



Trophic interactions between native and alien palaemonid prawns and an alien gammarid in a brackish water ecosystem

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Received 3 February 2015, revised 31 March 2015, accepted 1 April 2015, available online 26 November 2015

Abstract. Macroalgae are an important habitat for small mobile invertebrates such as gammarid amphipods and palaemonid prawns. Gammarid amphipods are important grazers of micro- and macroalgae whereas palaemonid prawns are feeding on macroalgae and small aquatic invertebrates including gammarids. Recently the invasive palaemonid prawn *Palaemon elegans* established in the Baltic Sea. As *P. elegans* occurs within the same habitats as the native *Palaemon adspersus*, it is expected that this invasion modifies the existing trophic interactions. To address this question, we experimentally investigated the feeding of the native *P. adspersus* and the invasive *P. elegans* on the benthic macroalga *Cladophora glomerata* and on the invasive gammarid amphipod *Gammarus tigrinus*. In the course of the experiment neither *G. tigrinus* nor *Palaemon* spp. had effects on filamentous macroalgae. The presence of prawns drastically increased the mortality of amphipods with no difference in the feeding efficiency between the two prawn species. To conclude, the alien prawn does not add an extra function to the trophic system of the coastal ecosystem of the Baltic Sea. Nevertheless, due to its progressively increasing densities and wide habitat range, *P. elegans* is expected to exert stronger predation pressure on gammarid amphipods as compared to *P. adspersus* alone.

Key words: Baltic Sea, invasive species, *Palaemon elegans*, *Palaemon adspersus*, *Gammarus tigrinus*, trophic interactions, predation.

INTRODUCTION

In aquatic systems with low species diversity, predation can be a strong structuring force (Flecker and Townsend, 1994; Worm and Myers, 2003), and the addition of an efficient predator may result in many direct and indirect effects leading to a reorganization of the entire food web (Carpenter et al., 1985). Nowadays the rates of bioinvasions are progressively increasing in the coastal seas around the world with decapod crustaceans being amongst the most notorious pests (Weis, 2011). When established, such predators may generate changes in trophic interactions of invaded systems equivalent to for instance coastal eutrophication or climate change (e.g. Grosholz et al., 2000). Although native species are better adapted to their environment, invasive species

may outcompete native species as they are often better foragers (Weis, 2011). When present at high numbers, predators may drastically reduce populations of herbivores and thereby indirectly facilitate blooms of ephemeral algae in coastal ecosystems (Eriksson et al., 2009; Sieben et al., 2011). Moreover, in the absence of invertebrate prey, introduced decapods may also feed on some macroalgal species and thereby cause shifts in the macroalgal community structure.

The invasive rockpool prawn *Palaemon elegans* established almost in the entire Baltic Sea recently (Janas and Maňkucka, 2010; Katajisto et al., 2013). Its Baltic population is genetically closer to the Mediterranean, Black Sea, and Caspian Sea populations than to the Atlantic population (Reuschel et al., 2010). This evidence clearly suggests that *P. elegans* is a non-native species in the Baltic Sea, which has been introduced by human activity. The ecological consequences

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of the large-scale and rapid invasion of *P. elegans* are barely known.

As the Baltic Sea is characterized by low numbers of benthic invertebrate predators and the invasive palaemonid has attained high densities in numerous habitats, the species is expected to have an effect on the food webs of the coastal sea. Earlier studies have shown that palaemonid prawns can feed on both benthic macroalgae and invertebrates (Hartnoll and Salama, 1992; Janas and Barańska, 2008; Moksnes et al., 2008; Lesutienė et al., 2014) with amphipods serving as their main food (Möller et al., 1985; Persson et al., 2008). As *P. elegans* occurs within the same habitats as the native *Palaemon adspersus*, the invasive palaemonid may outcompete the native palaemonid species. It is also expected that this invasion may modify the existing trophic interactions either due to the addition of a new function (i.e. preying on different organisms compared to the native prawn species) or intensification of the existing interactions (e.g. increasing predation pressure on amphipods). Additionally, *P. elegans* is also a valuable food for fish (Janas and Bruska, 2010; Gruszka and Więcaszek, 2011). As the effects of the prawn are expected to be context specific (Smaldon, 1979; Berglund, 1980), it is not possible to extrapolate findings of previous studies over the entire Baltic Sea.

