

Flexible microhabitat partitioning between hemi-sessile congeners

Jan Beermann^{1,*}, Karin Boos²

¹Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Biologische Anstalt Helgoland, PO Box 180, 27483 Helgoland, Germany

²MARUM – Center for Marine Environmental Sciences, University of Bremen, Leobener Strasse, 28359 Bremen, Germany

ABSTRACT: Microhabitat partitioning is a widespread mechanism that reduces competition and thus facilitates the coexistence of species. The extent to which microhabitat partitioning occurs depends on a variety of environmental parameters and biotic interactions. In the present study, we manipulated factors (animal density, presence of heterospecifics, and presence of predator cues) that potentially influence the differential use of microhabitats by 2 hemi-sessile congeners that coexist on small spatial scales at very high densities: the amphipod crustaceans *Jassa marmorata* and *J. herdmani*. In both species, the presence of heterospecifics had a clear effect on which part of an offered macroalga was preferably colonized, suggesting that the extent of microhabitat partitioning depends on the presence/absence of heterospecifics. Furthermore, 'predatory fish cues' in the seawater induced an avoidance behaviour, which should reduce the extent of habitat partitioning and inevitably increase competition between the species. The results clearly show some flexibility of habitat selection in, and thus habitat segregation between, the studied species, allowing for a trade-off between interspecific competition and predation pressure.

KEY WORDS: Amphipoda · Coexisting species · Interspecific competition · Intraguild interference · Marine fouling · Microhabitat partitioning · Predator avoidance

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

In addition to non-equilibrium mechanisms of coexistence (Connell 1978, Wilson 1990, 1994, Roxburgh et al. 2004), the reduction of competition by partitioning of resources ranks among the classic explanations for the coexistence of species (Schoener 1974, 1986). Spatial segregation and especially microhabitat partitioning has been observed for a broad range of ecologically similar species coexisting in the same habitats, e.g. birds (Barnes & Nudds 1990) and their parasites (Choe & Kim 1989), fish (Ebersole 1985, Davis 2000), insects (Nummelin et al. 1984), echinoderms (Sloan 1979), and trees (Clark et al. 1993). In addition, microhabitat partitioning can occur even within a single species, reducing competition or even cannibalism among different develop-

mental stages (Nummelin et al. 1984, Davis 2000). Although it is commonly assumed that microhabitat partitioning facilitates a stable coexistence of species, the phenomenon cannot be generalized (Jørgensen 2004).

Particular habitat preferences of a species are supposed to be adaptive, reflecting the species' higher evolutionary fitness in the preferred microhabitat (Martin 1998). Nonetheless, the differential distribution of species in distinct habitats does not necessarily imply an active selection behaviour but can also be due to habitat-specific recruitment success and/or mortality rates (Crowe & Underwood 1998). An active (behavioural) microhabitat partitioning can occur in the absence of competition (Barnes & Nudds 1990), can be induced by interaction with sympatric congeners (Choe & Kim 1989), or both (Ebersole

1985). Microhabitat partitioning is an evolutionary response to exploitative competition, intraguild interference, or intraguild predation, although the degree of its actual manifestation may depend on habitat structure and predation risk (Brown & Moyle 1991, Polis & Holt 1992, Hughes et al. 1994, Holt & Polis 1997, Arim & Marquet 2004, Janssen et al. 2007). A species' fitness in a specific microhabitat depends on environmental conditions, which are often subject to short-term changes. This implies that some flexibility in habitat selection should be favoured by evolutionary history.

Littoral amphipod crustacean species are ideal for testing the factors driving species coexistence because they often occur in dense heterogeneous assemblages. This is especially the case in suspension-feeding amphipods where several species coexist within the same habitat. Species of the genus *Jassa* Leach inhabit self-constructed tubes made of amphipod silk and deliberately incorporated detritus (Dixon & Moore 1997, Kronenberger et al. 2012). Individuals sit at their tube's openings and extend their prolonged antennae into the water column for unselective filter-feeding. The tubes are attached to nearly any kind of hard substratum, and multiple layers of tubes can form thick fouling mats with hundreds of thousands of individuals per m² (Franz 1989, Dixon & Moore 1997, Zintzen et al. 2008). The animals can be classified as hemi-sessile as they are able to escape from their tubes if disturbed or evicted by competitively superior conspecifics. Competitively inferior individuals, such as juveniles and small adults, leave their native habitat and disperse, thus reducing intraguild interference and promoting the colonization of new habitats, where they quickly settle and build new tubes (Franz & Mohamed 1989, Havermans et al. 2007). In addition, several *Jassa* species coexist in high densities. This coexistence may be corroborated by some degree of ecological differentiation with respect to microhabitat utilization and life-history traits (Beermann & Franke 2012, Beermann & Purz 2013).

