07$, $P < 0.05$; Fig. 2). There was no significant correlation between *G. tigrinus* abundances and length of *F. radicans* vegetative growth ($F = 1.37$, $P > 0.25$) or epiphyte cover ($F = 2.52$, $P > 0.1$).

**DISCUSSION**

Effective management of habitats invaded by multiple predators requires consideration of effects that are indirect, interactive, or complex in other ways (Nyström et al. 2001, Preston et al. 2012, Hervias et al. 2013, Doherty et al. 2015). Past studies on interactions among multiple aquatic invasive predators or competitors have provided examples of additive effects (Johnson et al. 2009, Preston et al. 2012), neutral interactions (Nyström et al. 2001), and negative effects (Jackson 2015). Multiple invaders from a common region of origin in particular are expected to facilitate each other’s populations and impacts (Gallardo and Aldridge 2015), which may be relevant to the crab and amphipod in this study (Table 1). However, in the case of *Palaemon elegans* and *Rhithropanopeus harrisii*, our laboratory experimentation produced results suggesting their effects are separate with no interactions. If these results are extrapolated to the broad marine environment, then management of harmful synergistic effects may not be considered a priority for regional ecological management. Results suggest that *P. elegans* needs consideration for its effects on grazers and native foundation species. *R. harrisii* needs consideration for a weaker separate effect on grazers and its predation on filter-feeders. *Fucus* as a habitat forming taxon is often a component in Baltic Sea conservation planning, for example, in Baltic marine protected areas (Virtanen et al. 2018). The Baltic Sea is already heavily impacted by *G. tigrinus*, so the presence of this grazer’s predators may in some ways be considered a positive feature during marine protected area planning or monitoring (or other conservation activities), even if the predators such as *P. elegans* are invasive. On the other hand, *G. tigrinus* as a prey item has become an important food source for Baltic Sea native fish (Daunys and Zettler 2006), and importantly, the invasive amphipod is found in coastal areas that previously lacked this ecological function (Herkül et al. 2016). So reduction of this prey’s abundances (and thus possibly also fish abundances) by invertebrate predators may indirectly affect regional fisheries management and conservation planning that prioritizes fish (e.g., Koljonen 2001), especially if, as in the case of the larger *R. harrisii*, the invertebrate predator may be less likely itself to be a food source.

Although invasive *Dreissena polymorpha* often cause severe impacts (Ricciardi 2003), their filter-feeding and water clarification function can be valuable in eutrophic conditions such as in the Baltic Sea (Bagdanaviciute et al. 2018). Thus, consideration of the effect we found of *R. harrisii* on *D. polymorpha* may be useful for water quality management in regions where they co-occur, for example, any region already with *D. polymorpha* that has recently been invaded by *R. harrisii* may expect some decrease in water quality,
management of which may be considered using means such as line farming of *D. polymorpha* (Friedland et al. 2019) or native mussels (Buer et al. 2020). Another effect to be considered caused by *D. polymorpha* and that will be impacted by mussel predation is the alteration of benthic habitat heterogeneity. Living and dead shells from mussels can affect other species by altering the structure of the benthos, and the shells may also change oxygenation of underlying sediments (Zaiko et al. 2009, Zaiko et al. 2010). Evidence suggests that Baltic Sea *R. harrisii* populations are affected strongly by temperature (possibly from reduced larval survival at low temperatures; Laughlin and French 1989) and thus levels of predation on *D. polymorpha* may also be driven largely by temperature. Unpredictable temperature changes from inter-annual seasonal variability will likely cause unpredictable crab-driven changes to this ecological system (Lehmann et al. 2011). Longer term climate-related temperature increases (Neumann 2010) will also likely increase crab abundance, distribution, and effects from the predation they cause.

Importantly, our study suggests that species invasion in the Baltic Sea may in some ways improve the state of native *Fucus radicans* algae (and likely also the closely related *Fucus vesiculosus*) due to a trophic cascade including *P. elegans* and *Gammarus tigrinus*. This was evident because when *P. elegans* was at high densities, there were lower densities of *G. tigrinus* grazers. *P. elegans* is known as a predator of amphipods (Kuprijanov et al. 2015), and here, we demonstrate this effect can be strong—*G. tigrinus* population sizes were stable or declining in the presence of *P. elegans* but its absence allowed population sizes to more than double. All treatments involved *F. radicans* losing biomass, but the loss was maximized at these high grazer densities.

Evidence suggests *R. harrisii* may also contribute to trophic cascades, but the predation effect was not interactive with effects from *P. elegans* and the effect from *R. harrisii* was weaker, with no effect on algal biomass being detected. This crab has a more varied diet (Nurkse et al. 2018) which in this experiment included not only *G. tigrinus* but also *D. polymorpha*. A highly varied diet in general may spread predation pressure more evenly among prey species limiting the potential for trophic cascades involving specific mid-trophic consumers.

