ECOLOGICAL DIFFERENTIATION AMONG AMPHIPOD SPECIES IN MARINE FOULING COMMUNITIES:

STUDIES ON SYMPATRIC SPECIES OF THE GENUS *JASSA* LEACH, 1814 (CRUSTACEA, AMPHIPODA)

Dissertation

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Introduction

With more than 10,000 species described to date (Lowry 2013), amphipods (Peracarida, Crustacea) represent one of the most diverse taxa of Crustacea. In marine benthic communities Amphipoda often exceed all other types of macrozoobenthos in terms of numerical abundance, species diversity and sometimes even biomass. Many amphipod species feature a high degree of ecological differentiation (niche specificity) which makes them particularly suited to document spatio-temporal changes in environmental conditions (e.g. Marques & Bellan-Santini 1993; Conlan 1994; Conradi & López-González 1999, 2001; Chintiroglou et al. 2004). This has resulted in a widespread use of amphipod species as 'bioindicators' of monitoring programmes in both freshwater and marine areas (e.g. Reish 1993; Thomas 1993; Linton & Warner 2003; Simpson et al. 2005).

Amphipods have also been reported to dominate marine fouling communities on artificial substrates such as ship wrecks, navigational aids, fish cages as well foundations of harbours and offshore constructions (Barnard 1958; Conradi et al. 1997; Zintzen et al. 2006; Greene & Grizzle 2007). Considering the scheduled large-scale introduction of wind power stations into the German Bight and many other coastal areas, amphipod fouling communities may increasingly influence the function of coastal marine ecosystems in the near future (Langhamer et al. 2009; Krone et al. 2013). Species of the genus *Jassa* Leach, 1814 (Ischyroceridae) usually represent the most frequent species in such amphipod fouling communities. They can reach remarkably high abundances of up to 800,000 ind./m² (Franz 1989; Scinto et al. 2007; Zintzen et al. 2008; Beermann & Franke 2011; Krone et al. 2013). *Jassa* species are classified as hemi-sessile filter feeders (Fig. 1.1). Specialised glands in the third and fourth pereopods produce 'amphipod silk', which is used by the animals to construct tubes that are firmly attached to the substrate. In this way *Jassa* individuals create their own

microhabitat (Conlan 1994; Dixon & Moore 1997; Kronenberger et al. 2012a, b). Sitting in their individual tubes, the animals feed more or less unselectively by extending their prolonged antennae out of the tubes into the water column. In densely crowded populations, these tubes are built in multiple layers attached to each other and can thus form thick mats with detritus incorporated (Caspers 1952; Barnard 1958; Dixon & Moore 1997). By this means, clean substrates can become quickly colonised by large numbers of *Jassa* individuals, either by immigration of animals from adjacent areas, but mainly by recruitment of dispersing juveniles from the water body (Franz & Mohamed 1989; Havermans et al. 2007).
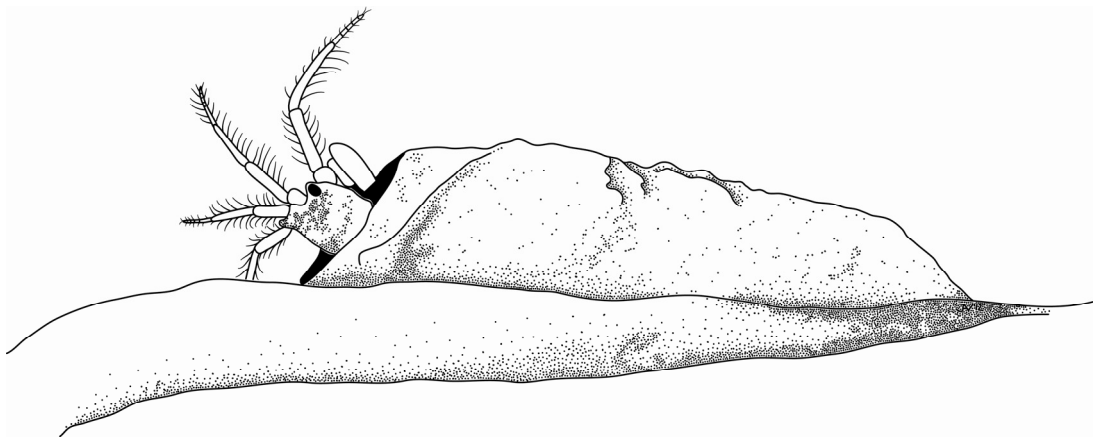
Figure 1.1 *In situ* habitus of *Jassa* sp. in its tube, antennae extended into the water column. (original drawing; based on a sketch of Dixon & Moore 1997)

Several *Jassa* species have been recognised to overlap in their geographical distributions. For example, five species of the genus are recorded for northern Europe: the two cosmopolitan species *J. marmorata* Holmes, 1903 and *J. slatteryi* Conlan, 1990, and three species (*J. falcata* (Montagu, 1808), *J. herdmani* (Walker, 1893) and *J. pusilla* (Sars, 1894)) which are restricted to north-western Europe (Conlan 1990; Beermann & Franke 2011). Additionally, some *Jassa* species even co-occur on small spatial scales. At Helgoland (German Bight, North Sea) the three species *J. falcata*, *J. marmorata* and *J. herdmani* are

known to coexist in the fouling communities around the island (Beermann & Franke 2012; Fig. 1.2, 1.3). Information on differences in biological and ecological traits among the species of the genus *Jassa* is still scarce. This is due to a former taxonomic confusion, as prior to a major revision of the genus by Conlan (Conlan 1989, 1990), *Jassa* individuals were attributed to a single species, '*Jassa falcata*' by Sexton & Reid (1951). This was broadly accepted in most ecological and taxonomic surveys up to the 1990s. In Conlan's revision (1989, 1990) several species were newly described or re-erected, and also voucher material of previous ecological studies on *Jassa* was examined. Conlan concluded that many studies on '*Jassa falcata*' in fact dealt with a mixture of species. For example, studies on '*J. falcata*' by Nair & Anger (1979b, 1980) at Helgoland in fact referred to a mixture of mainly *J. marmorata* and *J. herdmani*. Therefore, most ecological studies on *Jassa* published before 1990 must be considered with caution, because they possibly dealt with a mixture of species which probably differ in their biological/ecological traits.
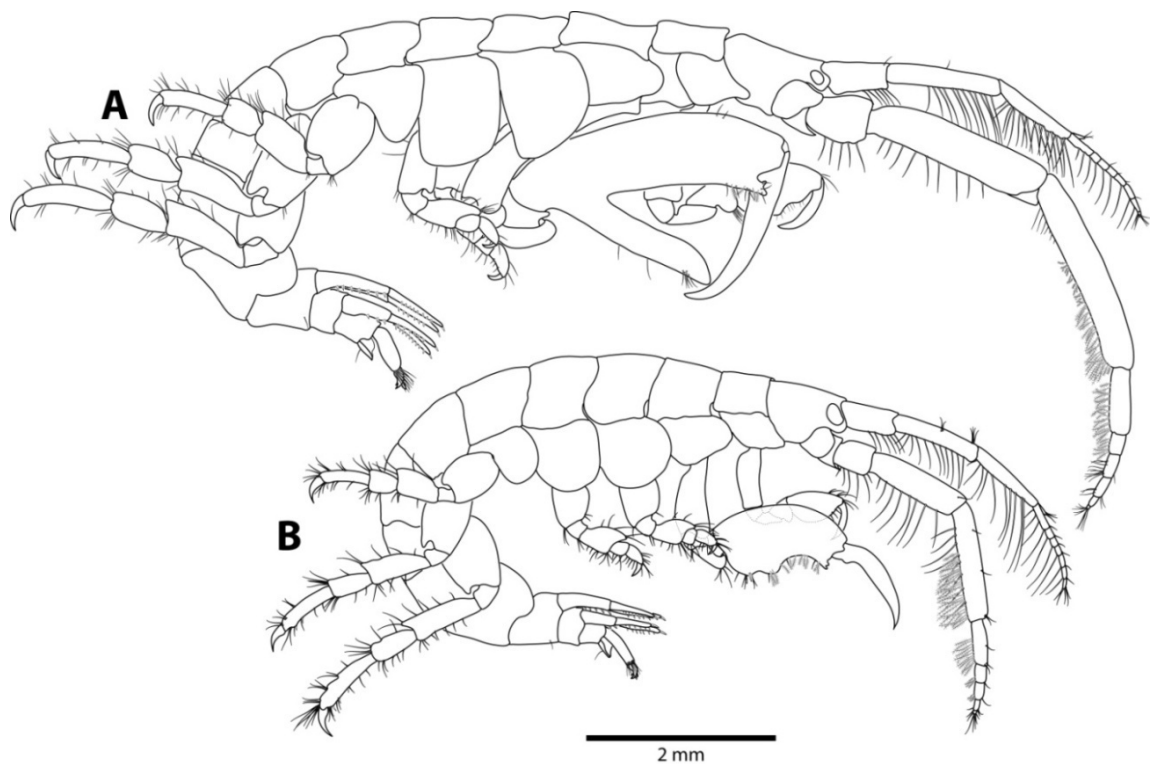
Figure 1.2 Habitus of *Jassa falcata* specimens from Helgoland, North Sea. A, adult male ('major form'); B, adult female. (original drawing)
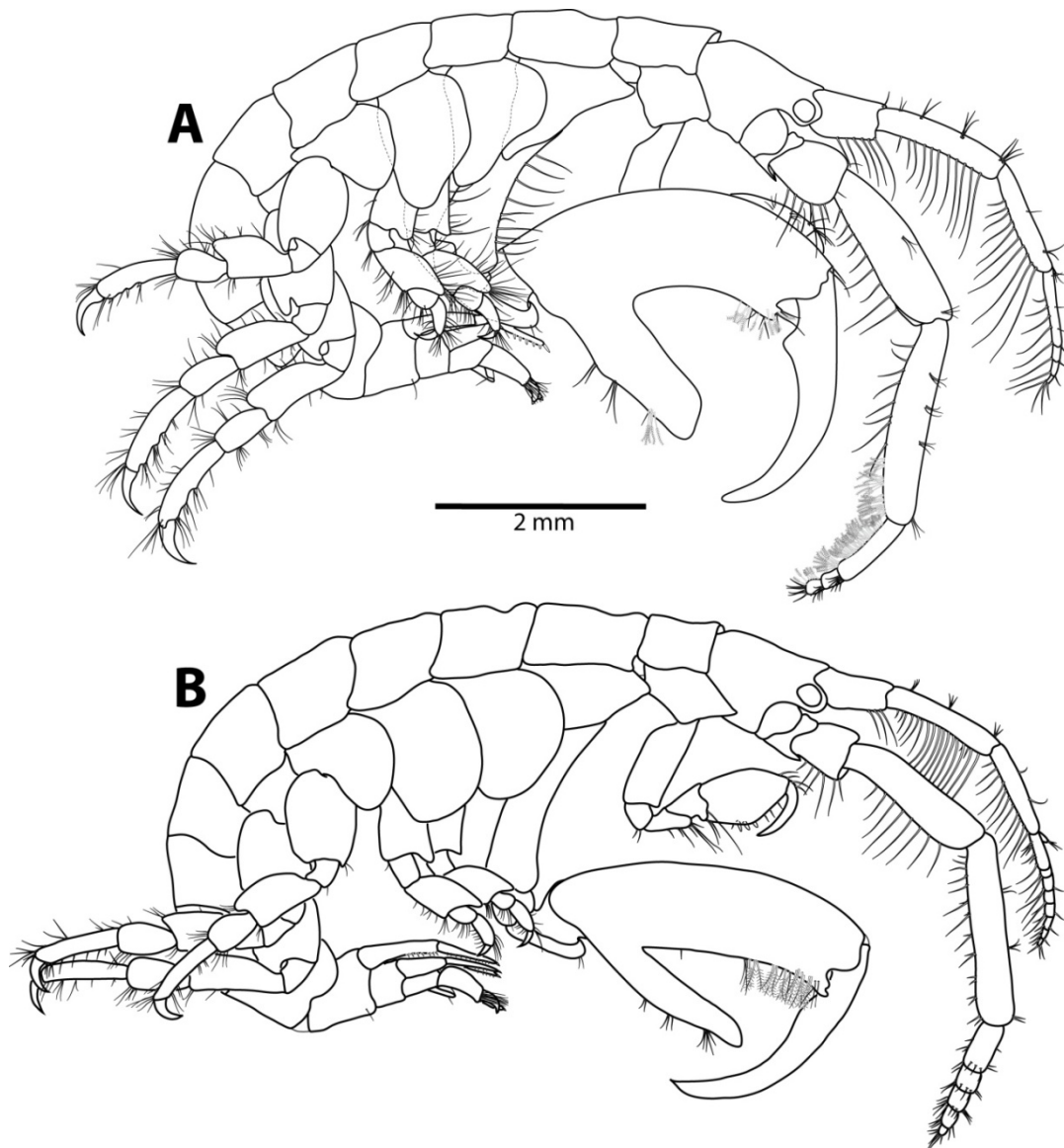
Figure 1.3 Habitus of 'major form' male *Jassa* specimens from Helgoland, North Sea. A, *J. marmorata*; B, *J. herdmani*. (original drawing)

The taxonomic confusion was caused by the high polymorphism of *Jassa* species. The sexes are highly dimorphic. Males are usually bigger in size and show several special characteristics (Fig. 1.2). The most conspicuous feature are the enlarged second gnathopods, which bear thumb-like protuberances on the propodi (referred to as 'thumbs'). This character develops with a terminal moult

(transition from 'non-thumbed' to 'thumbed' males) which marks the beginning of intense sexual activity. The animals ('cruising males') then leave their tubes, searching and attending receptive females as well as fighting other males, for the rest of their lives. Non-thumbed males (i.e. males before the final moult) can already display fully developed penes papillae, but prefer to stay in their tubes. Encounters with unattended receptive females may occur occasionally, but are repelled by the females (Borowsky 1983, 1985; Conlan 1989). Besides the sexual dimorphism, there is another distinct dimorphism in thumbed males: 'major form' males (or short: 'majors') are bigger in size and exhibit enlarged antennae 2 and second gnathopods with big thumbs, whereas 'minor form' males (or: 'minors') are smaller in body size and display smaller thumbs (Fig.1.4).