In the present paper, we studied the behavioural patterns associated with microhabitat partitioning in the 2 congeneric species *Jassa marmorata* Holmes, 1903 and *Jassa herdmani* (Walker, 1893), which coexist in marine fouling communities at the island of Helgoland (German Bight, North Sea) on a broad range of hard substrata. As the species can form dense tube aggregations with up to 1000 adult individuals per 100 cm² (Beermann 2014), we hypothesized that habitat partitioning is not affected by density (intraspecific effect) but is modified by direct

interference with heterospecifics (interspecific effect) as well as by the simulated presence of potential predators (predator avoidance). For this purpose, the microhabitat selection of the 2 congeners was tested in simple experimental set-ups in the laboratory.

MATERIALS AND METHODS

Animal collection and maintenance

Live specimens of *Jassa marmorata* and *J. herdmani* of the same size class (7.5 ± 0.5 mm body length) were collected in the field from navigational aids and harbour walls in the South Harbour of Helgoland in late summer 2012. The animals were kept in several plastic containers (20 × 20 × 6 cm) under constant laboratory conditions: 13°C water temperature, 12 h light:12 h dark, daily change of seawater, daily feeding with *Artemia*-nauplii and powder of dried *Ulva* thalli (oven-dried at 50°C for 5 h). All experiments were performed only with female individuals because behavioural responses largely relate to females, whereas the much more active males in natural situations follow females, seeking places where they can expect to encounter receptive individuals (Beermann & Franke 2012). Only specimens larger than 6 mm body length were used in the experiments because live specimens of smaller size cannot be safely determined to species level (for further details, see Conlan 1990, Beermann & Franke 2011). After 48 h under the above conditions, the animals were tested in different experimental set-ups described below. Each individual was used only once.

Experimental set-up

In all experiments, we used thalli of the green macroalga *Cladophora rupestris* (Linnaeus) Kützing 1843 as a substratum for settlement, thereby following the procedure of Beermann & Franke (2012). This filamentous algal species was chosen because it hosts *Jassa* species in the field and because its thalli survive detachment from the natural substratum for a long time in the laboratory. A preceding cleaning procedure made sure that the thalli were free of other organisms (e.g. small crustaceans, epibiotic algae). In different experimental set-ups, the amphipods were introduced into flat plastic containers (10 × 10 cm), each supplied with a centrally fixed algal thallus. After 24 h in the set-ups, allowing the

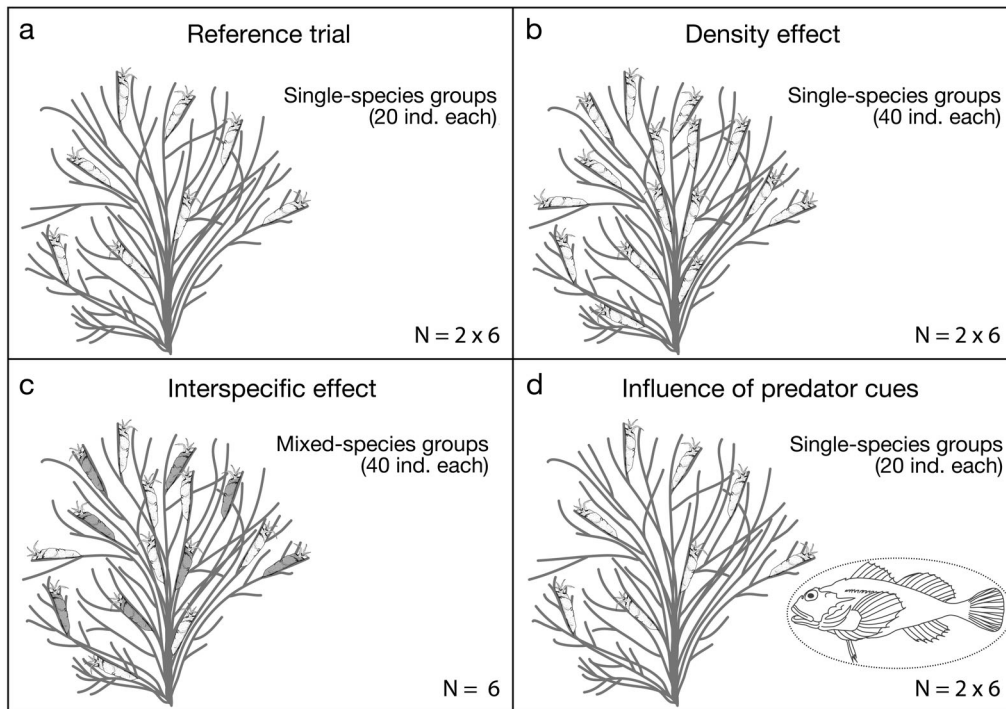


Fig. 1. Experimental set-ups for the study of microhabitat selection in *Jassa marmorata* and *J. herdmani*: (a) single-species reference set-up (low density), (b) single-species set-up with high animal density, (c) mixed species set-up (20 *J. marmorata* + 20 *J. herdmani*), (d) set-up identical to the reference trial, except for the presence of 'fish cues' in the seawater

amphipods to settle and build tubes, all individuals were checked for their local position and counted without manipulating or removing the thalli from the containers. Three different areas were distinguished for the evaluation: the peripheral area of the algal thallus (individual on or closely beneath the distal branches of the alga and thus visible to the observer), the central area of the algal thallus (individual completely hidden among the branches of the thallus and not visible from the outside), and the remaining area (individual not associated with the algal thallus). The different volumes of the microhabitat areas were considered as not influential because individuals in the field can occur in much higher densities (nearly 10-fold higher) in habitats described herein as 'central' and 'peripheral' areas of the algae.