It is difficult to assess the strength of interspecific interactions in a food web using only field observations because multiple types of interactions act at the same time (Scheffer et al., 2005; Speckman et al., 2005) and several prey and predator species are involved (Chapin et al., 1997; Pinnegar et al., 2000; Frank et al., 2007). Natural communities are complex systems with multiple trophic levels and nonlinear interactions between species. These interactions together with environmental variability can enhance or weaken the separate effects of a single species of interest (Schmitz, 2007). In the context of palaemonid invasion this can obscure the true effect of *P. elegans*.

Experimental studies can effectively reveal cause–effect relationships in a multitrophic system and assess intensities of various controls involved (Hunt and McKinnell, 2006). Although experiments where vegetation, herbivores, and predators are simultaneously manipulated can be regarded as an important tool to assess the relative strength of trophic interactions and cascade effects, such studies are still rare (e.g. Korpinen et al., 2007; Moksnes et al., 2008; Persson et al., 2008; Wernberg et al., 2013). Nevertheless, all these studies have specifically demonstrated critical roles of predation on invertebrate prey and macroalgae that would not have been revealed if only two trophic levels had been included into the experimental design.

In the current study we experimentally manipulated the presence of the filamentous macroalga *Cladophora glomerata*, the invasive amphipod *Gammarus tigrinus*,

the native prawn *P. adspersus*, and the invasive prawn *P. elegans* in order to test (1) whether *P. elegans* had different grazing and/or predation rates than *P. adspersus* and (2) whether the grazing and/or predation rates varied among mixed and single species assemblages. Based on earlier evidence, we expected that gammarid amphipods constitute an important food source for both prawn species. We also expected that due to its higher mobility (Berglund, 1980), the invasive prawn exerted stronger predation pressure on amphipods than the native species and due to its higher aggressiveness and higher efficiency in predator avoidance (Berglund and Bengtsson, 1981), it might induce elevated mortality in the native palaemonid. Finally, we predicted that due to the complementarity effect, assemblages containing both prawn species had higher grazing and/or predation rates compared to assemblages containing a single prawn species.

Methods

An outdoor aquarium experiment was performed adjacent to the Kõiguste Marine Biology Laboratory, the north-eastern Baltic Sea, in August 2012. Experimental organisms were collected from the northern (58°37.34'N, 22°51.78'E) and the southern coast (58°22.25'N, 22°58.77'E) of Saaremaa Island, north-eastern Baltic Sea. The palaemonid prawns *P. adspersus* and *P. elegans* and their prey *G. tigrinus* were collected with hand nets between 0 and 1 m depth. Only adult specimens were used in the experiment. Boulders overgrown with the green filamentous macroalga *Cladophora glomerata* were collected from the same areas. Prior to the beginning of the experiment, all invertebrates were removed from the algae and boulders by vigorously shaking the boulders in filtered sea water followed by a thorough visual inspection. Boulders with filamentous algae in the experiment served as an object of grazing for the palaemonid prawns and gammarid amphipods and as a refuge for gammarids.

The experiment was performed in 5-L aquaria filled with filtered surface water (salinity 5.5) from Kõiguste Bay. The following treatments and treatment levels were used: *Palaemon* community (*P. elegans*, *P. adspersus*, mixed, none), *Palaemon* density (1 or 2 individuals per aquarium, which corresponded to 14 and 28 ind m⁻² or 1.49±0.92 and 2.57±1.06 g m⁻² of dry biomass (mean±standard deviation), respectively), presence of macroalgae (vegetated boulders, unvegetated boulders), presence of gammarid amphipods (present, absent). Altogether 92 aquaria were used to deploy 23 treatments replicated four times (Table 1). The initial density of gammarids within the aquaria was 141 ind m⁻², the cover of macroalgae was set at 50% corresponding to the algal biomass of 3.43±0.85 g dw m⁻². Similar