1 mm
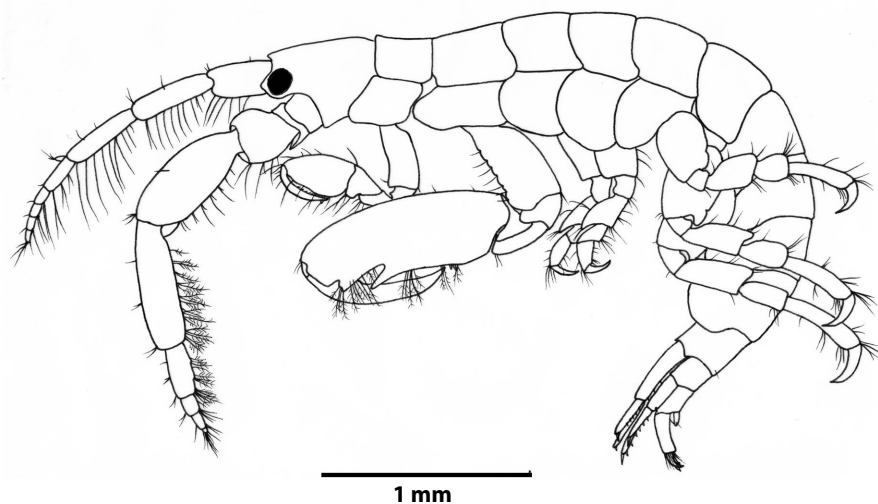
Figure 1.4 Habitus of a 'minor form' male of *Jassa slatteryi* from Malaga, Spain, Mediterranean Sea. (original drawing)

In densely crowded *Jassa* communities there is probably an intense interference competition among thumbed males for receptive females. Females can be mated only within a short period of 1-2 hours immediately after their moults (Borowsky 1983; Clark & Caudill 2001). The two male morphs represent different mating strategies. 'Majors' guard their mate by attending the female's

tube and evicting other males from its vicinity. 'Minor' males, in contrast, never fight and may act as 'sneaker males' to gain access to receptive females. However, the two different male morphs do not display evolutionary stable alternative reproductive strategies (ESS) as their alternative realization depends on the quality of food available during preceding developmental stages (Conlan 1989; Clark 1997; Kurdziel & Knowles 2002).

Only few studies have focussed on life cycle parameters of *Jassa* species, and the available data were mostly assessed from field observations on single-species populations of *J. marmorata* and *J. slatteryi* (Franz 1989; Clancy 1997; Jeong et al. 2007; Scinto et al. 2007). The only investigation of life cycle parameters of *Jassa* under controlled laboratory conditions, carried out by Nair and Anger (1979b) on '*Jassa falcata*', most probably dealt with a mixture of species (Conlan 1990). Two studies which were conducted at Helgoland (Karez & Ludynia 2003; Beermann & Franke 2012) produced a first evidence of some ecological differentiation among coexisting *Jassa* species. However, a detailed knowledge on species-specific biological and ecological traits, and how these might facilitate the coexistence of congeneric species is still largely missing.

A stable coexistence of species requires some differentiation in biological/ecological traits which reduces the degree of interspecific competition. Differentiation via partitioning of resources (particularly food and microhabitat) provides reasonable explanations for many cases of long-term coexistence (Hardin 1960; Harper et al. 1961; Schoener 1974, 1986). However, as natural communities are subjected to permanent changes, non-equilibrium mechanisms of coexistence may also be involved. For example, Connell's 'intermediate disturbance hypothesis' assumes that intermediate frequencies of disturbance in habitats result in the coexistence of fast colonisers with more competitive species (Connell 1978; Wilson 1990, 1994; Roxburgh et al. 2004).

In the current study, both field and laboratory experiments were performed to analyse possible differences in biological/ecological traits among the three *Jassa* species which co-occur at Helgoland. In detail, the investigation aimed to elucidate the following aspects:

- the succession of amphipod fouling communities in different environments
- seasonal changes in colonisation activity
- population structure of *Jassa* species in the field
- microhabitat selection of *Jassa* species and its interference with congeneric competitors and potential predators
- life history parameters of sympatric *Jassa* species

In a first one-year field experiment, PVC panels were immersed at different locations around Helgoland in spring and sampled monthly to track the seasonal succession (species diversity, abundances, population structure) of the amphipod fouling community under different environmental conditions, with a focus on the dominating *Jassa* species. In a second year-round field experiment, PVC panels were exposed for one month only each to study seasonal changes in the colonisation activity. Microhabitat selection of *J. marmorata* and *J. herdmani* on a macroalga was studied under controlled laboratory conditions. Effects of intra- and interspecific competitors and of a potential presence of predators were experimentally analysed. Furthermore, adults of the three sympatric *Jassa* species were kept in the laboratory to reveal possible differences among the species with respect to survival rate and moult intervals.

Overall, the experiments and observations were expected to contribute to a more detailed biological/ecological characterisation of sympatric *Jassa* species, thus giving support to their taxonomic distinction which so far has been based mainly on morphological traits.

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Materials & Methods

2.1 Colonisation and succession in the field

The annual succession of amphipod fouling communities in the field was studied on an artificial substrate, starting in March 2010. PVC panels of 10 x 10 cm were roughened on one side according to the procedure of Beermann & Franke (2012), and fixed in groups of 12 to special installations (Fig. 2.1.1). Six installations each represented a 'station'. Such stations were positioned at three different sites around Helgoland (12 x 6 x 3 = 216 panels in total; Fig. 2.1.2). The three locations differed with respect to environmental parameters, particularly water depth and degree of wave exposure. The first location was situated approximately 600 m north of the island at 10 meter water depth. The installations were attached to artificial wave breakers (so-called 'tetrapods') by SCUBA divers, one meter above the seafloor. The tetrapods were part of an experimental artificial reef structure at Helgoland (MarGate project) which was established in February 2010. The second location was situated directly above the first one, one meter below the water surface. The installations were fixed to moored buoys. This location was fully exposed to the surface turbulence and the tidal currents of up to 0.9 ms^{-1}. The third study site was located inside of the South Harbour of Helgoland. This location was considered as 'sheltered' as it was fully protected from waves by the harbour's walls and boulders and showed only weak tidal currents of up to 0.1 ms^{-1}. Sampling at the stations was carried out every month via boat and, at the 10 m station, by SCUBA diving. From each of the six installations of a station, a single panel was removed (= six replicates per month and location). This could be done without disturbing the local *Jassa* community as the individuals normally stayed within their tubes or clung to the substrate. The panels were put separately in sealable plastic bags and shock-frozen at -80°C until further processing, thus ensuring a perfect preservation of the animals' morphological characters. During the sampling procedure at the 10 m station in October, two panels were accidently

put into the same plastic bag by the collecting SCUBA diver. In this case, the arithmetic mean of the two panels was treated as a single replicate so that only five instead of six replicates were available. While still in frozen condition, the fouling on the smooth side of the panels was removed, i.e. only animals settled on the roughened sides were considered for the analysis. All amphipods and other vagile arthropods in the sample were determined to species level and counted. As juvenile amphipods are hardly distinguishable on the species or even the genus level, they were excluded from the analysis. In the genus *Jassa* only specimens bigger than 4 mm were considered, as smaller individuals cannot be determined without fail on the species level (Conlan 1990; Beermann & Franke 2011). For an in-depth analysis of the community structure of the *Jassa* species at Helgoland, the individuals of all *Jassa* species (≥ 4 mm; i.e. males and females with brood pouch) were classified with respect to sex (males, females), reproductive status (females with/without eggs, males with/without thumb), and, in case of thumbed males, with respect to reproductive forms (major/minor form males).

Starting in June 2011, a similar experiment was performed at the sheltered location in order to analyse the seasonality of early colonisation. For this purpose, only a single panel each was fixed to the six installations of this station. After one month of exposure, the panels were removed, processed as above, and replaced by clean panels. This procedure was repeated over a one-year period (6 x 12 = 72 panels in total). After each sampling event, any fouling was carefully removed from the station to exclude that short distance dispersal influences the colonisation of the test panels. All gathered material was treated and evaluated as above. However, for the analyses of abundances, *Jassa* individuals ≤ 4 mm were also counted and categorised as 'juvenile *Jassa* spp.'.
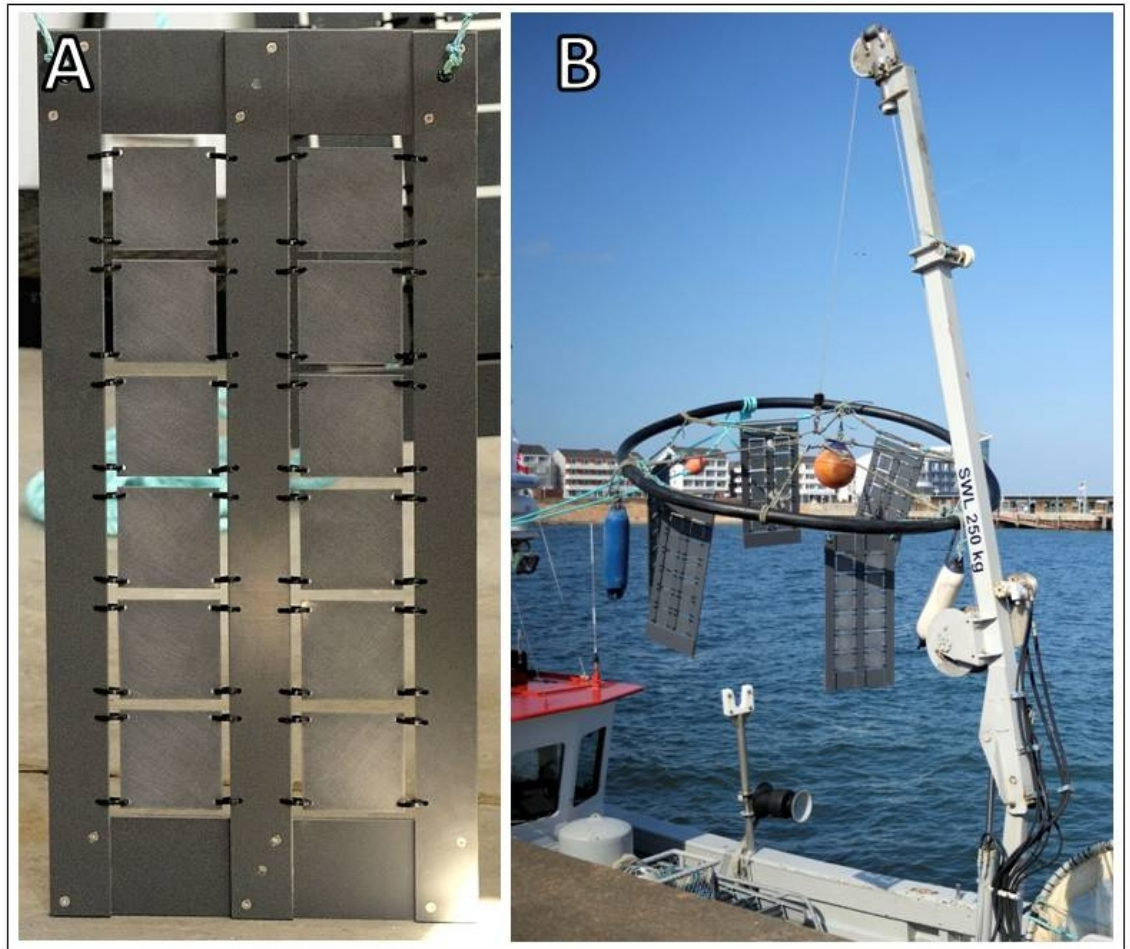
Figure 2.1.1 A) Installation with 12 test panels as used for the field experiment (before exposure). B) A 'station' consisting of six installations (before scuttling at the location in the South Harbour).
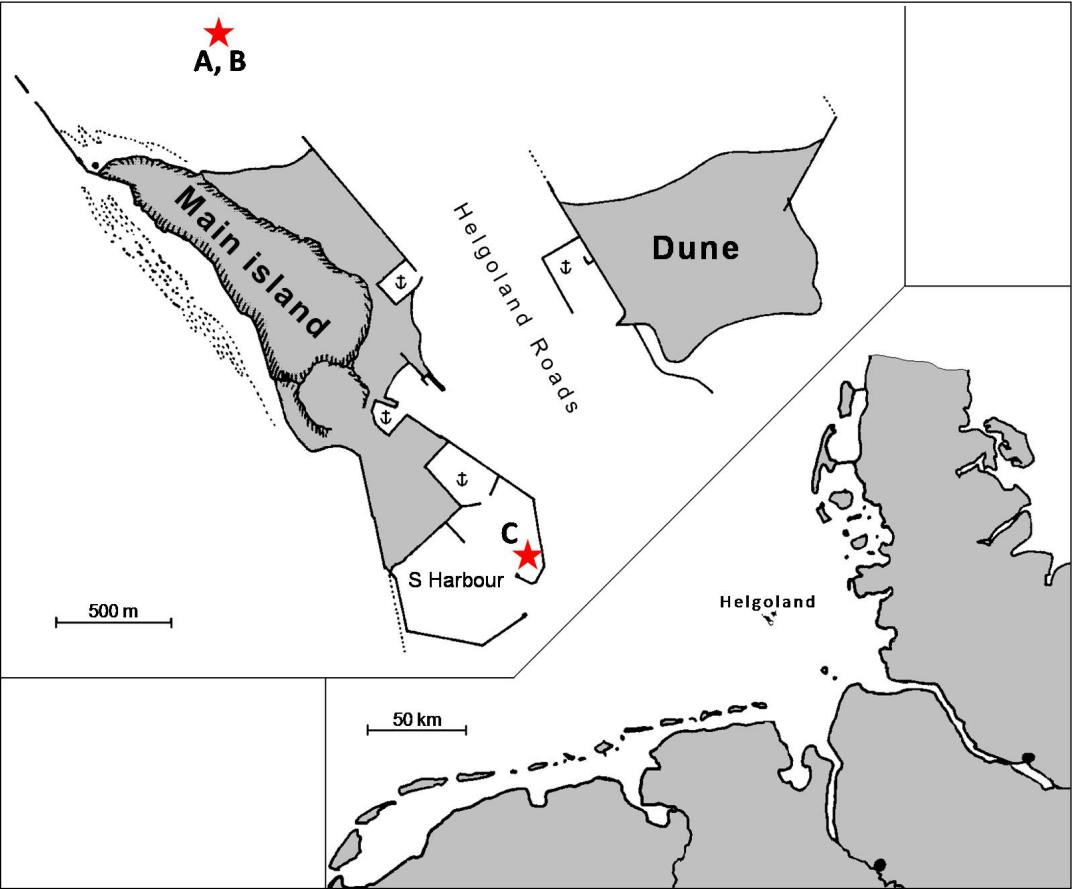
Figure 2.1.2 Map of Helgoland and its location in the German Bight. Asterisks indicate the position of the study sites: A, B) 10 m station and exposed location; C) sheltered location (modified from Beermann & Franke 2011).