The 2 species' microhabitat selection behaviour was studied for a reference situation and subsequently tested for density effects, interspecific effects, and the influence of 'predator cues', according to the following experimental set-ups which were run in parallel: (a) single-species trial with 20 individuals (reference trial; Fig. 1a); (b) single-species trial with 40 individuals (density effect; Fig. 1b); (c) mixed-species trial with 20 individuals of *J. marmorata* and 20 individuals of *J. herdmani* combined

(interspecific effect; Fig. 1c); and (d) single-species trial with 20 individuals of each species in incubated seawater (influence of predator cues; Fig. 1d). For the latter set-up, instead of filtered natural seawater, we used seawater from an aquarium (60 × 40 × 55 cm; running seawater system) which was inhabited by 5 specimens (ca. 10 cm body length) of the sea scorpion *Taurulus bubalis* (Euphrasen 1786), a common benthic predator of amphipods around Helgoland. The fish were kept in a tank with a constant flow of aerated seawater and were fed every second day with live specimens of the amphipods *Echinogammarus marinus* (Leach 1815) and *Gammarus locusta* (Linnaeus 1758). Six replicates were run per species for each experimental set-up.

Statistical analyses

The counted numbers of individuals were analysed in relation to different combinations of the fixed-effects factors 'area' (3 levels: central, peripheral, not on alga), 'species' (2 levels: *J. marmorata*, *J. herdmani*), 'density' (2 levels: low density, high density), 'composition' (2 levels: single-species trial, mixed-species trial), and/or 'water quality' (2 levels: clean,

incubated). In the analysis, we applied generalized linear mixed models (GLMM) with Poisson error structure and log-link function. The models were built in the following way: for the evaluation of microhabitat selection under the defined reference conditions (single species, low density), the counts were modelled as a function of species and area, including their interaction. For a density effect on the microhabitat selection, the counts of the 2 single-species set-ups (clean seawater) were modelled as a function of species, area, and density, including all possible interactions. An interspecific effect was evaluated by modelling the counts of both high-density set-ups as a function of species, area, and group composition which included all possible interactions. To evaluate an effect of predator cues, the counts of the 2 low-density trials were modelled as a function of species, area, and water quality including all possible interactions. The outcomes for the interactions of highest orders were of particular interest as they effectively allow for revealing possible effects of species identity, animal density, group composition, and/or water quality on the microhabitat selection. As a result of the microhabitat selection process in all experimental set-ups, we took the dependent nature of the data into account in all models by including the replicated trials as a random effects factor, thereby considering the grouped nature of the data within each replicate.

Due to occasional deaths in the course of the experiments, the number of individuals that had actively selected a specific area varied slightly at the end of each trial. Dead individuals were excluded from the analysis, and the subsequent imbalance in numbers was considered by including an offset term in the models. The offset variable comprised the total number of live individuals recorded at the end of each experiment. With respect to the log-link function in the Poisson models, the logarithm of the number of live animals was used as the offset term. The inclusion of the offset term also considered the imbalance of numbers of individuals per species when testing for a density effect (20 vs. 40 individuals of the same species per container) and for an interspecific effect (40 single-species individuals vs. 20 individuals of the same species in presence of 20 heterospecifics). Therefore, possible interfering effects of the factors 'density' and 'composition' were eliminated by the offset term, which considered the total number of live individuals per species and experiment.

All models were fitted in R (v. 2.14.0; R Development Core Team 2011) using the function 'glmer' from the R package 'lme4' (Bates et al. 2011). To confirm the assumptions of equally distributed residuals

and homogeneous variances, histograms, qqplots, and the residuals plotted against the fitted values were visually inspected (Quinn & Keough 2002). Neither of them indicated severe deviations from the assumptions, and slight irregularities in the patterns were considered negligible.

Overdispersion was checked in each model by comparing the residual deviance with the residual degree of freedom. Within the dataset used for testing for a density effect, overdispersion was a potential issue ($\chi^2 = 87.7$, $df = 60$, $p = 0.011$). However, the dispersion parameter of 1.462 was considered to be within an acceptable range (consensus: 0.8 to 1.6; R. Mundry pers. comm.).