Table 1. Experimental setup. Four replicates were analysed for each treatment

Treatment	Presence of vegetation	Presence of gammarids	<i>Palaemon</i> community	<i>Palaemon</i> density
1	No	No	<i>P. elegans</i> + <i>P. adspersus</i>	2
2	No	No	<i>P. elegans</i>	1
3	No	No	<i>P. elegans</i>	2
4	No	No	<i>P. adspersus</i>	1
5	No	No	<i>P. adspersus</i>	2
6	No	Yes	<i>P. elegans</i> + <i>P. adspersus</i>	2
7	No	Yes	<i>P. elegans</i>	1
8	No	Yes	<i>P. elegans</i>	2
9	No	Yes	<i>P. adspersus</i>	1
10	No	Yes	<i>P. adspersus</i>	2
11	No	Yes	None	0
12	Yes	No	<i>P. elegans</i> + <i>P. adspersus</i>	2
13	Yes	No	<i>P. elegans</i>	1
14	Yes	No	<i>P. elegans</i>	2
15	Yes	No	<i>P. adspersus</i>	1
16	Yes	No	<i>P. adspersus</i>	2
17	Yes	No	None	0
18	Yes	Yes	<i>P. elegans</i> + <i>P. adspersus</i>	2
19	Yes	Yes	<i>P. elegans</i>	1
20	Yes	Yes	<i>P. elegans</i>	2
21	Yes	Yes	<i>P. adspersus</i>	1
22	Yes	Yes	<i>P. adspersus</i>	2
23	Yes	Yes	None	0

values have been previously observed in the Kõiguste Bay area (Lauringson and Kotta, 2006). The density of *P. adspersus* and *P. elegans* was slightly higher in aquaria than in the field; however, when prawns are swarming in the field, the values match the experimental densities.

The wet weight of algae was determined prior to the experiment to the nearest 0.01 g. Before weighing, the algae and boulders were gently dried on plotting paper until the paper did not become wet any more. At the end of the experiment algae were removed from the boulders, and the boulders and algae were weighed separately. The initial weight of the algae was calculated by subtracting the weight of a boulder. Additional four replicates of boulders with algae were collected to obtain the ratio of wet to dry weight of algae. These algae were dried at 60°C for 48 h. The ratio of wet to dry weight of algae was used to convert the initial algal wet weight to dry weight.

The experiment lasted 48 h. The number of gammarid individuals was visually estimated in every 12 h. The experiment was terminated when at least in one experimental treatment about 50% of gammarids had been consumed. This was necessary to avoid total consumption of gammarids by prawns and to prevent

getting biased estimates of predation rate due to the changing prey densities. During the course of the experiment, the water temperature varied between 14 and 23°C following diel variation in the seawater temperature in Kõiguste Bay.

At the end of the experiment the test animals were counted and determined to the species level. In addition, the body length of prawns was measured from the tip of the rostrum to the tip of the telson. The total body length of palaemonid prawns used in the experiment was as follows (min, mean, max; mm): *P. elegans* 21.7, 38.5, and 49.5; *P. adspersus* 22.3, 38.7, and 51.0. The survival was calculated as the percentage of individuals of *G. tigrinus* and palaemonid prawns that were alive at the end of the experiment. In addition, all remaining algae were collected from the boulders and their dry weight was determined. The algal consumption was quantified as the change in the dry weight of algae between the start and the end of the experiment.

Factorial ANOVA with the density of prawns nested within the *Palaemon* community was used to investigate the separate and interactive effects of treatments on the macroalgal consumption and the survival of amphipods and palaemonid prawns. Post-hoc Bonferroni tests were used to analyse which treatment levels were statistically different from each other. Prior to analyses we checked the validity of the assumptions of ANOVA.

RESULTS

Only one prawn out of 128 specimens died. This indicates that experimental treatments had no clear effects on prawn mortality during the experiment.