Statistical analyses

The computer software GraphPad Prism (5.03), STATISTICA (8.0) and PRIMER (5.2.9) were used for calculations. All analyses were performed at a 95% confidence level.

The amphipod species diversity in the first field experiment was expressed by Simpson's diversity index for finite communities. It is calculated in the following way:

$$D = \sum \left(\frac{n_i[n_i - 1]}{N[N - 1]} \right)$$

n_i = number of individuals in the ith species; N = total number of individuals

This index is weighted towards the dominating species in a sample, and is little sensitive to species richness. It is thus considered to be one of the most meaningful and robust 'nonparametric' diversity indices (see Magurran 2004, and references therein). The value of D ranges from 0 to 1. As the diversity increases with decreasing D, the term 1-D is expediently used for graphical representations and statistical interpretations.

The D-values of the different stations were compared by a crossed two-way analysis of variance (ANOVA) with the factors 'month' (twelve levels) and 'location' (three levels: 10 m depth, exposed, sheltered), followed by Tukey's HSD post hoc test. The same procedure was applied for an analysis of the total number of species at the stations over time.

The numerical abundance of the three *Jassa* species was analysed using a crossed three-way ANOVA with the factors 'month' (twelve levels), 'location' (three levels: 10 m depth, exposed, sheltered) and 'species' (three levels: *J. falcata*, *J. marmorata*, *J. herdmani*). Tukey's post hoc procedure was then used to identify differences in detail.

Except for the analysis of the total number of species where the residuals had normal distribution (Kolmogorov-Smirnov test) and showed homogeneity of variances (Bartlett test), the variances in the performed analyses were

heterogeneous. These patterns could not be improved by the transformation procedures suggested by Zar (1996). Nevertheless, these nonconformities were accepted, as big MANOVAs with balanced design have been proven to be very robust (Underwood 1998).

The outcome of the second field experiment could not be analysed by using Simpson's index, because both species diversity and abundances were too low. Instead, a cluster analysis was applied on pooled data of amphipod species occurrences per month. Before calculation, the data were square root transformed to reduce the impact of extreme abundance values. The clustering was based on Bray-Curtis similarities with group-average linking. As the data for the total number of amphipod species did not meet the assumptions of an ANOVA, the months were compared with the nonparametric Kruskal-Wallis test, followed by Dunn's post hoc test.

The analysis of the different categories of *Jassa* individuals was conducted by comparing the medians of frequencies via Kruskal-Wallis and Mann-Whitney U test according to Sokal & Rohlf (1995). However, samples were only taken into account, if the replicates together comprised 100 or more specimens.

2.2 Microhabitat selection on a macroalga

Live specimens of *J. marmorata* and *J. herdmani* of the same size class were gathered in the field from navigational aids near to the island of Helgoland and from walls of the island's South Harbour in late summer 2011 and 2012. As *J. falcata* was generally rare in the field, the species had to be excluded from the experiments. The animals were then kept under constant laboratory conditions: 13°C, LD 12:12, daily change of seawater, daily feeding with *Artemia*-nauplii and powder of dried *Ulva*-thalli. Only specimens bigger than 6 mm were used in the experiments, as live specimens of smaller size cannot be safely determined to species level (for further details: Conlan 1990; Beermann & Franke 2011). Individuals were categorised into ('major') thumbed males, non-thumbed males and mature females. 'Minor' thumbed males were rare in the field and were thus excluded from the experiments. After 48 hours under the above conditions, the animals were tested in the different set-ups. Each individual was used only once.

2.2.1 Isolated individuals

In order to check for behavioural differences between animal categories and species, individuals of *J. marmorata* and *J. herdmani* (20 thumbed males, 20 non-thumbed males and 20 females of either species) were put singly into compartments (3 x 6 cm) each containing a small thallus fraction of the green macroalga *Cladophora rupestris*. This algal species was chosen because it hosts *Jassa* species in the field and because its thalli survive detachment from the substrate 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 etc.). After 24 hours in the setups, allowing the amphipods to settle and build tubes, all individuals were checked for their local position. Three different areas were distinguished for the evaluation: the peripheral area of the algal thallus (individual on or closely beneath the surface 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).

2.2.2 Groups of individuals

A similar experimental design was used to test the behaviour of animals (females only) which were kept together in small groups. In a first set-up, groups of 20 females of the same species were put in flat boxes (10 x 10 cm), each containing a thallus of *C. rupestris*. Six replicates were run per species. After 24 hours the experimental animals were checked for their positions as above. The outcome of this experiment was taken as reference point to evaluate possible effects of some factors on microhabitat selection. The second experiment was designed to test for a possible effect of animal density in the two species. The experimental set-up was identical to the first one (24 h, 6 replicates), except that group sizes were doubled (40 ind.). The results were then compared intraspecifically to the results of the first experiment. In a subsequent third experiment, the animals' behaviour was studied in mixed-species groups. 20 females of *J. marmorata* were placed together with 20 females of *J. herdmani* in the box (24 h, 6 replicates, evaluation as above) to test for direct interspecific effects. The outcome was than compared for each species to the results of the second experiment (single-species groups of 40 individuals each).

An additional fourth experiment was run to elucidate the possible influence of further environmental parameters on microhabitat selection in *J. marmorata* and *J. herdmani*. The set-up was identical to the reference experiment, except for the quality of the deployed seawater. Instead of filtered natural seawater, seawater from an aquarium was used which was inhabited by five 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). Data of this experiment with 'fish cues' in the medium were compared intraspecifically with the results of the reference experiment.

Statistical analyses

The computer software GraphPad Prism (5.03) and STATISTICA (8.0) were used for calculations. All analyses were performed at a 95% confidence level.

Chi-square tests were applied to test for differences in microhabitat selection between the three intraspecific categories of animals. To fulfil the prerequisites of calculation, data+1 were used. However, when comparing the distributional behaviour of the two species, the raw data of the categories in *J. herdmani* were pooled.

Microhabitat selection in grouped females were analysed with crossed two-way analyses of variance (ANOVA). The reference experiment was analysed interspecifically with respect to the factors 'species' (two levels: *J. marmorata*, *J. herdmani*) and 'area' (four levels: peripheral, central, not on alga, dead). The results of the set-up with groups of 40 individuals were divided by two (data/2), and then compared, for each species intraspecifically, to the results of the reference experiment with respect to the factors 'density' (two levels: 20 individuals, 40 individuals) and 'area' (see above). The data of the mixed-species groups were compared to those of single-species groups with 40 individuals. The behaviour of either species was analysed with respect to the factors 'composition' (mixed species, single species) and 'area' (see above). The outcome of the experiment using fish tank seawater was compared, for either species, with the results of the reference set-up with respect to the factors 'water quality' (two levels: filtered seawater, fish water) and 'area'. All analyses were followed by Tukey's post hoc tests to identify differences in detail. All residuals were normally distributed (Kolmogorov-Smirnov test) and variances of the reference and the 'fish water' group were homogeneous (Levene's test). In order to achieve variance

homogenity in the ANOVA with mixed vs. single species groups, data+3/8 was square root-transformed according to Zar (1996). Thereafter, variances passed Levene's test. No transformation could produce variance homogenity in the comparisons of different densities. This was caused by the cumulated presence of zero-values in the data for 'dead' and 'not on alga' groups. Nevertheless, the analyses were considered to be robust because of their fully balanced design and as the two concerned groups were only given minor importance in the interpretation of the results. Additionally, marginal P-values were regarded with caution.

2.3 Survival and moult intervals of adults

Adult individuals of *J. falcata*, *J. marmorata* and *J. herdmani* (i.e. thumbed 'major' males and females with brood pouch) of the same size classes (approx. 9 mm for males and 7 mm for females) were collected in the field from walls and navigational aids of Helgoland harbour in June 2010. Individuals were put separately in small bowls of 100 ml each, containing a piece of meshed gauze (2 x 1 cm). They were kept under constant laboratory conditions (LD 12:12, daily exchange of seawater) and fed a mixed diet of *Artemia*-nauplii and powder of dried *Ulva* thalli. In the bowls, the animals acted quite naturally, building tubes or (in the case of thumbed males) clinging on the gauze, respectively. The experiments were performed at two different temperature regimes, 8°C and 18°C, with 42 specimens (21 males + 21 females) of each of the three species (42 x 3 x 2 = 252 individuals in total). As only 42 thumbed males of *J. falcata* were found in the field, this number was chosen as the standard. Each individual was checked daily until death for mortality and (in the case of females) for moults. Specimens which died at the first day of observation, probably due to non-visible injuries suffered during the sampling process, were excluded from the analysis.

Statistical analyses

The computer software GraphPad Prism (5.03) and STATISTICA (8.0) were used for calculations. All analyses were performed at a 95% confidence level.

Mortality of adult specimens was plotted over time and survival rates were then compared with a Logrank test (Mantel-Cox) between the three *Jassa* species as well as between sexes for the two temperature regimes.

The total number of moults as well as the mean lengths of intermoult periods per individual were tested using crossed two-way analyses of variance (ANOVA) with respect to the factors 'species' (three levels: *J. falcata*, *J. marmorata* and *J. herdmani*) and 'temperature' (two levels: 8°C and 18°C). Before the ANOVA, data (data+1 for number of moults) were log-transformed.

Thereafter error terms passed normality tests (D'Agostino and Pearson, Kolmogorov-Smirnov) and variances were homogeneous (Bartlett test). For more detailed analyses Tukey's post hoc test was used.

Individual lengths of moult intervals over time were analysed, comparing linear regression slopes (F test).

Results

3.1 Colonisation and succession in the field

3.1.1 Annual succession

All panels (brought out in March 2010) were quickly covered with tubes, built by individuals of *Jassa* species. The degree of coverage increased at all three locations over time, reaching a maximum in August, after which time no further changes were observed till the end of the experiment (March 2011). At the 10 m station and at the exposed location, *Jassa* tubes clearly dominated the fouling community. Panels from the 10 m station exhibited a lower degree of coverage by *Jassa* tubes (up to only 80%) and this coverage was rather flat, whereas up to 100% coverage with voluminous tufts of tubes (approx. 3-4 cm height; Fig. 3.1.1) occurred at the exposed location. Algae and sessile animals (bryozoans, hydrozoans, ascideans, barnacles, bivalves and tubiculous polychaetes) were rare and, if present, were partly covered or even completely overgrown by *Jassa* tubes. At the sheltered location, however, the ascidean species *Ciona intestinalis* (Linnaeus, 1767) and *Ascidiella aspersa* (Müller, 1767) covered up to 90% of the panel surfaces, but these accumulations were in turn partly covered and marbled by *Jassa* tubes.