To establish the significances of individual terms (i.e. the interaction terms), likelihood ratio tests (LRT; R function 'anova' with argument 'test' set to 'Chisq') were used to compare the deviances of the full models with those of the corresponding models not comprising the respective term of interest.

RESULTS

Reference trial

In the reference set-up with single-species groups of 20 females each, a significant interaction of the factors 'species' and 'area' was detected ($LRT_{\text{species:area}}: \chi^2 = 53.376$, $df = 2$, $p < 0.0001$). Both species preferred the algae over the remaining parts of the container, but females of *Jassa marmorata* were equally distributed over central and peripheral parts of the algae ($p = 0.442$), whereas females of *J. herdmani* were significantly more abundant in the peripheral than in the central parts of the thalli ($p < 0.0001$, Fig. 2a). The comparison between the species showed that *J. marmorata* settled more frequently in the central parts than *J. herdmani* ($p < 0.0001$), and *J. herdmani* chose the peripheral parts more often than *J. marmorata* ($p < 0.0001$). No differences between the species were found for the number of individuals having settled elsewhere in the container ($p = 0.4038$).

Density effect

The direct comparison of high density trials with the reference experiment revealed a non-significant 3-way interaction ($LRT_{\text{species:area:density}}: \chi^2 = 3.900$, $df = 2$, $p = 0.142$). This result indicates that microhabitat selection was unaffected by increased group sizes in both *J. marmorata* and *J. herdmani*. However, pairwise com-

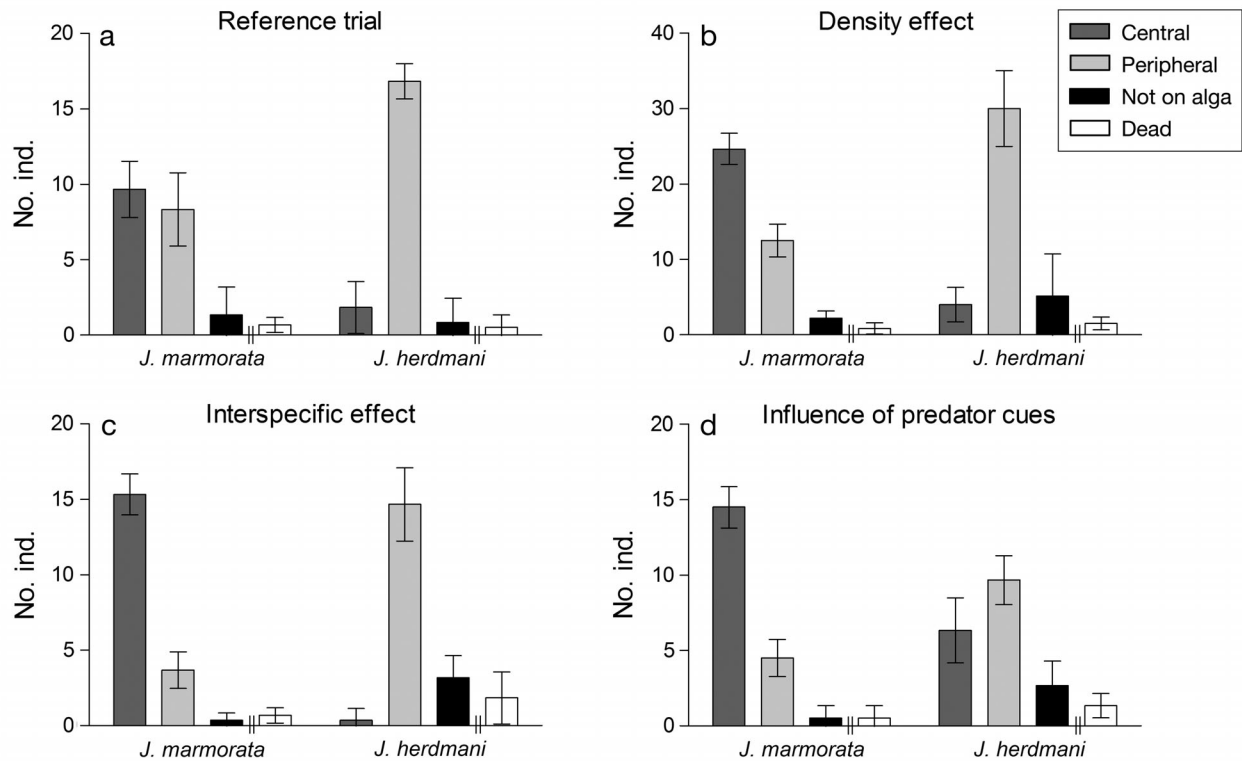


Fig. 2. Spatial distribution of female *Jassa marmorata* and *J. herdmani* on a macroalga (*Cladophora rupestris*) in different experimental set-ups: (a) densities of 20 individuals per species, (b) densities of 40 individuals per species, (c) mixed-species groups at densities of each 20 conspecific together with 20 heterospecific individuals (40 individuals in total), (d) densities of 20 individuals per species, being subjected to incubated seawater which contained fish cues of the sea scorpion *Taurulus bubalis*. Presented data include the number of deceased individuals for informational and graphical reasons, although these individuals were not part of the analyses (see 'Statistical analyses' for details); means \pm SD (each N = 6)

parisons of groups revealed some slight differences in distributional patterns for *J. marmorata*. At high densities, individuals of *J. marmorata* settled significantly more often in the central parts than at the peripheral parts of the algal thalli ($p < 0.0001$; Fig. 2b), whereas no significant difference was found at low densities (see reference trial above). In the statistical analysis, this detected change in the observed spatial distribution was not powerful enough to result in an overall significant density effect.

