

ORIGINAL ARTICLE

Relationships between mechanical disturbance and biomass of the invasive amphipod *Gammarus tigrinus* within a charophyte-dominated macrophyte community

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Baltic Sea; *Chara aspera*; gammarid amphipod; mechanical disturbance; non-native species; recovery.

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Abstract

Disturbance may alter the resistance of communities to non-indigenous species as it frees space and removes competitively superior species. In a factorial field experiment we studied how different types of mechanical disturbance affected the biomass level of the non-indigenous amphipod *Gammarus tigrinus* in a brackish water charophyte community. Mechanical disturbance affected the biomass of *G. tigrinus* with a time lag between disturbance and response of the gammarid species. In general, all types of disturbance reduced gammarid biomasses. The effect persisted until the end of the experiment regardless of the recovery of macrophyte communities in terms of species number and biomass of benthic invertebrate and plant species. Thus, a possible cause of reduced biomass of the gammarid amphipods relates to the decreased biomass of *Chara aspera* and its structural changes. This indicates that the dominance of *G. tigrinus* in a low saline system has less to do with strong species interactions (e.g. competitive displacement) than with habitat-level processes (e.g. changes in habitat structural characteristics and food supply).

Introduction

Non-native species are ranked among the greatest threats to global biodiversity (Bax *et al.* 2003), with coastal marine systems being the most invaded systems on the planet (Carlton 1996). Earlier studies have shown that successful exotics may render previously stable systems unbalanced and unpredictable (Carlton 1996; Ruiz *et al.* 1997) and severely affect the structure and functioning of invaded ecosystems (Ricciardi & Cohen 2007; Orav-Kotta *et al.* 2009). Despite the importance of coastal invasions, marine non-native species are much less well studied than terrestrial and freshwater counterparts (Groscholz 2002).

Dating back as far as 1958, Elton realized that species-rich communities should be more stable and less susceptible to non-native species compared to species-poor communities (Elton 1958). To date most of the smaller-scale experimental work has supported this biotic resistance hypothesis (e.g. Stachowicz *et al.* 1999, 2002) and

the observed inverse relationship is explained by more efficient utilization of available resources by highly diverse communities (Levine & D'Antonio 1999) and/or the sampling effect, i.e., the occurrence of suppressive species increases with diversity (Wardle 2001). Competition with an ecologically similar native species is an obvious example of such biotic resistance (Kotta *et al.* 2001; Kotta & Ólafsson 2003).

Disturbance may alter the resistance of communities to non-native species as it frees space and removes competitively superior species, thus relaxing competitive interactions among non-native and resident species (Shea & Chesson 2002). Nevertheless, non-native species often seem to have idiosyncratic and context-specific characters, urging experimental studies on how disturbance affects the population dynamics of these species. Even more, the role of disturbance in the success of non-native species has initiated a long debate because non-native species could be considered the drivers or consequences of

biological changes (Didham *et al.* 2005 and references therein).

Due to its short geological history, the Baltic Sea biota has a low number of species (e.g. Segerstråle 1957). Despite high numbers of non-native species, the coastal biota shows no loss of biodiversity and, even more, non-native species actually expand ecosystem functioning (Kotta *et al.* 2006; Reise *et al.* 2006). In recent years the range of non-native amphipods has increased tremendously in the Baltic Sea. Crustacean invaders seem to expand their distribution at the expense of the resident species of the area, suggesting strong competitive interactions among resident and non-native species (Jazdzewski *et al.* 2002; Szaniawska *et al.* 2003; Orav-Kotta *et al.* 2009).

Although the exotic *Gammarus tigrinus* Sexton was occasionally found in the southern Baltic Sea in the mid-1970s, it was not until the early 2000s that the species expanded its distribution throughout virtually the entire Baltic (Herkül *et al.* 2009). A recent climate change may have facilitated this rapid range expansion, as elevated winter storms are expected to increase the amount of drifting macroalgae, an efficient transport vector of amphipod crustaceans in the water column (Biber 2007). More importantly, extensive erosion and alteration of depositional coasts has been observed in the Baltic Sea in recent years (Orviku *et al.* 2003). The lack of evidence for sea level rise during this period suggests that such erosion is largely due to the recent increased storminess in the Eastern Baltic Sea. Severe storms efficiently erode sediment and destroy benthic macrophyte communities, thereby facilitating the large-scale spread of the non-native species through relaxation of competitive interactions. Besides these episodic extreme disturbances, benthic communities are impoverished by increasing intensities of smaller mechanical stressors, mainly of human origin, such as trampling by feet, boating and dredging.