Figure 3.1.1 Artificial panels (10 x 10 cm) after five months of exposure (March to August) at the three different locations: 10 m station (A), exposed location (B), sheltered location (C).

Species diversity

In the course of the one-year experiment, 27 amphipod species from 13 families were found associated with the panels (Tab. 3.1.1). In addition, 13 further vagile arthropod species belonging to five higher taxonomic groups occurred (Tab. 3.1.2): decapod crustaceans (three species), isopod crustaceans (four species), tanaid crustaceans (one species), pantopods (four species), and insects (one species). The panels were quickly colonised by high abundances of amphipod species and only few other crustaceans and pycnogonids, which were less diverse and showed lower abundances than the amphipods (see Appendix).

Table 3.1.1 Amphipod species with family affiliation found in the fouling communities during the first field experiment.

Ampeliscidae
Ampelisca diadema (Costa, 1853)
Amphilochidae
Amphilochus manudens Bate, 1862
Gitana sarsi Boeck, 1871
Aoridae
Aora gracilis (Bate, 1857)
Calliopiidae
Apherusa bispinosa (Bate, 1857)
Apherusa jurinei (Milne-Edwards, 1830)
Calliopius laeviusculus (Krøyer, 1838)
Caprellidae
Caprella linearis (Linnaeus, 1767)
Caprella mutica Schurin, 1935
Pariambus typicus (Krøyer, 1844)
Phtisica marina Slabber, 1769
Cheirocratidae
Cheirocratus sundevallii (Rathke, 1843)
Corophiidae
Crassicorophium bonelli (Milne-Edwards, 1830)
Monocorophium acherusicum (Costa, 1857)
Monocorophium insidiosum (Crawford, 1937)
Monocorophium sextonae (Crawford, 1937)
Dexaminidae
Dexamine spinosa (Montagu, 1813)
Dexamine thea Boeck, 1861
Gammaridae
Gammarus locusta (Linnaeus, 1758)
Gammarellidae
Gammarellus angulosus (Rathke, 1843)
Gammarellus homari (Fabricius, 1779)
Ischyroceridae
Jassa falcata (Montagu, 1808)
Jassa herdmani (Walker, 1893)
Jassa marmorata Holmes, 1903
Stenothoidae
Metopa pusilla Sars, 1892
Stenothoe monoculoides (Montagu, 1815)
Lysianassidae
Tryphosella sarsi Bonnier, 1893

**Table 3.1.2** Further vagile Arthropoda found in the fouling communities during the first field experiment.

Decapoda
Cancer pagurus (Linnaeus, 1758)
Eualus pusiolus (Krøyer, 1841)
Pisidia longicornis (Linnaeus, 1767)
Isopoda
Idotea granulosa Rathke, 1843
Idotea pelagica Leach, 1815
Janira maculosa Leach, 1814
Munna kröyeri Goodsir, 1842
Tanaidacea
Tanais dulongii (Audouin, 1826)
Pantopoda
Achelia echinata Hodge, 1864
Anoplodactylus pygmaeus (Hodge, 1864)
Callipalene brevirostris (Johnston, 1837)
Nymphon brevirostre Hodge, 1863
Insecta
Clunio marinus Haliday, 1855

The fouling communities at the three locations differed significantly in terms of total amphipod species number ($F_{2,179} = 266.91$; $P < 0.0001$), but also fluctuations between months were detected ($F_{11,179} = 69.77$; $P < 0.0001$). The duration of exposure (ranging between 1 and 12 months) affected the community differently depending on the location, i.e. there was a significant interaction of the factors 'location' and 'month' ($F_{22,179} = 8.93$; $P < 0.0001$). A direct comparison between the locations revealed that the exposed station exhibited the lowest number of amphipod species. From June 2010 on, the amphipod species number at the exposed station was significantly lower than at both the sheltered station (Fig. 3.1.2; each $P < 0.01$) and the 10 m station (each $P < 0.001$). The 10 m station showed the highest number of amphipod species. From October 2010 on, the amphipod species number at this station was always significantly higher than at the sheltered location (each $P < 0.01$).
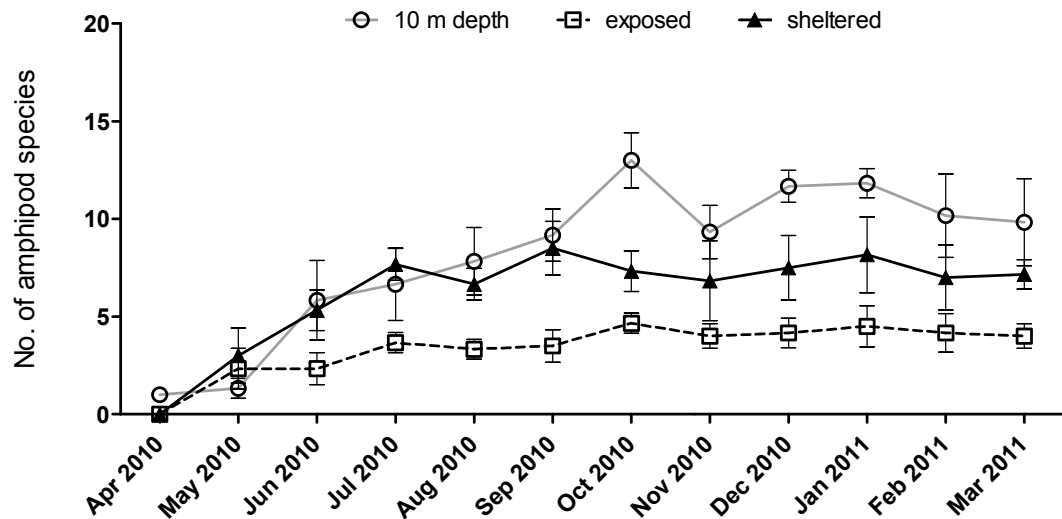
Figure 3.1.2 Total number of amphipod species at the three different locations over time (means ± SD).

The calculated Simpson's index revealed clear differences in amphipod diversity among locations and months (both $P < 0.0001$; Tab. 3.1.3). The duration of exposure affected the amphipod diversity at the locations differently ($P < 0.0001$). In general, diversity was lowest at the exposed location (Fig. 3.1.3). From July on, amphipod diversity at this location even significantly decreased, reached minimum values in September and October (each $P < 0.005$), and then showed only little fluctuations over the following months (each $P > 0.05$). From September 2010 to February 2011, the amphipod diversity at the exposed location was significantly lower than at the sheltered location and at the 10 m station (each $P < 0.01$). No significant differences were found between the two latter stations, although the diversity was tendentially higher at the 10 m station. Only in May, the 10 m station showed the lowest diversity of the three locations (exposed: $P < 0.0001$; sheltered: $P < 0.005$).
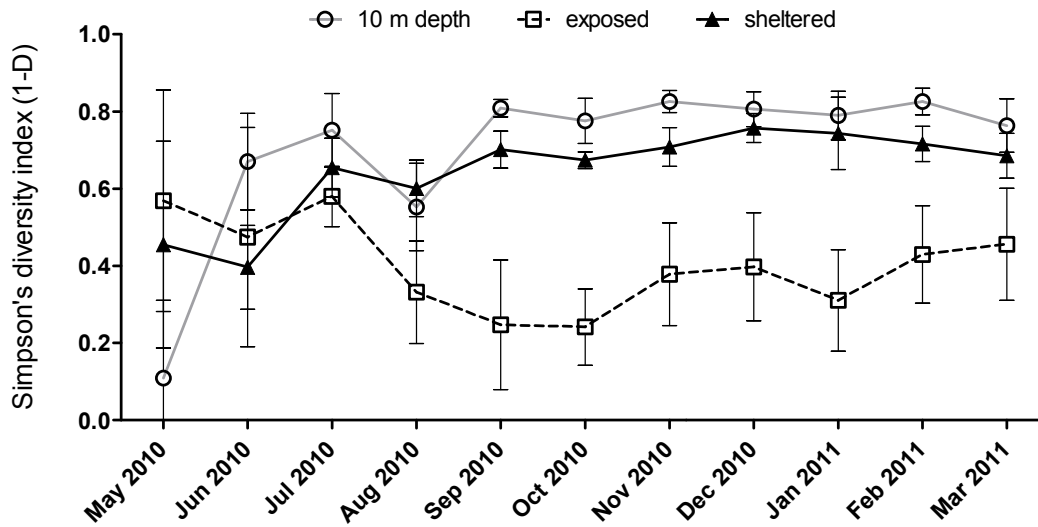
Figure 3.1.3 Amphipod species diversity, expressed by Simpson's diversity index at the different locations over time (not shown: April 2010; means ± SD).

Table 3.1.3 Results of two-way ANOVA for amphipod species diversity (Simpson's index) recorded over the first field experiment.

Factors & interactions	*df*	MS	F	*P*
Month	10	0.1409	8.7971	**< 0.0001**
Location	2	1.6412	102.4229	**< 0.0001**
Month x location	20	0.1435	8.9567	**< 0.0001**
Error	164	0.0161		

Abundances of *Jassa* species

All three stations were rapidly colonised by the three locally known *Jassa* species. The abundance values of *Jassa* species showed a clear dependence on the factors 'species', 'location' and the duration of exposure (each $P < 0.0001$; Tab. 3.1.5). Moreover, the species were differently affected by the factors 'location' and 'month' (duration of exposure). The overall least abundant species was *Jassa falcata*. At the 10 m station, however, its abundance exceeded those of the other two species, although this was statistically significant only in August (*J. marmorata*: $P < 0.0005$; *J. herdmani*: $P < 0.0001$; Fig. 3.1.4). Abundances of

J. falcata clearly peaked in August 2010 (compared to July and September: each *P* < 0.0001) when water temperature was at its maximum. *Jassa falcata* was also abundant at the exposed location, where specimens temporarily occurred in higher numbers than at the 10 m station (July: *P* < 0.0005), but then strongly decreased (Fig. 3.1.5).
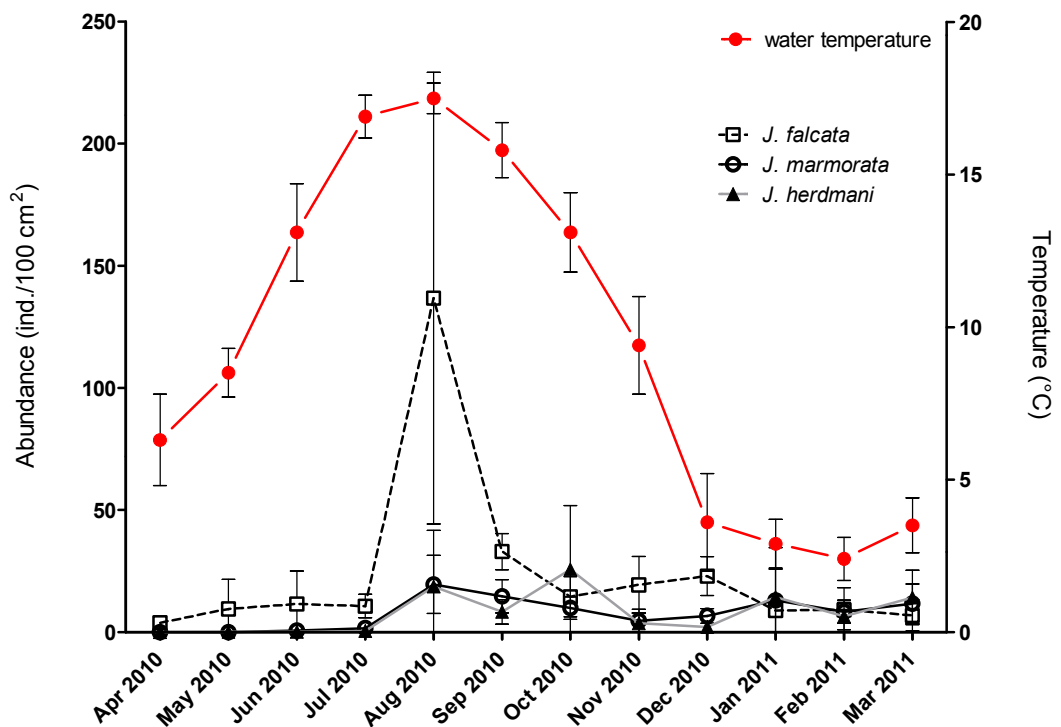
Figure 3.1.4 Abundances of *Jassa* species (> 4 mm) at the 10 m station (means ± SD). The sea surface water temperature at Helgoland is plotted on a monthly basis (means ± SD).

Jassa marmorata was the most abundant species at the exposed as well as the sheltered location. In July the abundances of *J. marmorata* where higher at the sheltered than at the exposed location (*P* < 0.05), while the situation was inverse over the following months (all *P* < 0.005, except for November: *P* = 0.0865). At both the sheltered (Fig.3.1.6) and the exposed location (Fig. 3.1.5), the abundances of *J. marmorata* showed a clear peak in August. The numbers rapidly

increased from July to August at both locations (each *P* < 0.005). In November, however, the abundances of *J. marmorata* at both locations dropped rapidly to a minimum, significantly differing from those in October (each *P* < 0.0001).