There can be complex food web implications when an invasive prey species becomes highly abundant. For example, if a predator species starts relying strongly on a single invasive prey species as a food source, this provides the requirements for prey-switching (Murdoch 1969, Doherty et al. 2015). In New Zealand, invasive cats were reliant on invasive rabbits for prey, but when disease abruptly decimated the invasive prey, the enlarged predator populations abruptly switched to preying on and endangering native prey populations (Norbury 2001, Murphy et al. 2005). More experimentation would be needed to understand the potential for prey-switching in the marine food web of the current study, but there is the potential for a prey-switching process to occur if enlarged *P. elegans* abundances were prevented from relying on invasive amphipod prey. Similarly, the process of hyperpredation can occur when introduction of a dominant invasive prey boosts predator populations (Courchamp et al. 2000, Ringler et al. 2015) that reduce/control invasive prey, but spillover predation on less-dominant native prey populations can be severe (Courchamp et al. 2000, Ringler et al. 2015). Further research could determine if such a process driven by *P. elegans* predation could impact Baltic Sea native prey such as the amphipods *Gammarus oceanicus*, *Gammarus salinus*, and *Gammarus zaddachi* (Herkül et al. 2016). Overall, our experiment included only a subset of species that are present in the natural community and further research would be useful to test the generality of these results using experimentation in the field or in the laboratory using different numbers/combinations of species.

An important implication of our results is the possibility that the wide range of native invertebrates (Korpinen et al. 2010, Dijkstra et al. 2012, Westerbom et al. 2019) and fish (Borg et al. 1997) that use *Fucus* as food and habitat are currently relying on invasive predators to cause a trophic cascade that prevents declines in this facilitation. In other words, the potential for algal facilitation of native species is significantly linked with the potential for predation of the algal consumers, which are largely invasive. In some cases, grazers benefit algal primary foundation species by preferentially grazing the epiphytes which at high cover may reduce the fitness of the host foundation species (Lubchenco 1983). This does not, however, appear to have occurred in the present study where...
the only correlation of G. tigrinus grazers was a negative one with biomass of the foundation species alga. The lack of correlation between G. tigrinus grazers and epiphytes may be due to selective grazing of senescent algal tissue (Kotta et al. 2006b) that may facilitate algal productivity but leave overall algal biomass stable. But in general, from the current analyses, it can only be concluded that if any effects of G. tigrinus occur on biomass and facilitation potential from the algae we studied, the effects will likely be negative.

Although epiphyte cover was not correlated with G. tigrinus, epiphytes were significantly affected by P. elegans, which increased their cover. This is a finding commonly made during experiments on this predator (Moksnes et al. 2008, Persson et al. 2008). These epiphytes provide habitat and food for native species (Wikström and Kautsky 2007) via the process of secondary facilitation (Thomsen et al. 2018). However, as discussed above, there was no significant correlation between abundances of prey/graizers and cover of epiphytes, so the reason for the positive relationship between the predator and epiphytes is not clear. It may be due to some kind of complex amphipod grazing change, for example, a predator-induced density-independent grazing rate reduction (Reynolds and Sotka 2011).

Although the signal within the data of predator and grazer effects was clear, this occurred within aquaria that had high mortality of D. polymorpha (overall mean 81%) and negative F. radicans biomass change (~24%). Seasonal Fucus algal biomass losses are common (Graiff et al. 2015) but these aquaria may also have had some sub-optimal conditions for mussels and algae (Kraufvelin 1999), for example, low planktonic food supply for D. polymorpha. However, when considering F. radicans vegetative tissue length, the majority of replicates had positive values. The greatest increases occurred in treatments that included R. harrisii, which is an omnivore that grazes F. radicans (Jormalainen et al. 2016). This result suggests such grazing may stimulate new vegetative growth (Black 1976) and produce shorter more dense algal bushes, which may in turn affect the species using the bushes as habitat (Schagerström et al. 2014). Variability in algal tissue properties such as from vegetative vs non-vegetative tissue can significantly affect algal mortality and population sizes; pruning of algal tissue such as that which was likely done by R. harrisii may decrease plant mortality in some contexts (Black 1976, Demes et al. 2013), but severe grazing causes algal detachment. Although P. elegans is also omnivorous, the results suggest that in some ways it affects F. radicans in ways that are opposite to the ways that the crab affects F. radicans, because significantly reduced vegetative tissue length increases occurred when the shrimp was present. This finding is probably not caused by indirect effects involving G. tigrinus grazing, indicated by the non-significance of the attempt to correlate G. tigrinus density with F. radicans vegetative tissue length.

To conclude, in the heavily invaded system of the Baltic Sea simulated in this experiment, effects of the invasive predators we manipulated were separate. However, unpredictable effects still need consideration and a multi-species approach to management is required mostly due to a significant trophic cascade including one predator species and one prey, both invasive. The results are directly applicable to some currently highly invaded Baltic Sea regions and will become applicable to nearby regions as these invaders continue to spread. By using a comprehensive experimental approach to unravel the dynamics occurring, the general dynamics revealed may be used to guide research of similar dynamics in other systems, which may be not only marine but also freshwater and terrestrial. These results have reinforced findings from previous studies demonstrating the importance of understanding in particular novel tropic cascades that can have far reaching ecological and economic implications.

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