Interspecific effect

The comparisons of the animals' behaviour in mixed- vs. single-species set-ups at high densities showed a significant 3-way interaction ($LRT_{\text{species:area:composition}}: \chi^2 = 18.773$, $df = 2$, $p < 0.0001$). When confronted with *J. herdmani* and in comparison to the single-species trials, individuals of *J. marmorata* were found less often in the peripheral parts ($p = 0.0333$, Fig. 2c) and more often (although statistically

not significant: $p = 0.0769$) in the central parts of the alga. Individuals of *J. herdmani* in turn were found less often in the central parts ($p = 0.0197$) but settled more frequently at locations elsewhere in the container than in the central parts of the algal thallus ($p = 0.0025$). This particular difference was not observed in the single-species treatment. In both species, the overall preferences of settling in the central parts (*J. marmorata*) or in the peripheral parts (*J. herdmani*) remained the same in the presence of the respective heterospecific.

Influence of predator cues

The analysis of the animals' behaviour in clean seawater vs. a medium which contained 'predator cues' of *Taurulus bubalis* revealed a significant 3-way interaction ($LRT_{\text{species:area:water quality}}: \chi^2 = 7.228$, $df = 2$, $p = 0.027$). In direct comparison to the reference trials, *J. marmorata* settled more often in the central parts of the thallus ($p = 0.0192$) and less often in the

peripheral parts ($p = 0.0089$, Fig. 2d) when subjected to incubated seawater. No difference was detected between the numbers of individuals that were not found on algae ($p = 0.144$). The same pattern was found for *J. herdmani*, which settled more frequently in the central parts and less frequently in the peripheral parts of the algal thallus ($p = 0.0002$ and $p = 0.0019$, respectively) than in the reference experiment. In addition, clearly more individuals of *J. herdmani* settled elsewhere in the container ($p = 0.0185$). However, individuals of *J. herdmani* in the incubated seawater still preferred the peripheral parts over the central parts of the alga ($p = 0.0428$).

DISCUSSION

There are several examples of closely related amphipod species that co-occur on small spatial scales (e.g. Fenchel & Kolding 1979, Skadsheim 1983, Lancellotti & Trucco 1993, Huang et al. 2007). A stable co-occurrence requires physiological, morphological, or/and behavioural trade-offs among competing species (Tilman 1987). *Jassa* species are hemi-sessile filter feeders. In densely crowded fouling communities, these species compete primarily for space as a limited resource. Hence, spatial segregation probably acts as a form of resource partitioning, reducing interspecific competition and thus facilitating a stable coexistence (Connell 1983, Schoener 1983, 1986). In our reference trial, female *J. marmorata* used both the peripheral and the central parts of the algal thallus, whereas female *J. herdmani* were restricted to the peripheral parts. This is in accordance with the findings of Beermann & Franke (2012) and most likely represents a form of microhabitat partitioning. As *Jassa* males are in intense competition with other males for receptive females, seeking the vicinity of the females' tubes most likely increases the chances for reproductive success. The observed patterns in female groups (present study) were similar to those in the mixed-sex groups tested by Beermann & Franke (2012). In accordance with the findings for isolated individuals in the latter study, this result confirms the assumption that the positioning of *Jassa* females also determines the spatial distribution of conspecific males.

Altered microhabitat utilization

At an increased density, the pattern observed for *J. marmorata* slightly changed in favour of the

central algal parts, whereas *J. herdmani* remained unaffected. When the 2 congeners were confronted with each other in the mixed-species trial, there was a clear interspecific effect: the distribution of both *J. marmorata* and *J. herdmani* was more strongly affected by the presence of heterospecific than by conspecific individuals. When individuals of *J. marmorata* encountered those of *J. herdmani*, they scarcely settled in peripheral parts. *J. herdmani*, in turn, avoided central algae parts but started building tubes elsewhere in the container. This obvious reinforcement of the microhabitat partitioning between the 2 species may be supported by the differential escaping behaviours observed in *J. marmorata* and *J. herdmani* in response to mechanical disturbance: *J. marmorata* seeks shelter among the branches of an algal thallus, whereas *J. herdmani* swims away (Beermann & Franke 2012). Direct interference between the 2 species in the peripheral parts of the thallus thus may be expected to result in a displacement of individuals of *J. marmorata* from the peripheral to the central parts for settlement, whereas *J. herdmani* typically would swim away and settle again in the peripheral parts or elsewhere in the experimental container.