Jassa herdmani reached its highest abundance values at the exposed location, although the species remained always less frequent than the dominating *J. marmorata* (Tab. 3.1.4). This difference was statistically significant from July to October and from December to January (each *P* < 0.005), but not in November (*P* = 0.3048), February (*P* = 0.2528) and March (*P* = 0.0505). The abundance of *J. herdmani* at the exposed location increased significantly from July to August (*P* < 0.0001). Although a similar pattern was observed for *J. herdmani* at the sheltered location (Fig. 3.1.6), this was statistically non-significant because of the species' low abundances at this location in general (*P* = 0.1805).
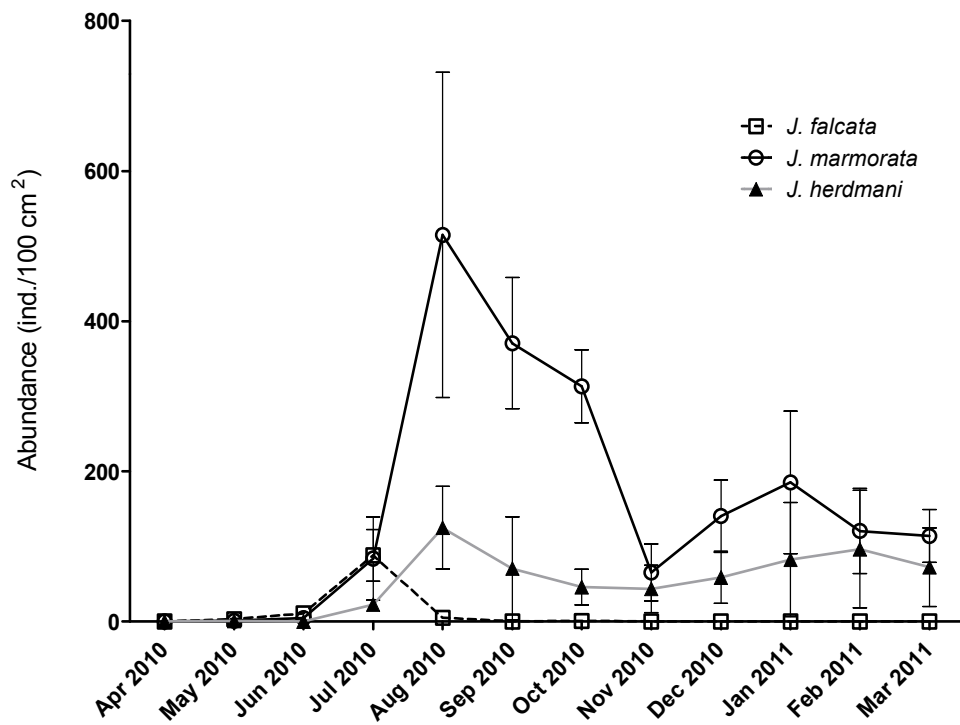
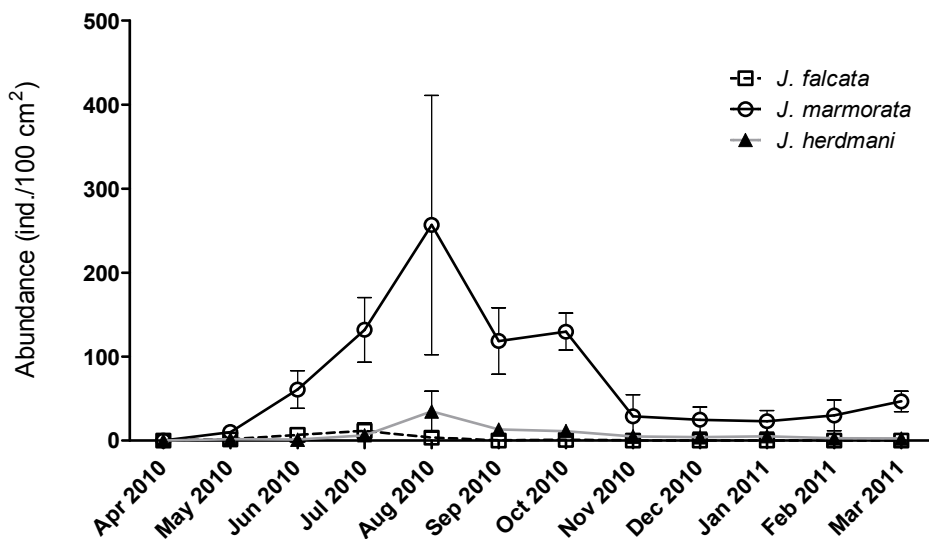**Figure 3.1.5** Abundances of *Jassa* species (> 4 mm) at the exposed location (means ± SD).

Figure 3.1.6 Abundances of *Jassa* species (> 4 mm) at the sheltered location (means ± SD).

Table 3.1.4 Abundances of *Jassa* species (> 4 mm) in the first field experiment (means ± SD).

		10 m depth	exposed	sheltered
Apr 2010	*J. falcata*	3.8 ± 2.6	0.0	0.0
	J. marmorata	0.0	0.0	0.0
	J. herdmani	0.0	0.0	0.0
May 2010	*J. falcata*	9.5 ± 12.2	3.2 ± 1.7	1.5 ± 1.8
	J. marmorata	0.0	1.0 ± 0.9	10.3 ± 2.9
	J. herdmani	0.2 ± 0.4	0.7 ± 1.0	1.8 ± 1.2
Jun 2010	*J. falcata*	11.5 ± 13.6	10.8 ± 5.9	6.8 ± 4.4
	J. marmorata	0.7 ± 1.0	4.7 ± 5.2	60.8 ± 22.2
	J. herdmani	0.2 ± 0.4	0.2 ± 0.4	1.2 ± 1.3
Jul 2010	*J. falcata*	10.7 ± 4.8	88.3 ± 34.4	11.5 ± 9.5
	J. marmorata	1.7 ± 1.6	83.8 ± 55.4	131.8 ± 38.5
	J. herdmani	0.5 ± 0.5	22.7 ± 7.3	6.3 ± 1.8
Aug 2010	*J. falcata*	136.8 ± 92.5	5.0 ± 3.9	3.5 ± 3.4
	J. marmorata	19.5 ± 11.9	515.0 ± 216.7	256.7 ± 154.3
	J. herdmani	18.7 ± 23.0	125.0 ± 55.1	34.8 ± 24.2
Sep 2010	*J. falcata*	33.0 ± 7.4	0.2 ± 0.4	0.2 ± 0.4
	J. marmorata	14.7 ± 6.8	370.8 ± 87.3	118.5 ± 39.6
	J. herdmani	8.3 ± 5.0	70.7 ± 68.7	13.2 ± 4.8
Oct 2010	*J. falcata*	14.5 ± 8.2	0.7 ± 1.6	0.8 ± 1.3
	J. marmorata	9.9 ± 4.6	313.3 ± 48.6	129.8 ± 22.0
	J. herdmani	25.7 ± 26.2	46.0 ± 23.7	11.3 ± 7.5
Nov 2010	*J. falcata*	19.3 ± 11.6	0.0	0.0
	J. marmorata	4.7 ± 4.7	65.5 ± 38.0	29.0 ± 25.8
	J. herdmani	3.7 ± 4.3	43.7 ± 31.6	5.0 ± 6.8
Dec 2010	*J. falcata*	23.0 ± 7.9	0.0	0.0
	J. marmorata	6.7 ± 3.0	140.3 ± 48.1	25.0 ± 15.0
	J. herdmani	2.2 ± 1.9	58.8 ± 34.7	4.0 ± 3.2
Jan 2011	*J. falcata*	8.8 ± 1.6	0.0	0.0
	J. marmorata	13.0 ± 12.8	185.3 ± 95.1	23.0 ± 12.9
	J. herdmani	14.3 ± 20.3	82.5 ± 76.1	5.2 ± 4.3
Feb 2011	*J. falcata*	9.2 ± 9.2	0.2 ± 0.4	0.0
	J. marmorata	8.3 ± 4.8	120.8 ± 56.7	30.0 ± 18.3
	J. herdmani	6.5 ± 5.6	96.5 ± 78.2	2.7 ± 2.3
Mar 2011	*J. falcata*	6.8 ± 6.4	0.0	0.0
	J. marmorata	11.7 ± 8.1	114.2 ± 35.2	46.8 ± 12.2
	J. herdmani	14.2 ± 11.1	72.5 ± 52.5	2.5 ± 1.4

Table 3.1.5 Results of the three-way ANOVA for *Jassa* spp. abundances in the first field experiment.

Factors & interactions	df	MS	F	P
Month	11	63078.0554	46.5287	**< 0.0001**
Location	2	214042.3998	157.8858	**< 0.0001**
Species	2	287431.6493	212.0205	**< 0.0001**
Month x location	22	14183.6775	10.4624	**< 0.0001**
Month x species	22	27162.7932	20.0363	**< 0.0001**
Location x species	4	128677.0237	94.9171	**< 0.0001**
Month x location x species	44	16702.4844	12.3203	**< 0.0001**
Error	537	1355.6781		

Structure of *Jassa* populations

a) *Jassa falcata*

Relevant data on population structure are given here only for those species and months when abundances where high enough to allow for meaningful statements.
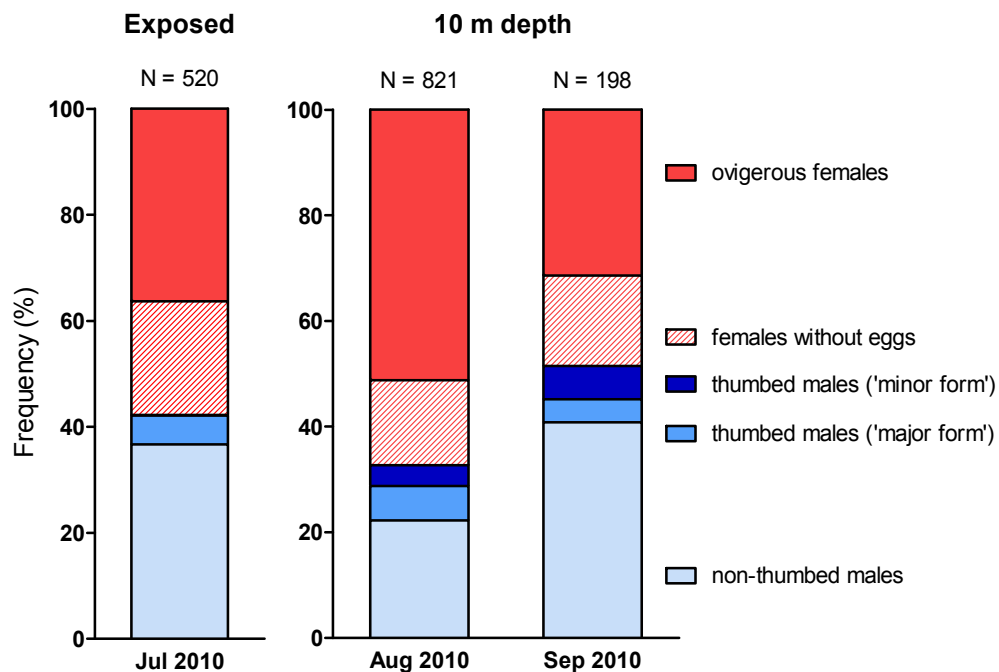
Jassa falcata populations at the 10 m station showed a clear surplus of females in August 2010 ($P < 0.005$; Fig. 3.1.7). In September and at the same location, however, the sex ratio was balanced ($P = 0.6304$), i.e. the proportion of males increased significantly from August to September ($P < 0.01$). At the exposed location the sex ratio of *J. falcata* in July did not differ significantly from 1:1 ($P = 0.1321$) and did not differ from that of *J. marmorata* at the same time and station ($P = 0.7483$).

In August and September, the majority of female *J. falcata* at the 10 m station carried eggs in their brood pouch ($P < 0.05$). This pattern was also observed for the exposed location in July, and no difference was found between *J. falcata* and *J. marmorata* ($P = 0.6991$).

Among male *J. falcata* collected at the 10 m station in August and September, there was a clear dominance of non-thumbed over thumbed males ($P < 0.01$). The difference between August and September was statistically not significant ($P = 0.0931$). However, at the exposed location in July, the proportion

of thumbed males was significantly higher in *J. marmorata* than in *J. falcata* ($P < 0.05$).

The ratio of 'majors' to 'minors' at the 10 m station did not differ significantly from 1:1 both between August ($P = 0.4225$) and September ($P = 0.2876$). At the exposed location, however, significantly more 'majors' than 'minors' occurred ($P < 0.005$), similar to the situation in *J. marmorata* ($P = 0.9999$).