Earlier studies have shown that *G. tigrinus* tolerates broad environmental conditions (Pinkster *et al.* 1977; Wijnhoven *et al.* 2003; Devin & Beisel 2007) and has low habitat selectivity (Bousfield 1973; Daunys & Zettler 2006); therefore, it may potentially inhabit very different types of coastal habitat. However, in the coastal reach of the Northern Baltic Sea, the species is becoming a dominant mesoherbivore in the sheltered charophyte communities (Herkül *et al.* 2009). Being extremely fragile, such charophyte habitats are potentially very sensitive to any type of mechanical disturbances.

In an *in situ* experiment, we studied how different types of mechanical disturbance affected the biomass level of *G. tigrinus* in a brackish water charophyte community. We predict that a moderate mechanical disturbance leav-

ing a significant proportion of the charophyte canopy intact may increase the biomass of the non-native amphipod as the majority of native herbivores are expected to be sensitive to such stress. Consequently, the competitive interactions among non-native and resident species are expected to be weakened (e.g. Herkül *et al.* 2006). *Gammarus tigrinus* is an opportunistic species and is therefore expected to be less severely affected by mechanical disturbance than the resident species. We also predict that due to the phytophilous nature of *G. tigrinus*, the disturbances associated with mechanical removal of vegetation or sediment will significantly reduce the biomass of the non-native species.

Study Area

Rame Bay is a shallow and semi-enclosed bay in the Northeastern Baltic Sea (58.5749° N, 58.5671° E; surface area 4 km²). The maximum depth of the area is 1.5 m but most of the bay is shallower than 1 m. The bottom is composed of fine sand and a thick layer of finely fractioned silt. Salinity varies between 3 and 5 and is highly dependent on rainfall. Being sheltered, Rame Bay provides excellent habitat for luxurious charophyte populations together with aquatic phanerogams. The most widespread species is *Chara aspera* Willd., which dominated the entire sheltered part of the bay (Torn & Martin 2003). The non-native amphipod *Gammarus tigrinus* only recently invaded Rame Bay and 2 years after establishment (i.e., at the beginning of this study) it made up the majority of gammarid abundance and biomass in the bay.

Material and Methods

Experimental procedures

The experiment was carried out from June 2007 to July 2008. Experimental plots (1.5 × 1.5 m) were established within a dense *Chara aspera* community at 1 m depth. Mechanical disturbance was applied once in June 2007 and involved the following treatment levels: (i) control (i.e., undisturbed plots), (ii) cutting the tips of plants, (iii) removal of plants, (iv) mixing of the sediment surface layer, (v) removal of the surface sediment layer. We used a full random design. For the second treatment, the upper 5 cm of the vegetation was cut by a diver. For the third treatment, plants were removed gently by hand. These two treatments mimic the foraging of herbivorous birds. For the fourth treatment, sediment was mixed together with vegetation to approximately 0.1 m depth. Mixing of the sediment surface layer was used to imitate the influence of motorboat anchoring, running of scooters and/or trampling. And finally, for the fifth treatment,

the sediment layer was removed down to about 0.1 m depth. Removal of the sediment layer represents disturbances due to dredging and/or ice scrape that also result in the removal of vegetative layer. The plots were sampled in July, August, September and October 2007, and July 2008. For each treatment level and sampling occasion three replicate biomass samples were collected, totaling 75 samples. A SCUBA diver collected samples by gently removing the biota within the algal canopy and sediment epifauna using a 20 × 20 cm frame. Samples were stored at −20 °C. In the laboratory all macrophytes and benthic invertebrates were determined to the species level. The dry weight of species was obtained after drying the individuals at 60 °C for 2 weeks (Torn *et al.* 2010).

Statistical analyses

Repeated measures ANOVA (StatSoft Inc 2007) was used to compare the effect of different types of disturbance (levels: tips cut, plants removed, sediment mixed, sediment removed and control) on species number and biomass among different months (from July 2007 to July 2008). The Mauchly sphericity test was used to check the assumption of equality of variance. We used the following multivariate tests to seek the statistical significance of different types of experimental disturbance on vegetation biomass: Wilks' lambda, Pillai–Bartlett trace and Hotelling–Lawley trace tests. These tests were used as they do not make the strict, often unrealistic, assumptions about the structure of the covariance matrix. As all these tests resulted in similar significance levels, only the output of the Wilks' lambda test (as the most commonly used) was reported. A *post-hoc* Fisher LSD test was used to analyse which treatment levels were statistically different from each other.