The present results indicate quantitative changes in microhabitat selection as a response to the presence of interspecific competitors, even if animal densities are relatively low. In the field, i.e. at much higher densities (Beermann 2014), the described behavioural responses may thereby contribute significantly to a small-scale spatial segregation of the studied *Jassa* species. However, the comparatively low animal densities in the current experiments may have reduced competition among individuals. Thus, an occurrence of strong intraspecific and/or further interspecific effects under field conditions cannot be excluded.

Predator avoidance behaviour

In addition to competition effects, the presence of waterborne chemical cues clearly influenced the microhabitat selection of *J. marmorata* and *J. herdmani*. In the presence of 'fish cues' in the seawater, *J. marmorata* strongly avoided peripheral algal parts and concentrated on the central areas. In contrast to their clear preference of the peripheral parts in filtered natural seawater, individuals of *J. herdmani* also settled more often in central parts of the algal thalli when subjected to incubated seawater.

Thus, both species showed a clear response to a probable presence of a predator by seeking shelter for settlement.

Predator avoidance behaviours have commonly been observed among aquatic invertebrates such as gastropods (McCarthy & Fisher 2000, Turner & Montgomery 2003, Jacobsen & Stabell 2004) and crustaceans (Main 1987, Holomuzki & Short 1988, Lindén et al. 2003, Zamzow et al. 2010). Also, amphipods have been demonstrated to avoid predatory fish species by altering their behaviour in response to waterborne 'fish cues' (kairomones). However, most studies have dealt with freshwater *Gammarus* species (e.g. Andersson et al. 1986, Holomuzki & Hoyle 1990, Wudkevich et al. 1997, Penuto & Keppler 2008), whereas only few investigations have observed direct predator avoidance (e.g. Zamzow et al. 2010) or responsive behaviours (e.g. Reynolds & Bruno 2013) in amphipod species in marine environments. The modes of avoidance behaviours may depend on different environmental parameters, such as sediment quality (Baumgärtner et al. 2003), and may change as a result of habituation to the stimulus (Holomuzki & Hatchett 1994). Furthermore, cues released by wounded conspecifics can induce avoidance behaviours as well (Wudkevich et al. 1997, Wisenden et al. 2001). All these possible influences on *Jassa* settlement behaviour must be considered thoroughly in future surveys.

Our results represent the first evidence of a predator-avoidance behaviour in tube-building amphipod communities. This behaviour must be taken into account when assessing the spatial distribution of *Jassa* individuals in the field because aggregation at 'safer' areas could come along with changes in competitive relationships among the congeners (Holt 1984) and with reduced access to food (Scheffer 1997), especially in filter feeders. Further predator cue experiments on *Jassa* spp. need to clarify the situation for mixed-species trials and identify how this may depend on the density and/or numerical ratio of species. Possible outcomes may also depend on the species identity of the provided algal thalli. Small marine herbivores have been shown to select for chemically defended algae species, reducing the risk of fish predation (Hay et al. 1988, 1990, Duffy & Hay 1994). Although *Jassa* species are filter feeders, the 2 species could differ in their respective habitat preferences or may display differential resource utilisation when settling on chemically more or less defended algae species.

CONCLUSIONS

The small-scale spatial segregation of the coexisting amphipods *Jassa marmorata* and *J. herdmani* on complex structures such as algal thalli contributes significantly to a partitioning of space—an important limiting resource in fouling communities—and, thus, a reduction in interspecific competition and/or intra-guild predation between the species. Both studied species showed some flexibility in their habitat utilisation, responding to the presence of interspecific competitors as well as to potential predators. The predator-avoidance behaviour of the 2 species (settling in the central parts of algal thalli) probably results in an increase in interference competition. Flexible habitat selection thus may be considered a trade-off between a number of parameters such as competition and predation pressure, allowing for fitness-maximizing adaptations to changing environmental conditions.

Acknowledgements. We thank the crew of the RV 'Aade' for their help in the field and colleagues Heinz-Dieter Franke (Helgoland, Germany), Martin Thiel (Coquimbo, Chile) and Roger Mundry (Leipzig, Germany) for valuable comments and suggestions. J.B. was financially supported by a scholarship of the Free University of Berlin (Elsa-Neumann-Stipendium of the Federal State of Berlin). Furthermore, we are grateful to 3 anonymous reviewers for constructive comments on the manuscript.