Figure 3.1.7 Population structure of *J. falcata* (specimens > 4 mm) at the exposed location in July, and at the 10 m station in August and September. The individuals were classified with respect to sex, reproductive status (females with/without eggs; thumbed/non-thumbed males) and male morph ('major'/'minor' form of thumbed males).

b) *Jassa marmorata*

At the exposed location, the sex ratio of *J. marmorata* in July was biased in favour of females ($P < 0.05$; Fig. 3.1.8). However, the sex ratio differed significantly over time ($H_{K-W} = 40.97$; $P < 0.0001$). In August and September, for example, the sampled populations exhibited more males than females ($P < 0.005$). At the sheltered location, the sex ratio also differed significantly between the months ($H_{K-W} = 31.19$; $P < 0.0005$). In July males and females were equally abundant ($P = 0.8182$; Fig. 3.1.9), while e.g. in September significantly fewer females than males were recorded ($P < 0.005$).

At the exposed location, ovigerous females were found throughout the year. In July, the percentage of females carrying eggs in their brood pouch (ovigerous females) did not differ significantly from that of females with empty pouches ($P = 0.1797$). The number of ovigerous females relative to the overall number of females varied over time ($H_{K-W} = 28.97$; $P < 0.0005$). In August, e.g., the percentage of ovigerous females was significantly higher than in September and February (each $P < 0.05$). A similar pattern was observed for the sheltered location. Although ovigerous and non-ovigerous females were equally abundant in July ($P = 0.3095$), their ratio differed significantly among the months ($H_{K-W} = 49.20$; $P < 0.0001$). The number of ovigerous females clearly decreased from August to January, when egg-carrying females were completely missing. In direct comparison, ovigerous females were relatively more frequent at the exposed than at the sheltered location. This difference was statistically significant from September 2010 to March 2011 (each $P < 0.05$).

At both locations, males with thumbs on their 2nd gnathopods represented only a minority among the overall number of males. The relative number of thumbed males varied significantly among the months at both the exposed ($H_{K-W} = 33.89$; $P < 0.0001$) and the sheltered location ($H_{K-W} = 40.98$; $P < 0.0001$). At both locations, there was a trend towards fewer thumbed males in the winter months. Significant differences were found for the sheltered location between

August/September and December to February, and for the exposed location between July/August and December/January (each $P < 0.05$). A direct comparison between the two locations showed that thumbed males were more common at the sheltered location, although this difference was statistically significant only in August and September (both $P < 0.005$).

Among thumbed males which were found at the exposed location, 'major form' males were more frequent than 'minors', but this ratio varied over the months ($H_{K-W} = 41.02$; $P < 0.0001$). 'Majors' and 'minors' were equally frequent in October ($P = 0.6991$) as well as in November ($P = 0.2963$), and in March there was even a clear bias in favour of 'minor form' males ($P < 0.05$). Significant differences in the 'minor'/'major' ratio over the months were also found at the sheltered location ($H_{K-W} = 45.36$; $P < 0.001$), although 'major form' males were clearly dominant (Fig. 3.1.9). Only in March, 'majors' and 'minors' were equally frequent ($P = 0.2615$).
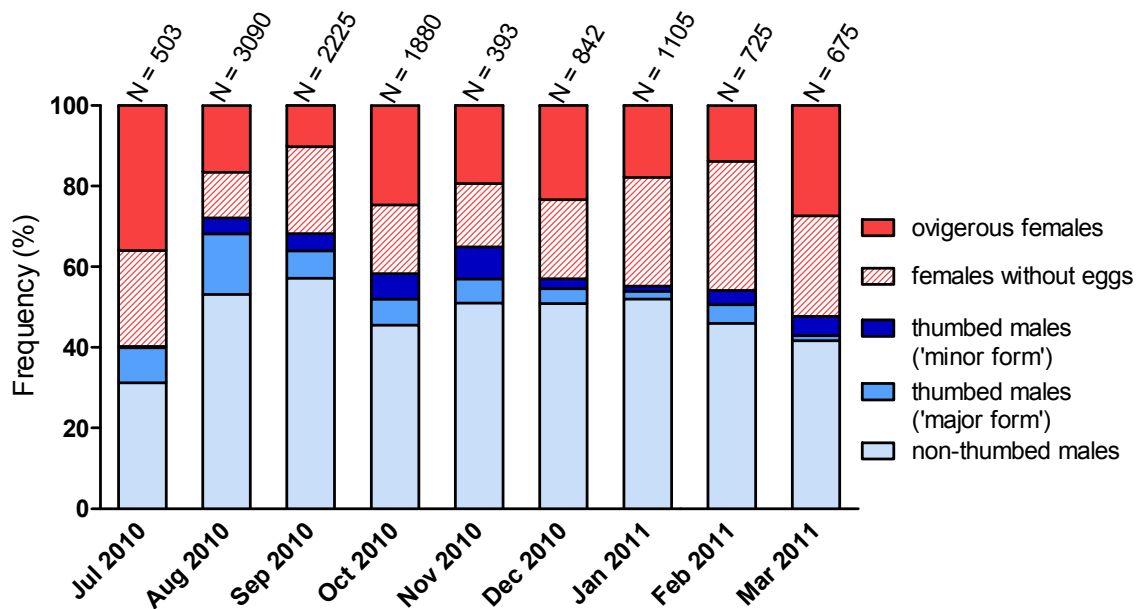
Figure 3.1.8 Population structure of *J. marmorata* (specimens > 4 mm) at the exposed location from July 2010 to March 2011. The individuals were classified with respect to sex, reproductive status (females with/without eggs; thumbed/non-thumbed males) and male morph ('major'/'minor' form of thumbed males).
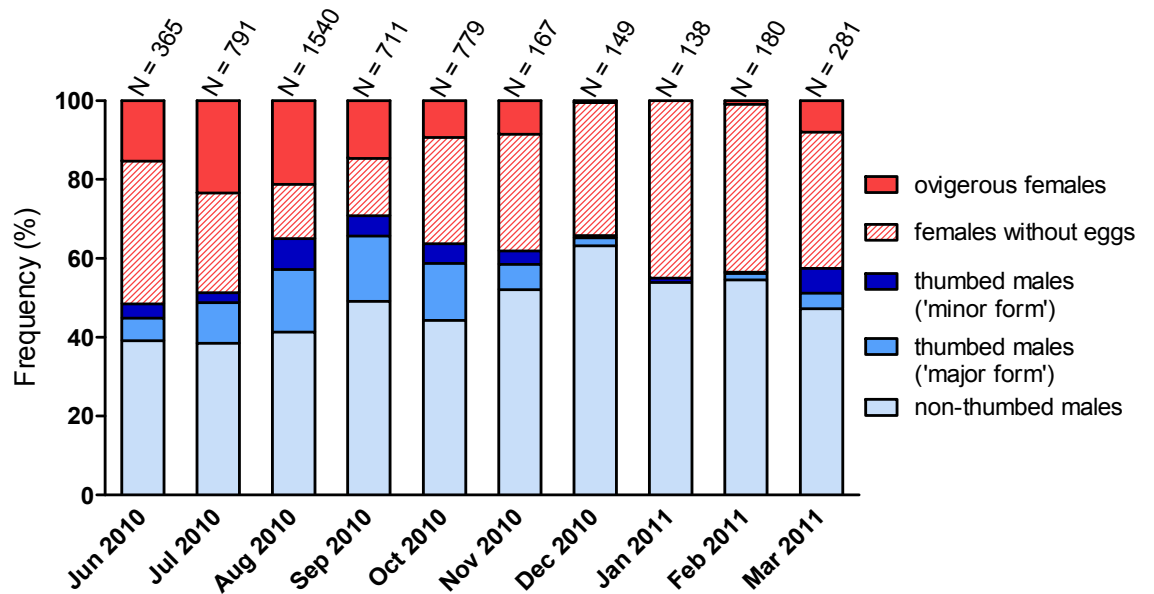
Figure 3.1.9 Population structure of *J. marmorata* (specimens > 4 mm) at the sheltered location from June 2010 to March 2011. The individuals were classified with respect to sex, reproductive status (females with/without eggs; thumbed/non-thumbed males) and male morph ('major'/'minor' form of thumbed males).

c) *Jassa herdmani*

At the exposed location, the sex ratio of *J. herdmani* differed significantly among the months ($H_{K-W} = 23.71$; $P < 0.005$). Whereas the sexes were equally frequent in August ($P = 0.3939$), significantly more females than males were found in October ($P < 0.01$). This pattern was in clear contrast to that observed in *J. marmorata* ($P < 0.005$).

The portion of egg-bearing females also varied significantly over the months ($H_{K-W} = 32.71$; $P < 0.0001$). In August, most females had eggs in their pouches ($P < 0.005$), while in the winter months from January to March the majority of females exhibited empty pouches.

Throughout the year thumbed males were less frequent than non-thumbed males, but their ratios varied significantly over the months ($H_{K\text{-}W}$ = 27.49; $P < 0.0005$). From August to March the percentage of thumbed males decreased; significant differences occurred between August and February/March as well as between September/October and March (each $P < 0.05$). At the exposed location in August, the proportion of thumbed males relative to the total number of males was higher in *J. herdmani* than in *J. marmorata* ($P < 0.005$).

The ratio of the two male morphs differed significantly between the months ($H_{K\text{-}W}$ = 29.70; $P < 0.0001$). For example, the percentage of 'major' males exceeded that of 'minor' males in August ($P < 0.01$), whereas the two male morphs were equally frequent in September ($P = 0.5211$) and January ($P = 0.9360$).
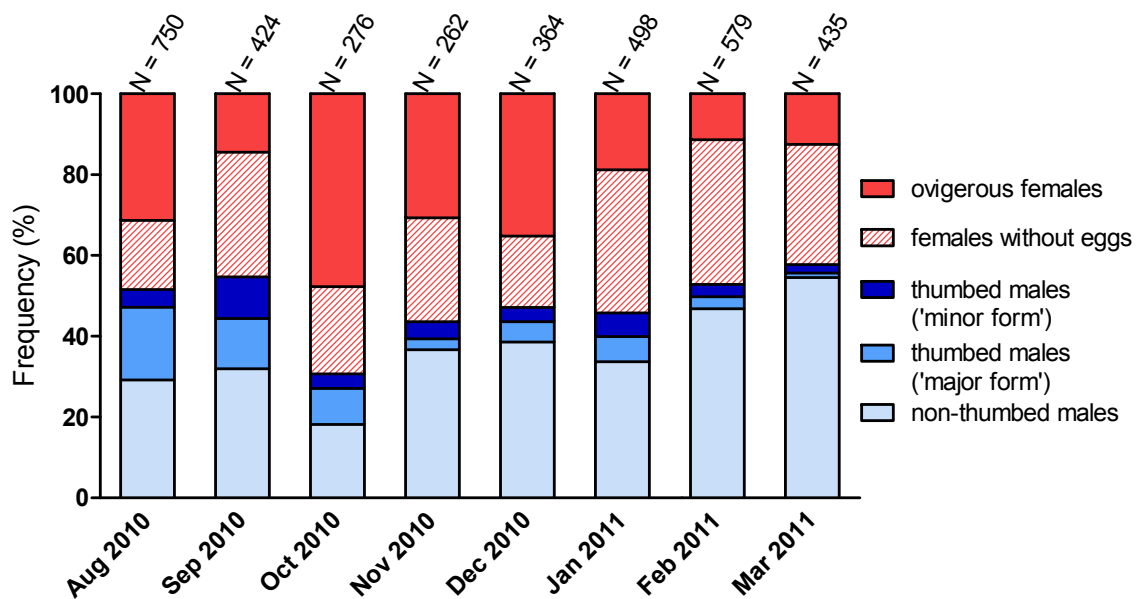

Figure 3.1.10 Population structure of *J. herdmani* (specimens > 4 mm) at the exposed location from August 2010 to March 2011. The individuals were classified with respect to sex, reproductive status (females with/without eggs; thumbed/non-thumbed males) and male morph ('major'/'minor' form of thumbed males).

3.1.2 Monthly colonisation over the annual cycle

In this experiment the panels were exposed in the field for a period of one month only. The degree of coverage varied strongly with the annual time of exposure. Whereas a distinct fouling by *Jassa* tubes was recorded on the panels in July (up to 40% coverage), the extent of fouling decreased towards November, when hardly any tubes were found attached to the panels (Fig.3.1.11).
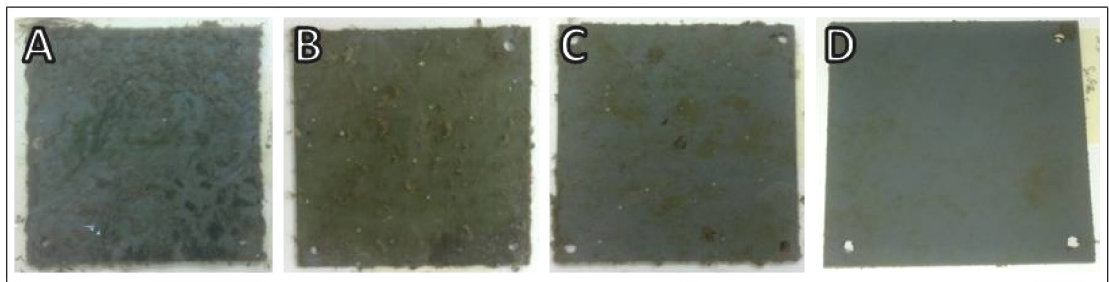
Figure 3.1.11 Artificial panels (10 x 10 cm) after one month of exposure during different times of the year: July (A), August (B), September (C) and November (D).