Multivariate data analyses on plant and invertebrate communities were performed by the statistical program PRIMER version 6.1.5 (Clarke & Gorley 2006). Similarities between each pair of samples were calculated using a zero-adjusted Bray–Curtis coefficient. This coefficient is known to outperform most other similarity measures and enables samples containing no organisms at all to be included (Clarke *et al.* 2006). Non-metric multidimensional scaling analysis (MDS) was used to visualize the dissimilarities between treatments and times.

Results

The studied benthic invertebrate communities were characterized by a few taxa. The plots contained mainly the amphipods *Gammarus tigrinus*, *Gammarus salinus* Spooner, *Gammarus zaddachi* Sexton, *Gammarus oceanicus* Segerstråle, *Gammarus locusta* (Linnaeus), the isopod *Asellus aquaticus* (Linnaeus), the snails *Bithynia tentaculata*

(Linnaeus), *Hydrobia ulvae* (Pennant), *Lymnaea peregra* (Müller), *Theodoxus fluviatilis* (Linnaeus), the cockle *Cerastoderma glaucum* (Poiret) and larvae of Chironomidae, Coleoptera, Odonata and Trichoptera. *Gammarus tigrinus* was by far the most dominant herbivore species and constituted 98% of gammarid biomass, with moderate biomasses from June to September and high biomasses in October.

Mechanical disturbance affected the biomass of *G. tigrinus* with a 4-month time lag between disturbance and response of the gammarid species (Fig. 1, Table 1). Regardless of type, the disturbed communities had significantly lower gammarid biomasses than control communities in October 2007 (repeated measures ANOVA, *post-hoc* Fisher LSD test: control *versus* disturbed plots $P < 0.001$) and in July 2008 (repeated measures ANOVA, *post-hoc* Fisher LSD test: control *versus* disturbed plots $P = 0.023$ – 0.025 , except for control *versus* tips cut treatment $P = 0.071$).

Mechanical disturbance had no effect on the species number of benthic invertebrates and the biomasses of any other invertebrate species including juvenile gammarids (repeated measures ANOVA, separate disturbance effect and disturbance × time interaction $P > 0.05$) (Fig. 2).

The studied macrophyte communities contained mainly the charophyte *Chara aspera*, the chlorophytes *Cladophora glomerata* (L.) Kütz. and *Ulva intestinalis* L. and the higher plants *Najas marina* L. and *Potamogeton*

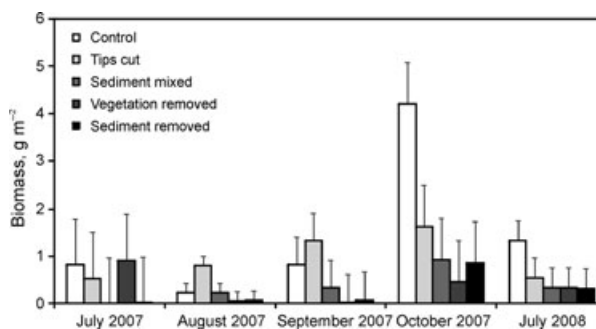


Fig. 1. Seasonal variation in average ($\pm 95\%$ CI) biomass of *Gammarus tigrinus* for the studied disturbance treatments in 2007–2008.

Table 1. Repeated measures ANOVA multivariate test of significance for the effect of disturbance on biomasses of *Gammarus tigrinus* in 2007–2008.