During the course of the experiment, we observed that the studied *Palaemon* species did not graze on the filamentous *C. glomerata* (Table 2). Neither did prawns

Table 2. Three-way ANOVA on the effects of gammarids (factor levels: absent, present), *Palaemon* community (factor levels: no prawn, *P. elegans*, *P. adspersus*, mixed community of *P. elegans* and *P. adspersus*), and *Palaemon* density (factor levels: 0, 1, 2 individuals per aquarium) on the macroalgal consumption

Effect	SS	DF	MS	F	p
Gammarids	0.00	1	0.00	0.00	0.97
<i>Palaemon</i> community	0.05	3	0.02	1.20	0.32
Gammarids × <i>Palaemon</i> community	0.05	3	0.02	1.16	0.34
<i>Palaemon</i> density (nested in <i>Palaemon</i> community)	0.02	2	0.01	0.79	0.46
Gammarids × <i>Palaemon</i> density (nested in <i>Palaemon</i> community)	0.03	2	0.01	1.11	0.34
Error	0.48	36	0.01		

indirectly affect the biomass of macroalgae through the removal of the mesoherbivore *G. tigrinus*. Moreover, there were no differences in the algal consumption between single and mixed species prawn treatments and between different palaemonid densities (Table 2).

Prawns significantly reduced the survival of gammarids (Table 3, Table 4, Fig. 1). Over 90% of the gammarid amphipods survived when prawns were absent. In the presence of the predatory palaemonid, the survival of gammarids was reduced to 55%. There was no difference in the feeding activity between the two studied prawn species and the presence of macroalgae did not modify the feeding rates of palaemonid prawns (Table 3). Moreover, the predation of prawns on gammarid amphipods did not vary among single and mixed *Palaemon* species treatments (Table 4) and prawn density had no effect on the survival of *G. tigrinus*.

Table 3. Three-way ANOVA on the effects of vegetation (factor levels: absent, present), *Palaemon* community (factor levels: no prawn, *P. elegans*, *P. adspersus*, mixed community of *P. elegans* and *P. adspersus*), and *Palaemon* density (factor levels: 0, 1, 2 individuals per aquarium) on the survival of gammarids. Statistically significant effect ($p < 0.05$) is indicated in bold

Effect	SS	DF	MS	F	p
Vegetation	485	1	485	0.76	0.39
<i>Palaemon</i> community	9 189	3	3 063	4.77	0.007
Vegetation × <i>Palaemon</i> community	245	3	82	0.13	0.94
<i>Palaemon</i> density (nested in <i>Palaemon</i> community)	625	2	312	0.49	0.62
Vegetation × <i>Palaemon</i> density (nested in <i>Palaemon</i> community)	81	2	41	0.06	0.94
Error	23 772	37	643		

Table 4. Bonferroni post hoc comparisons between the factor levels of *Palaemon* community following three-way ANOVA presented in Table 3. Statistically significant differences ($p < 0.05$) are indicated in bold

	<i>P. elegans</i>	<i>P. adspersus</i>	No prawn
Mixed community	1.00	1.00	0.01
<i>P. elegans</i>		1.00	0.04
<i>P. adspersus</i>			0.02

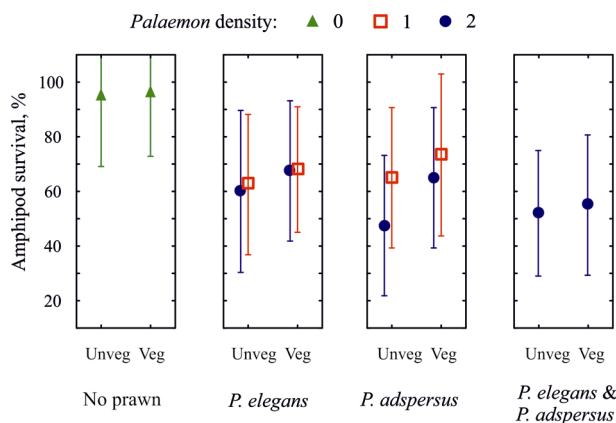


Fig. 1. Effect of vegetation (factor levels: absent, present; denoted as unveg and veg), *Palaemon* community (factor levels: no prawn, *P. elegans*, *P. adspersus*, mixed community of *P. elegans* and *P. adspersus*) and *Palaemon* density (factor levels: 0, 1, 2 individuals per aquarium) on gammarid survival. Vertical bars denote 0.95 confidence intervals.