Amphipod species diversity

A total number of 11 amphipod species from six different families and a single mysid crustacean species were found on the panels after one month of exposure each (Tab. 3.1.6; Fig. 3.1.12). All recorded amphipod species were already known from the first experimental set-up (see Tab. 3.1.1). With the exception of February, when all panels remained completely unsettled, the set-up was quickly colonised by amphipod species. Both spectrum and abundances of species changed with the month of exposure (Fig. 3.1.12).
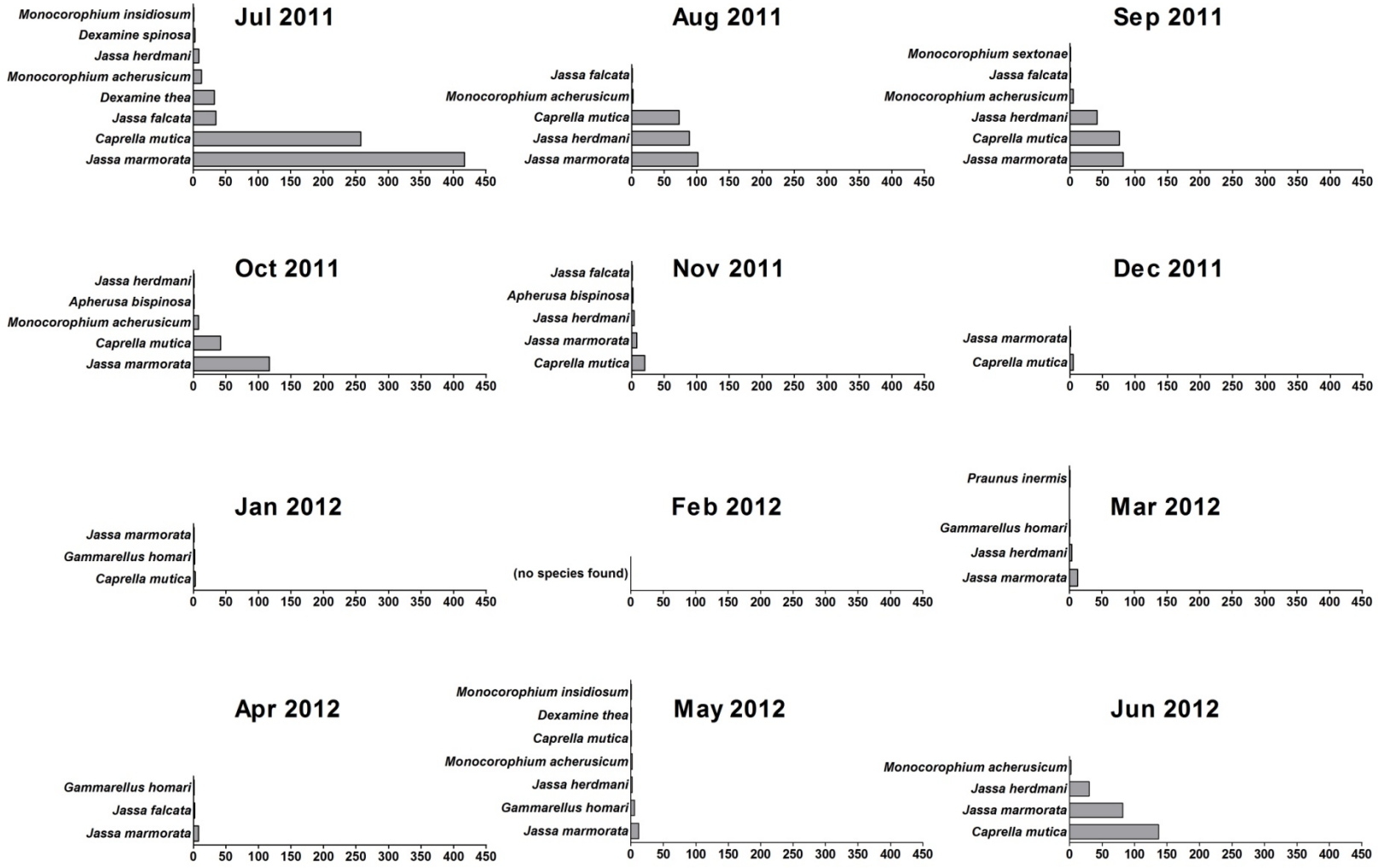
Figure 3.1.12 Seasonal changes (July 2011 - June 2012) in the abundances of amphipod species and further vagile arthropods found on the panels after one month of exposure (pooled replicates).

Table 3.1.6 Crustacea (amphipod species with family affiliation, and a single mysid species) found in the fouling communities of the second field experiment.

Calliopiidae
Apherusa bispinosa (Bate, 1857)
Caprellidae
Caprella mutica Schurin, 1935
Corophiidae
Monocorophium acherusicum (Costa, 1857)
Monocorophium insidiosum (Crawford, 1937)
Monocorophium sextonae (Crawford, 1937)
Dexaminidae
Dexamine spinosa (Montagu, 1813)
Dexamine thea Boeck, 1861
Gammarellidae
Gammarellus angulosus (Rathke, 1843)
Ischyroceridae
Jassa falcata (Montagu, 1808)
Jassa herdmani (Walker, 1893)
Jassa marmorata Holmes, 1903
further vagile Crustacea:
Mysida
Praunus inermis (Rathke, 1843)

The total number of amphipod species recorded varied significantly with the seasonal time of exposure (H_{K-W} = 60.87; $P < 0.0001$; Fig. 3.1.13). This was mainly due to differences between summer and winter months. Most species were found from July to November, while no species occurred in February. Panels which were removed after 3-4 months of exposure (first experiment) in June and July, respectively, harboured only a slightly higher number of amphipod species than those exposed for only one month in June and July ($P < 0.05$).

The species composition showed a high degree of similarity among the months, based on Bray-Curtis similarity of transformed data. February 2012 excluded, the cluster analysis divided the months mainly into two fractions: a 'winter/spring' fraction from November to May, and a 'summer/autumn' fraction from July to October 2011, including June 2012 (Fig. 3.1.14).
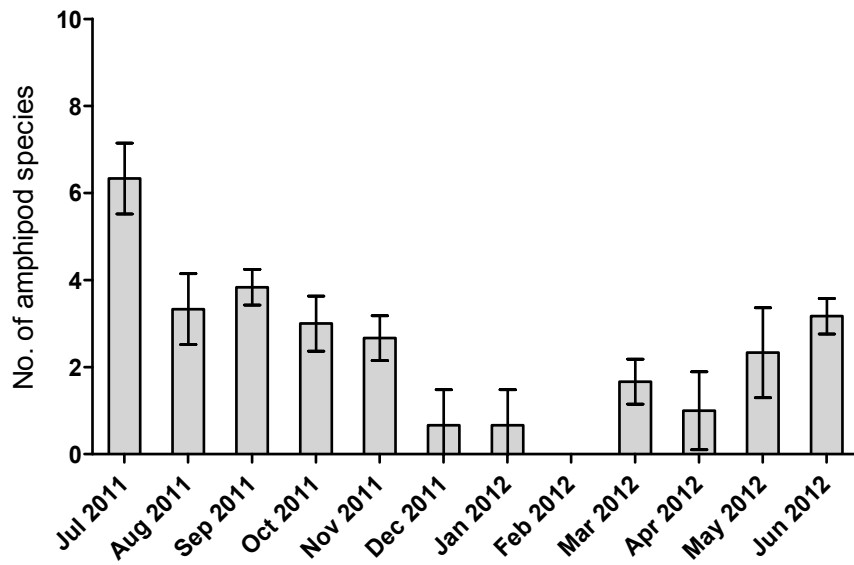
Figure 3.1.13 Number of amphipod species recorded on test panels as a function of the month of exposure (means ± SD).
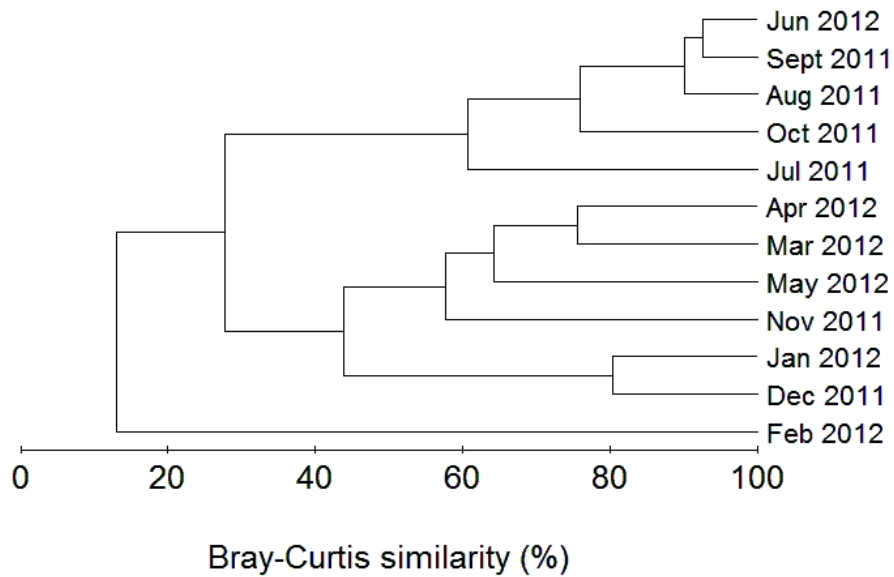
Figure 3.1.14 Species composition on the test panels after one-month exposure: cluster analysis based on Bray-Curtis similarity of amphipod species between the months.

Abundances of *Jassa* species

Species of the genus *Jassa* were the most abundant amphipods. Both the species affiliation and the specific month of exposure had a significant effect on the abundances (Tab. 3.1.8). There was also a highly significant interaction of the two factors. All three *Jassa* species were found associated with the panels. The most abundant species was *J. marmorata* (Fig. 3.1.15; Tab. 3.1.7). Due to the generally low abundances, however, this was statistically significant only for July ($P < 0.0001$) and October ($P < 0.001$). Juvenile individuals of *Jassa* (≤ 4 mm) without clear species affiliation were highly abundant from July to September 2011 and in June 2012. Juveniles occurred throughout the year. They decreased in abundance from July to October ($P < 0.0001$) and showed very low abundance values in the winter months. Their abundances increased again in late spring, when the water temperature was above 10°C.
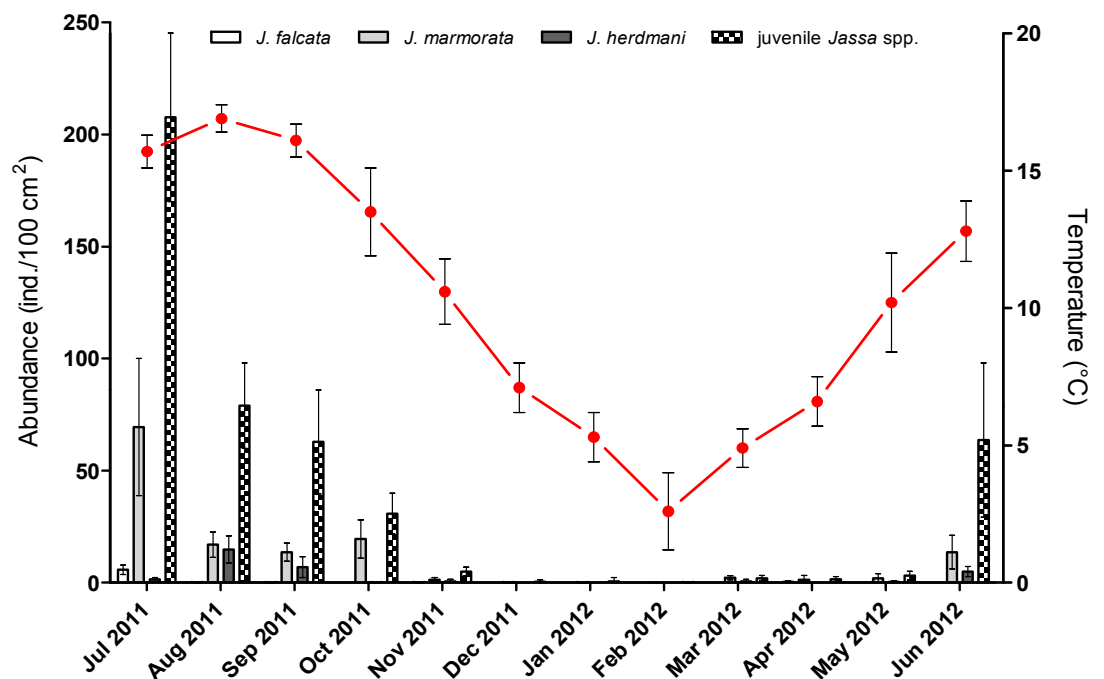
Figure 3.1.15 Abundances of *Jassa* species (> 4 mm) and their juveniles per month. The sea surface water temperature at Helgoland is plotted on a monthly basis from July 2011 to June 2012 (means ± SD).

Table 3.1.7 Abundances of *Jassa* spp. and juveniles on test panels after a one-month exposure (means ± SD).