Effect	SS	Df	MS	F	P
Intercept	35.70	1	35.70	121.35	<0.001
Disturbance	16.44	4	4.11	13.98	<0.001
Error	2.94	10	0.29		
TIME	16.92	4	4.23	15.40	<0.001
TIME × disturbance	20.06	16	1.25	4.56	<0.001
Error	10.99	40	0.27		

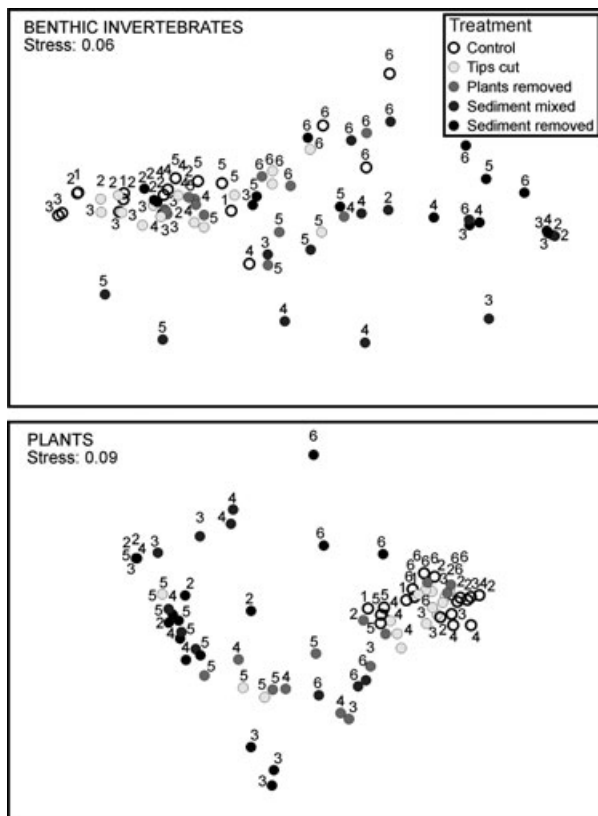


Fig. 2. Multidimensional scaling analysis (MDS) ordination of benthic invertebrate and macrophyte biomasses. Increasing distances between points denote larger dissimilarities among treatments and times. The time code is as follows: 1: June 2007, 2: July 2007, 3: August 2007, 4: September 2007, 5: October 2007, 6: July 2008.

pectinatus L. *Chara aspera* was by far the most dominant macrophyte species and constituted 96% of total plant biomass, with high biomasses from June to September and moderate biomasses in October.

Mechanical disturbance affected the biomass of *C. aspera* instantaneously and the effects persisted until the end of the experiment (Fig. 3, Table 2). Similarly to *G. tigrinus*, the disturbed communities had significantly lower biomasses compared with control communities. The disturbances associated with mechanical removal of vegetation or sediment had the largest impact on the charophyte community throughout the experiment (repeated measures ANOVA, *post-hoc* Fisher LSD test: control versus heavily disturbed plots $P < 0.001$). Disturbances that only partly damaged the plants had minor effects in 2007 and the communities had recovered by July 2008.

Mechanical disturbance also reduced the species number of macrophytes (Fig. 4, Table 3). In general, the disturbances associated with mechanical removal of vegetation or sediment had significantly lower species number compared with other treatments in 2007

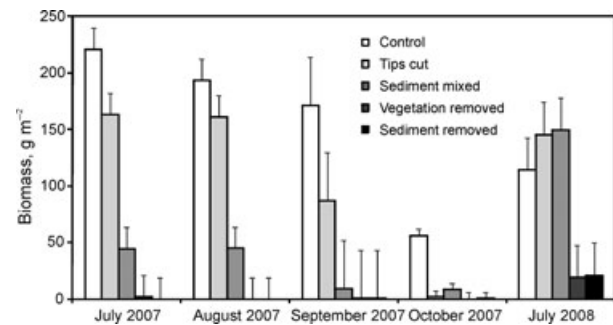


Fig. 3. Seasonal variation in average ($\pm 95\%$ CI) biomass of *Chara aspera* for the studied disturbance treatments in 2007–2008.

Table 2. Repeated measures ANOVA multivariate test of significance for the effect of disturbance on biomasses of *Chara aspera* in 2007–2008.

Effect	SS	Df	MS	F	P
Intercept	311,731	1	311,731	2081	<0.001
Disturbance	258,034	4	64,509	431	<0.001
Error	1498	10	150		
TIME	61,465	4	15,366	32	<0.001
TIME $\times$ Disturbance	89,820	16	5614	12	<0.001
Error	19,113	40	478		

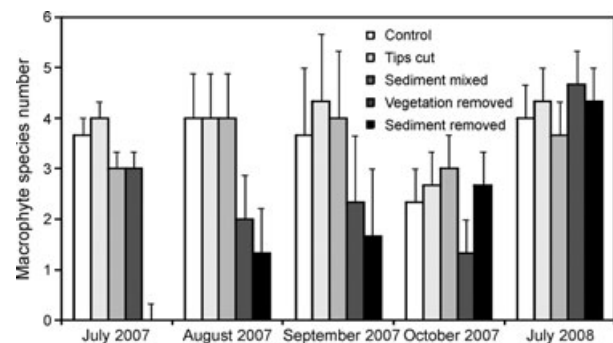


Fig. 4. Seasonal variation in average ($\pm 95\%$ CI) species number of macrophytes for the studied disturbance treatments in 2007–2008.