DISCUSSION

Our experiment demonstrated that *P. elegans* represented a similar function as *P. adspersus*, the only palaemonid previously present in the ecosystem of the north-eastern Baltic Sea. Both palaemonid prawns exerted a strong predatory pressure on gammarid amphipods. Contrastingly, the impacts of *P. elegans* on the native *P. adspersus* and on the macroalga *C. glomerata* were negligible. This suggests that the invasion does not necessarily lead to the reorganization of trophic interactions in the coastal sea unless *P. elegans* colonizes areas where *P. adspersus* is absent or found at low densities. Nevertheless, *P. elegans* tolerates hypoxia and low salinity better (Taylor and Spicer, 1987; Janas et al., 2013) and establishes in areas previously uninhabited by native palaemonid prawns or other invertebrate predators of similar size, for example in the Vistula Lagoon in the southern Baltic Sea (Ezhova et al., 2005) and in the eastern part of the Gulf of Finland in the northern Baltic Sea (I. Kuprijanov, unpublished material). Consequently, in such habitats the invasive palaemonid presents a new function and thereby affects the stability of local food webs (Long et al., 2011).

It has been suggested that in case of a lack of prey, palaemonid prawns can switch to an algal diet (Jephson et al., 2008). Our study suggested otherwise but this may reflect the short time frame of our experiment. In the southern Baltic Sea, the diet of *P. elegans* regularly consists of filamentous algae including *Cladophora* spp. (Janas and Barańska, 2008). However, the volume of animal food always exceeds algal food at the southern Baltic coast (Janas and Barańska, 2008), and the proportion of filamentous algae in the food of *P. adspersus*

and *P. elegans* may differ largely between areas (Jephson et al., 2008).

In the present study, no strong effect of vegetation on gammarid survival emerged. This certainly cannot hint the lack of such effect in the field, where conditions for escapee are substantially better than in a spatially limited aquarium. Normally, the native *P. adspersus* does not inhabit unvegetated areas whereas *P. elegans* can be found in the full range of coastal habitats regardless of macrophyte cover (Katajisto et al., 2013). Thus, when *P. elegans* reaches high densities in unvegetated habitats, it may exert an elevated predatory pressure on gammarid amphipods in such habitats.

In the present experiment, predator density had no effect on gammarid mortality. Gammarids may have reduced their time spent out of hiding places in response to higher prawn densities or alternatively, actively swimming gammarids may have been cropped at efficiencies indifferent of predator densities in the studied range. This may indicate that palaemonid food was a limiting factor at both studied shoaling densities and possibly even at lower densities than observed in the present study. Our study suggests that if a shoal of prawns with the density within the studied range (14–28 ind m⁻²) remained at a place for about 48 h, local gammarid population would be reduced by approximately 50% and the palaemonids might have to change their feeding grounds to meet their nutritional demands.

Previous laboratory experiments have demonstrated that *P. elegans* is able to effectively prey on gammarids (*G. locusta*) less than 8 mm in total length (Persson et al., 2008). In our study, slightly larger amphipods were successfully consumed by both species of palaemonid prawns. In predatory crustaceans, the size of chela defines the range of size of invertebrate prey (Mariappan et al., 2000). Individuals with bigger chelae are expected to attack larger prey (e.g. Elner, 1980), whereas those with smaller chelae catch fast-moving prey and exhibit more generalistic feeding patterns (Seed and Hughes, 1995; Yamada and Boulding, 1998). In addition to having relatively larger chelae, *P. adspersus* has also been shown to grow slightly faster and bigger compared to *P. elegans* (Berglund, 1980); however, the size difference seemed insufficient to cause an effect in our study. As to finding immobile food items *P. elegans* has been shown to be quicker than *P. adspersus* (Berglund, 1980). In our experiment, however, both species caught live amphipods with equal efficiency and differences between single and mixed species treatments were insignificant. Still, in mixed species treatments, food intake by one given prawn species may have been changed by the vicinity of the other species.

Although gammarids were heavily consumed by prawns in our study, it seems possible that *G. tigrinus*

can compensate for high mortality by a very broad reproduction period, high reproduction rate, and short development time. The native gammarids have a later start of breeding, smaller brood size, and longer maturation time (Kotta et al., 2010; Sareyka et al., 2011; Jänes et al., 2015). Therefore, the expanding *P. elegans* population could have stronger effects on native gammarids than on *G. tigrinus*. The invasive gammarid, in turn, may potentially facilitate the invasive predator by offering a more abundant food source than the less productive native prey species. The distribution range and abundance of native gammarids have already decreased due to negative effects of the invasive *G. tigrinus* (Kotta et al., 2010) and the invasion of *P. elegans* may further suppress the populations of native gammarid species.