LITERATURE CITED

- Andersson KG, Brönmark C, Herrmann J, Malmqvist B, Otto C, Sjöström P (1986) Presence of sculpins (*Cottus gobio*) reduces drift and activity of *Gammarus pulex* (Amphipoda). *Hydrobiologia* 133:209–215
- Arim M, Marquet A (2004) Intra-guild predation: a widespread interaction related to species biology. *Ecol Lett* 7: 557–564
- Barnes GG, Nudds TD (1990) Temporal variation in microhabitat relationships among grebes and coots. *Wilson Bull* 102:99–108
- Bates D, Maechler M, Bolker B (2011) lme4: linear mixed-effects models using S4 classes. R package version 0999375-42, <http://CRAN.R-project.org/package=lme4>
- Baumgärtner D, Koch U, Rothaupt KO (2003) Alteration of kairomone-induced antipredator response of the freshwater amphipod *Gammarus roeseli* by habitat. *J Chem Ecol* 29:1391–1401
- Beermann J (2014) Spatial and seasonal population dynamics of sympatric *Jassa* species (Crustacea, Amphipoda). *J Exp Mar Biol Ecol* 459:8–16
- Beermann J, Franke HD (2011) A supplement to the amphipod (Crustacea) species inventory of Helgoland (German Bight, North Sea): indication of rapid recent change. *Mar Biodivers Rec* 4(e41):1–15
- Beermann J, Franke HD (2012) Differences in resource utilization and behaviour between coexisting *Jassa* species

- (Crustacea, Amphipoda). *Mar Biol* 159:951–957
- Beermann J, Purz AK (2013) Comparison of life history parameters in coexisting species of the genus *Jassa* (Amphipoda, Ischyroceridae). *J Crustac Biol* 33:784–792
- Brown LR, Moyle PB (1991) Changes in habitat and microhabitat partitioning within an assemblage of stream fishes in response to predation by Sacramento squawfish (*Ptychocheilus grandis*). *Can J Fish Aquat Sci* 48:849–856
- Choe JC, Kim KC (1989) Microhabitat selection and coexistence in feather mites (Acari: Analgoidea) on Alaskan seabirds. *Oecologia* 79:10–14
- Clark DB, Clark DA, Rich PM (1993) Comparative analysis of microhabitat utilization by saplings of nine tree species in neotropical rain forest. *Biotropica* 25:397–407
- Conlan KE (1990) Revision of the crustacean amphipod genus *Jassa* Leach (Corophioidea: Ischyroceridae). *Can J Zool* 68:2031–2075
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat* 122:661–696
- Crowe TP, Underwood AJ (1998) Testing behavioural 'preference' for suitable microhabitat. *J Exp Mar Biol Ecol* 225:1–11
- Davis JLD (2000) Spatial and seasonal patterns of habitat partitioning in a guild of southern California tidepool fishes. *Mar Ecol Prog Ser* 196:253–268
- Dixon IMT, Moore PG (1997) A comparative study on the tubes and feeding behaviour of eight species of corophioid Amphipoda and their bearing on phylogenetic relationships within the Corophioidea. *Philos Trans R Soc Lond B* 352:93–112
- Duffy JE, Hay ME (1994) Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. *Ecology* 75:1304–1319
- Ebersole JP (1985) Niche separation of two damselfish species by aggression and differential microhabitat utilization. *Ecology* 66:14–20
- Fenchel TM, Kolding S (1979) Habitat selection and distribution patterns of five species of the amphipod genus *Gammarus*. *Oikos* 33:316–322
- Franz DR (1989) Population density and demography of a fouling community amphipod. *J Exp Mar Biol Ecol* 125: 117–136
- Franz DR, Mohamed Y (1989) Short-distance dispersal in a fouling community amphipod crustacean, *Jassa marmorata* Holmes. *J Exp Mar Biol Ecol* 133:1–13
- Havermans C, De Broyer C, Mallefet J, Zintzen V (2007) Dispersal mechanisms in amphipods: a case study of *Jassa herdmani* (Crustacea, Amphipoda) in the North Sea. *Mar Biol* 153:83–89
- Hay ME, Renaud PE, Fenical W (1988) Large mobile versus small sedentary herbivores and their resistance to seaweed chemical defenses. *Oecologia* 75:246–252
- Hay ME, Duffy JE, Fenical W (1990) Host-plant specialization decreases predation on a marine amphipod: an herbivore in plant's clothing. *Ecology* 71:733–743
- Holomuzki JR, Hatcher LA (1994) Predator avoidance costs and habituation to fish chemicals by a stream isopod. *Freshw Biol* 32:585–592
- Holomuzki JR, Hoyle JD (1990) Effect of predatory fish presence on habitat use and diel movement of the stream amphipod, *Gammarus minus*. *Freshw Biol* 24:509–517
- Holomuzki JR, Short TM (1988) Habitat use and fish avoidance behaviors by the stream-dwelling isopod *Lirceus fontinalis*. *Oikos* 52:79–86
- Holt RD (1984) Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am Nat* 124: 377–406
- Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. *Am Nat* 149:745–764
- Huang YM, Amsler MO, McClintock JB, Amsler CD, Baker BJ (2007) Patterns of gammaridean amphipod abundance and species composition associated with dominant subtidal macroalgae from the western Antarctic Peninsula. *Polar Biol* 30:1417–1430
- Hughes JA, Ward D, Perrin MR (1994) Predation risk and competition affect habitat selection and activity of Namib Desert gerbils. *Ecology* 75:1397–1405
- Jacobsen HP, Stabell OB (2004) Antipredator behaviour mediated by chemical cues: the role of conspecific alarm signalling and predator labelling in the avoidance response of a marine gastropod. *Oikos* 104:43–50
- Janssen A, Sabelis MW, Magalhães S, Montserrat M, van der Hammen T (2007) Habitat structure affects intraguild predation. *Ecology* 88:2713–2719
- Jorgensen EE (2004) Small mammal use of microhabitat reviewed. *J Mammal* 85:531–539
- Kronenberger K, Moore PG, Halcrow K, Vollrath F (2012) Spinning a marine silk for the purpose of tube-building. *J Crustac Biol* 32:191–202
- Lancellotti DA, Trucco RG (1993) Distribution patterns and coexistence of six species of the amphipod genus *Hyale*. *Mar Ecol Prog Ser* 93:131–141
- Lindén E, Lehtiniemi M, Viitasalo M (2003) Predator avoidance behaviour of Baltic littoral mysids *Neomysis integer* and *Praunus flexuosus*. *Mar Biol* 143:845–850
- Main KL (1987) Predator avoidance in seagrass meadows: prey behavior, microhabitat selection, and cryptic coloration. *Ecology* 68:170–180
- Martin TE (1998) Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* 79: 656–670
- McCarthy TM, Fisher WA (2000) Multiple predator-avoidance behaviours of the freshwater snail *Physella heterostropha pomila*: responses vary with risk. *Freshw Biol* 44: 387–397
- Nummelin M, Vepsäläinen K, Spence JR (1984) Habitat partitioning among developmental stages of waterstriders (Heteroptera: Gerridae). *Oikos* 42:267–275
- Pennuto C, Keppler D (2008) Short-term predator avoidance behavior by invasive and native amphipods in the Great Lakes. *Aquat Ecol* 42:629–641
- Polis GA, Holt RD (1992) Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol Evol* 7: 151–154
- Quinn GGP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org
- Reynolds PL, Bruno JF (2013) Multiple predator species alter prey behavior, population growth, and a trophic cascade in a model estuarine food web. *Ecol Monogr* 83:119–132
- Roxburgh SH, Shea K, Wilson JB (2004) The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* 85:359–371
- Scheffer M (1997) On the implications of predator avoidance.