Table 3. Repeated measures ANOVA multivariate test of significance for the effect of disturbance on the species number of macrophytes in 2007–2008.

Effect	SS	Df	MS	F	P
Intercept	730.080	1	730.080	1479.892	<0.001
Disturbance	35.387	4	8.847	17.932	<0.001
Error	4.933	10	0.493		
TIME	27.653	4	6.913	16.862	<0.001
TIME $\times$ Disturbance	37.547	16	2.347	5.724	<0.001
Error	16.400	40	0.410		

(repeated measures ANOVA, *post-hoc* Fisher LSD test: control *versus* heavily disturbed plots $P < 0.05$). Macrophyte species number within the heavily disturbed plots had recovered by July 2008. Mechanical disturbance did not affect the biomasses of other macrophyte species (repeated measures ANOVA, separate disturbance effect and disturbance $\times$ time interaction $P > 0.05$; Fig. 2).

Discussion

We predicted that a moderate mechanical disturbance that leaves the charophyte community almost intact but at the same time significantly impoverishes native invertebrate communities, may increase the biomass of the non-native amphipod because the competitive interactions are relaxed. However, our experiment did not support this prediction, as the biomass of *Gammarus tigrinus* was significantly reduced under all of the different types of mechanical disturbance, whereas the native species were not affected. The result suggests that the dominance of *G. tigrinus* in our system has less to do with strong species interactions, such as competitive displacement, than with habitat-level processes, such as changes in habitat structural characteristics and food supply (e.g. Kotta *et al.* 2000, 2004, 2008b). Moreover, the experiment demonstrated that *G. tigrinus* constituted most of the benthic invertebrate biomass. This would indicate that it is unlikely that *G. tigrinus* is influenced by competition from the native fauna, as the native fauna is simply too sparse to have significant competitive interactions with *G. tigrinus*.

Although there is solid evidence that disturbance enhances the densities of non-native species both in terrestrial and aquatic ecosystems, the results are not fully consistent. The effects of disturbance are known to be scale-specific, with strong positive effects often associated at small spatial scales but not at larger scales (Thompson *et al.* 2001; Gross *et al.* 2005). At small spatial scales the disturbance opens space in the community, which is then quickly used by the opportunistic non-native and native species and consequently animal densities at the community level are increased. On the other hand, disturbance does not enhance the likelihood of a species to become dominant, as high disturbance probably wipes out any species including the opportunistic species. Such patterns can be explained by purely statistical processes using neutral models with no species-specific interactions involved (Herben 2009). However, the neutral model does not predict that the non-native species should prevail in the absence of disturbance.

The Northeastern Baltic Sea is a physically limited environment. Strong natural disturbances due to low salinity, temperature extremes and ice scrape have resulted in impoverished benthic communities, with

many native and alien species inhabiting the area at the edge of their tolerance limits (Kotta *et al.* 2008a). In such environments, competitive interactions are not expected to play a large role; rather, habitat characteristics should be responsible for shifts in the benthic communities. In our experiment the strong link between the biomass of *Chara aspera* and *G. tigrinus* suggests a strong affinity of non-native gammarids to pristine charophyte habitats. Nevertheless, none of the disturbance treatments had any significant effect on the biomass of native species and thus the expectation that the majority of native herbivores are sensitive to environmental stresses does not hold true. We may also argue that the resistance of native species is an inevitable consequence of natural selection, as only the fittest can cope with the permanent environmental stresses presented by the Baltic Sea environment (Herkül *et al.* 2006).