Two species with very similar ecological niches are expected to either partition their limiting resources or not to occur sympatrically (MacArthur and Levins, 1967). In the North Sea, both prawn species share the range but partition their habitats (Berglund and Bengtsson, 1981). In the Gulf of Gdansk, the southern Baltic Sea, the distribution patterns show a retreat of *P. adspersus* from extensive areas after the invasion of *P. elegans* (Grabowski, 2006). In the north-eastern Baltic Sea, however, the two prawn species coexist in soft and hard bottom habitats and within a wide range of depths (Katajisto et al., 2013; Kuprijanov and Kotta, 2013). Contrary to the southern Baltic Sea, vegetated areas are widespread in the shallow habitats of the north-eastern Baltic Sea and are highly trophic. Therefore, the two prawn species may likely benefit from abundant food resources and accordingly weak interspecific competition in their sympatric summer habitat. It may be that prawns are only limited by predation in their wintering areas (Pihl, 1982; Gruszka and Więcaszek, 2011). Moreover, our experiment was focussed on the gammarid–palaemonid interactions whereas in field conditions the decapod predators are exposed to multiple prey species and are themselves preyed by fish. Thus, further community level, longer-term, and seasonally explicit experiments would provide more detailed knowledge on the roles of palaemonid prawns in the Baltic Sea coastal ecosystems.

To conclude, our study demonstrated how an introduction of a closely related species strengthens an existing function of a palaemonid predator in a food web. Both palaemonid species strongly preferred gammarids over filamentous green algae and preyed on invertebrates at an equal rate. Our results hint that the predatory function of the invasive palaemonid may largely overlap that of the local species, which could lead to niche partitioning or outcompeting processes between these two species. Additionally, the larger habitat range of the invasive species may intensify the top-down control of crustacean herbivores in an

extensive range of coastal areas of the Baltic Sea presently lacking such predator.

ACKNOWLEDGEMENTS

This work was financed by Institutional research funding IUT02-20 of the Estonian Research Council. The project has received funding from BONUS project BIO-C3 and the joint Baltic Sea research and development programme (Art 185), funded jointly from the European Union's Seventh Programme for research, technological development and demonstration and from the Estonian Research Council. We would like to thank V. Druzhinin and J. Kuprijanova for assisting in field-work, setting up the experiment, and laboratory analyses.

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Kohaliku ja võõrliigist kreveti ning võõrliigist kirpvähi toitumissuhted riimveelises ökosüsteemis

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Makrovetikad on väikestele selgrootutele, nagu kirpvähilised ja krevetilised, oluliseks elupaigaks. Kirpvähilised on rannikumeres tähtsad herbivoorid, samas kui krevetilised võivad käituda nii kiskjate kui ka herbivooridena. Hiljuti Läänemere põhjaossa jõudnud võõrliik elegantne krevett (*Palaemon elegans*) asustab kohaliku läänemere krevetiga (*P. adspersus*) sarnaseid elupaiku ja võib oletada, et elegantse kreveti invasioon muudab olemasolevaid toitumissuhteid. Elegantse kreveti mõjude väljaselgitamiseks uuriti eksperimentaalselt kohaliku liigi ja võõrliigi toitumissurvet makrovetikatele ning võõrliigist vöotkirpvähile (*Gammarus tigrinus*). Eksperimendi käigus ei avaldanud kumbki krevetiliik ega ka vöotkirpvähk makrovetikatele mõju. Krevettide esinemine suurendas drastiliselt kirpvähkide suremust, kuid kahe krevetiliigi toitumise intensiivsuses ei esinenud erinevust. Tulemustest võib järeldada, et võõrliigist krevett ei esinda Läänemere põhjaosas uut ökoloogilist funktsiooni, kuid üha laieneva leviku ja kasvava asustustiheduse tõttu võib elegantne krevett avaldada kirpvähkidele tugevamat kiskluse survet, kui seda suudab kohalik läänemere krevett üksi.