- Aquat Ecol 31:99–107
- Schoener TW (1974) Resource partitioning in ecological communities. *Science* 185:27–39
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Schoener TW (1986) Resource partitioning. In: Kikkawa J, Anderson DK (eds) *Community ecology: patterns and process*. Blackwell Scientific Publications, Melbourne
- Skadsheim A (1983) The ecology of intertidal amphipods in the Oslofjord. Distribution and responses to physical factors. *Crustaceana* 44:225–244
- Sloan NA (1979) Microhabitat and resource utilization in cryptic rocky intertidal echinoderms at Aldabra Atoll, Seychelles. *Mar Biol* 54:269–279
- Tilman D (1987) The importance of the mechanisms of interspecific competition. *Am Nat* 129:769–774
- Turner AM, Montgomery SL (2003) Spatial and temporal scales of predator avoidance: experiments with fish and snails. *Ecology* 84:616–622
- Wilson JB (1990) Mechanisms of species coexistence: twelve explanations for Hutchinson's 'paradox of the plankton': evidence from New Zealand plant communities. *NZ J Ecol* 13:17–42
- Wilson JB (1994) The 'intermediate disturbance hypothesis' of species coexistence is based on patch dynamics. *NZ J Ecol* 18:176–181
- Wisenden BD, Pohlman SG, Watkin EE (2001) Avoidance of conspecific injury-released chemical cues by free-ranging *Gammarus lacustris* (Crustacea: Amphipoda). *J Chem Ecol* 27:1249–1258
- Wudkevich K, Wisenden BD, Chivers DP, Smith RJF (1997) Reactions of *Gammarus lacustris* to chemical stimuli from natural predators and injured conspecifics. *J Chem Ecol* 23:1163–1173
- Zamzow JP, Amsler CD, McClintock JB, Baker BJ (2010) Habitat choice and predator avoidance by Antarctic amphipods: the roles of algal chemistry and morphology. *Mar Ecol Prog Ser* 400:155–163
- Zintzen V, Norro A, Massin C, Mallefet J (2008) Spatial variability of epifaunal communities from artificial habitat: shipwrecks in the southern Bight of the North Sea. *Estuar Coast Shelf Sci* 76:327–344

Editorial responsibility: James McClintock, Birmingham, Alabama, USA

*Submitted: June 19, 2014; Accepted: November 13, 2014
Proofs received from author(s): January 12, 2015*