Macrophytes provide important habitat and food resources for a variety of associated mobile animals. This is consistent with our study (and our second hypothesis) in which dense charophyte communities supported high biomasses of the non-native gammarid species. It is generally believed that mobile herbivores respond more strongly to the amount of available resources than the diversity of plants providing it (Parker *et al.* 2001; Christie *et al.* 2009), suggesting that mesoherbivores often have a broad diet and selectivity is rare (Cruz-Rivera & Hay 2001). The results of our experiment also hint that the gammarid amphipods are generalist foragers, as high densities of *G. tigrinus* did not match with macrophyte species number but rather to the biomass of *C. aspera*. It is plausible that besides food value, dense charophyte communities support high structural complexity and thus provide better value as a refuge from predators (Orav-Kotta & Kotta 2004; Kinzler & Mayer 2006; Christie *et al.* 2009).

Most aquatic macrophytes are seasonal, providing habitats of limited duration (Pihl *et al.* 1996; Kiirikki & Lehvo 1997), whereas species of gammarid amphipods have a lifespan of approximately up to 3 years (e.g. Wilhelm & Schindler 1996). Gammarids may therefore show a preference for macrophytes with higher longevity, such as charophytes, over ephemeral algae. However, due to the poor nutritional value of charophytes, grazers often just live within their bushes and feed on the epiphytes attached to the host plant (Coops & Doef 1996; Kotta *et al.* 2004). The low levels of herbivory are also related to the unpalatability or resistance of the algae. According to Hunter (1976), fresh *Chara* are heavily calcified, which may greatly reduce their appeal to herbivores. In the course of decomposition the cell walls of the algae become less resistant to herbivory and the concentration of nutrients increases in the decomposing material as a result of increased microbial activity (Hunter 1976; Buchsbaum

et al. 1991). As a consequence, the charophytes may occasionally become more attractive to benthic invertebrates, especially in the late autumn months, when gammarids are known to consume a significant number of charophytes (Van den Berg 1999; Noordhuis *et al.* 2002; Kotta *et al.* 2004). By October, the density of filamentous algae had notably declined in the study area. The abundant population of *G. tigrinus* that had relied on these algae was forced to switch to an alternative diet. Compared with other macroalgae in the area, the decomposing charophytes seemed to be the most rewarding food for gammarid amphipods. Thus, high aggregation of *G. tigrinus* within the *Chara* stands in October may be explained by high mobility of *G. tigrinus*, ensuring high dispersal out of macrophyte beds and quick utilization of rewarding habitats (e.g. Jørgensen & Christie 2003; Salovius *et al.* 2005). Mechanical disturbance resulted in lower gammarid biomasses but such stress affected only the qualities of adult habitats, whereas effects on juveniles were not found. The statistical differences in the gammarid biomasses between disturbed and undisturbed plots in October may be explained partly as a statistical sampling effect, as it corresponds with the peak biomass of *G. tigrinus*.

However, *G. tigrinus* retained elevated biomasses within undisturbed charophyte communities in July 2008, a year after the disturbance. Although the communities of *C. aspera* have recovered from moderate disturbances (i.e., levels: tips cut, sediment mixed), *G. tigrinus* had a systematically lower biomass in disturbed communities than in control treatment and the biomasses did not vary among disturbance levels. Thus, a high biomass of charophytes does not necessarily ensure that it will be colonized by a high number of *G. tigrinus*. Instead, the availability of resources and/or structural properties of charophytes may better explain the recovery of gammarid amphipods in the disturbed charophyte habitat. Repeated measures ANOVA analysis showed that mechanical disturbance had no effect on the algal resource availability, as assessed by a ratio of the biomass of macroalgae to the biomass of *G. tigrinus* (repeated measures ANOVA, separate disturbance effect and disturbance $\times$ time interaction $P > 0.05$). In the light of this evidence, the lack of recovery of gammarid amphipods a year after the disturbance hints that the three-dimensional structure of charophyte canopy rather than absolute or relative algal quantity determines the patterns of *G. tigrinus* in the studied habitat.

Conclusions

To conclude, mechanical disturbance affected the biomass of *Gammarus tigrinus* but with a significant time lag, possibly reflecting the seasonal dynamics of the gammarid amphipods and macroalgae. In general, the disturbed

communities had significantly lower gammarid biomasses than control communities throughout the experiment. A possible cause of reduced biomass of the gammarid amphipods relates to the decreased biomass of *C. aspera* and its structural changes but not to the diversity of macrophyte communities and the biomasses of macrophyte and benthic invertebrate species. Thus, the dominance of *G. tigrinus* in our system has less to do with strong species interactions, such as competitive displacement, than with habitat-level processes, such as changes in habitat structural characteristics and food supply.

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