	J. falcata	*J. marmorata*	*J. herdmani*	juv. *Jassa* spp.
Jul 2011	5.8 ± 2.1	69.5 ± 30.6	1.5 ± 0.8	207.7 ± 37.6
Aug 2011	0.2 ± 0.4	17.0 ± 5.6	14.8 ± 6.0	79.0 ± 19.1
Sep 2011	0.2 ± 0.4	13.7 ± 4.1	7.0 ± 4.7	62.8 ± 23.2
Oct 2011	0	19.5 ± 8.5	0.2 ± 0.4	30.8 ± 9.1
Nov 2011	0.2 ± 0.4	1.3 ± 1.0	0.7 ± 0.8	5.0 ± 1.9
Dec 2011	0	0.2 ± 0.4	0	0.5 ± 0.8
Jan 2012	0	0.2 ± 0.4	0	0.7 ± 1.6
Feb 2012	0	0	0	0.2 ± 0.4
Mar 2012	0	2.2 ± 1.0	0.7 ± 0.8	2.0 ± 1.3
Apr 2012	0.3 ± 0.5	1.3 ± 2.0	0	1.7 ± 1.0
May 2012	0	2.0 ± 2.0	0.3 ± 0.5	3.2 ± 2.0
Jun 2012	0	13.7 ± 7.4	5.0 ± 2.3	63.7 ± 34.4

Table 3.1.8 Results of two-way ANOVA for abundances of *Jassa* spp. in the second field experiment.

Factors & interactions	*df*	MS	F	*P*
Month	11	10385.2433	104.1264	**< 0.0001**
Species	3	21508.0868	215.6484	**< 0.0001**
Month x species	33	4799.4681	48.1213	**< 0.0001**
Error	240	99.7368		

<u>Population structure of *J. marmorata*</u>

Statements on the population structure were only possible for *J marmorata* and the four months from July to October, when abundance values were sufficiently high.

The sex ratio of *J. marmorata* did not differ from 1:1 ($P > 0.05$) and did not vary significantly among the months ($H_{K-W} = 7.74$; $P = 0.0516$; Fig. 3.1.16). This corresponds to the situation found in the first field experiment.

The percentage of egg-bearing females differed among the months ($H_{K-W} = 13.36$; $P < 0.005$). In July most females were ovigerous ($P < 0.005$), whereas in August the majority of females had empty brood pouches ($P < 0.01$).

Thumbed males were always more frequent than non-thumbed males ($P < 0.05$). The proportions of thumbed males ($H_{K-W} = 4.79$; $P = 0.1872$) as well as the proportions of the two male morphs ($H_{K-W} = 4.58$; $P = 0.2052$) did not differ among the months. However, 'majors' were significantly more frequent than 'minors' in July, but were equally common in October ($P = 0.8089$).
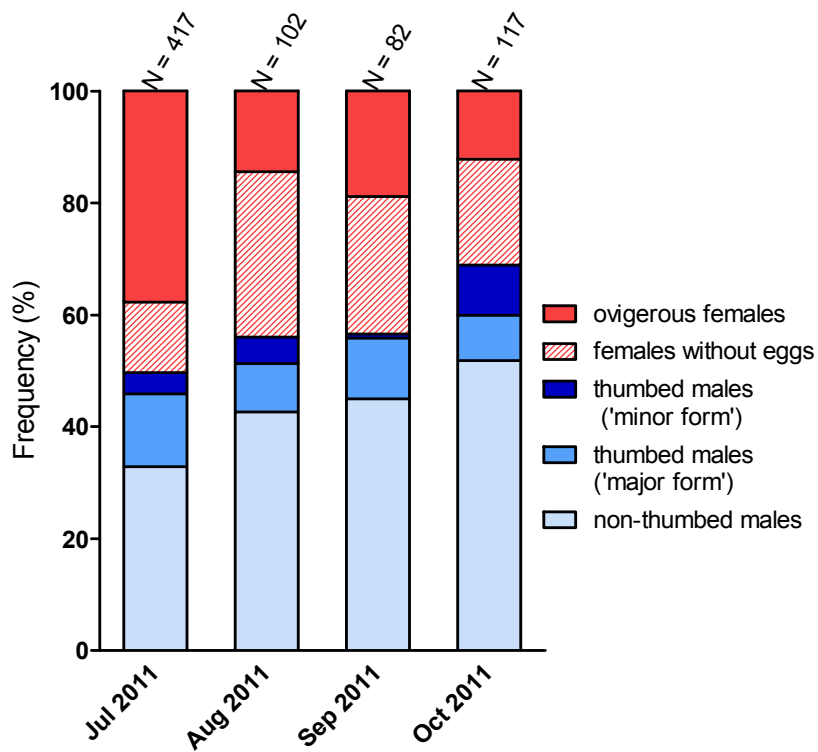
**Figure 3.1.16** Population structure of *J. marmorata* (specimens > 4 mm) after one month of exposure from July 2011 to October 2011. The individuals were classified with respect to sex, reproductive status (females with/without eggs; thumbed/non-thumbed males) and male morph ('major'/'minor' form of thumbed males).

3.2 Microhabitat selection on a macroalga

3.2.1 Isolated individuals

Singly kept individuals of both species preferred the thallus over the remaining parts of the container. *Jassa herdmani* (pooled data of all categories) chose the peripheral parts of the macroalgae over the central parts ($\chi^2_1 = 31.98$; $P < 0.0001$), and no differences were detected for this species between the three categories of animals ($\chi^2_6 = 2.331$; $P = 0.8868$; Fig. 3.2.1). In *J. marmorata*, thumbed as well as non-thumbed males also settled more often in the peripheral parts and therefore did not differ in behaviour from individuals of *J. herdmani* ($\chi^2_{12} = 6.254$; $P = 0.9027$). Females of *J. marmorata*, however, preferred the central over the peripheral parts of the thalli and therefore differed significantly from their males ($\chi^2_6 = 23.18$; $P < 0.001$) as well as from females of *J. herdmani* ($\chi^2_3 = 19.55$; $P < 0.0005$).
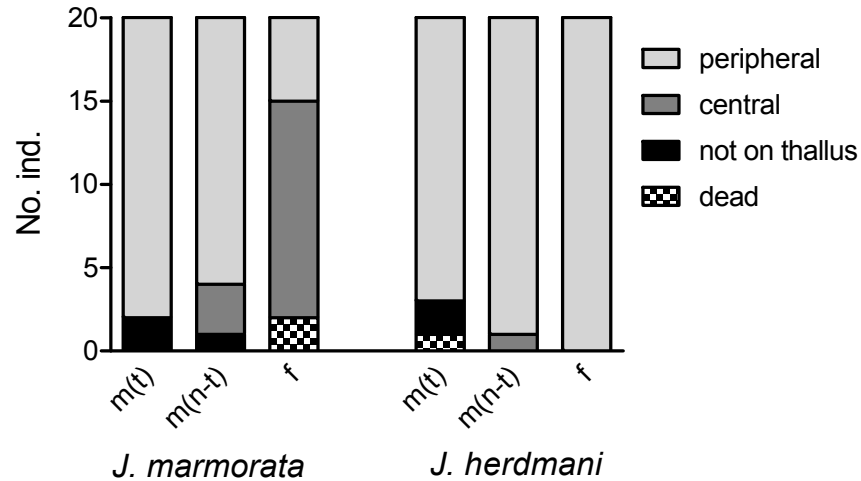
Figure 3.2.1 Spatial distribution of isolated specimens of *J. marmorata* and *J. herdmani* on a macroalga. Individuals were classified as thumbed males (**m(t)**), non-thumbed males (**m(n-t)**) and females (**f**). Peripheral and central parts of the algal thallus were distinguished as well as the remaining parts of the test box and dead individuals.

3.2.2 Groups of individuals

In the reference set-up with single-species groups of 20 females each, a significant interaction of the factors 'species' and 'area' was detected ($P < 0.0001$; Tab. 3.2.1). Both species preferred the alga over the remaining parts of the container, but females of *J. marmorata* were equally distributed over central and peripheral parts of the algae ($P = 0.8346$) whereas females of *J. herdmani* were significantly more abundant in the peripheral than in the central parts of the thalli ($P < 0.0005$; Fig. 3.2.2). The comparison between the species showed that *J. marmorata* settled more frequently in the central parts than *J. herdmani* ($P < 0.0005$), whereas *J. herdmani* chose more often the peripheral parts than *J. marmorata* ($P < 0.0005$). No differences between the species were found for the number of dead individuals ($P = 0.9999$).
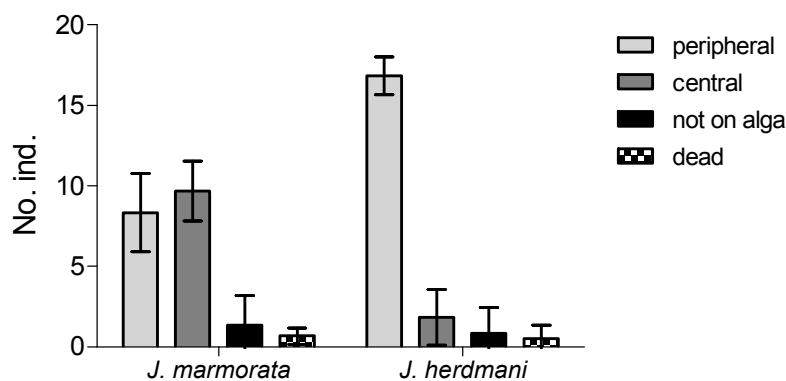
Figure 3.2.2 Spatial distribution in single-species groups (20 ind.) of female *J. marmorata* and *J. herdmani* on a macroalga. The algal thallus was categorised into peripheral and central parts and distinguished from remaining parts of the container; means ± SD (N = 6).

Table 3.2.1 Results of two-way ANOVA for the microhabitat selection of single-species groups (20 ind.) of *J. marmorata* and *J. herdmani* (interspecific comparison).

Factors & interactions	df	MS	F	P
Species	1	0.0001	0.0001	0.9999
Area	3	371.6667	143.8709	**<0.0001**
Species x area	3	133.8889	51.8279	**<0.0001**
Error	40	2.5833		

The set-ups with single species-groups of 40 females showed a significant interaction of the factors 'density' and 'area' in *J. marmorata* ($P < 0.005$) but not in *J. herdmani* ($P = 0.0979$; Tab. 3.2.2). In groups of 40 individuals, female *J. marmorata* settled relatively more often in the central parts of the thalli than in groups of only 20 individuals ($P < 0.05$; Fig. 3.2.3). Accordingly, *J. marmorata* chose the central parts over the peripheral parts at the increased density ($P < 0.0005$).
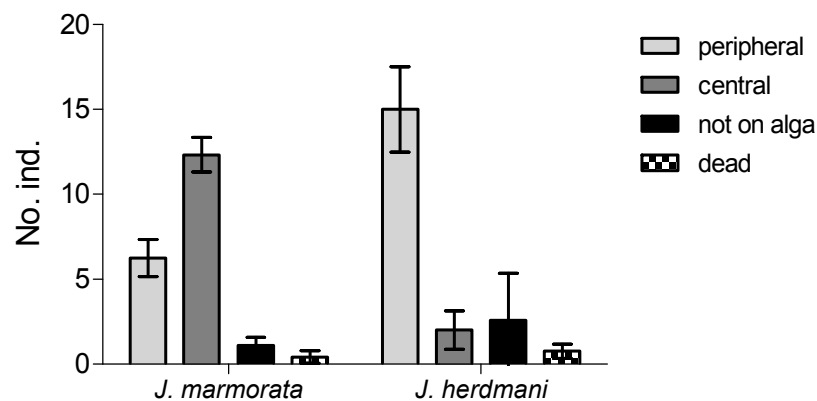

Figure 3.2.3 Spatial distribution in single-species groups of 40 individuals of female *J. marmorata* and *J. herdmani* on a macroalga (halved data); means ± SD (N = 6).

Table 3.2.2 Results of two-way ANOVAs for the microhabitat selection in single-species groups consisting of 40 individuals each. The two species were each compared intraspecifically with the reference group.

Factors & interactions	*df*	MS	F	*P*
J. marmorata				
Density	1	0.0052	0.0026	0.9591
Area	3	302.0190	153.9768	**<0.0001**
Density x Area	3	11.5746	5.9010	**<0.005**
Error	40	1.9614		
J. herdmani				
Density	1	0.0833	0.0288	0.8660
Area	3	634.5972	219.6154	**<0.0001**
Density x Area	3	6.4861	2.2446	0.0979
Error	40	2.8895		

The intraspecific comparisons of the animals' behaviour in mixed- vs. single-species set-ups with 40 individuals, showed a significant interaction of the factors 'composition' and 'area' in both *J. marmorata* ($P < 0.0001$) and *J. herdmani* ($P < 0.05$; Tab. 3.2.3). When mixed with *J. herdmani*, individuals of *J. marmorata* were found less often in the peripheral parts ($P < 0.005$), and more often ($P = 0.0870$, statistically not significant; Fig. 3.2.4) in the central parts of the alga compared to the single-species situation. Despite the significant interaction of the factors in *J. herdmani*, the post hoc test revealed no further significance between the factors. This is probably due to the transformation procedure, which may generate some loss in the power of the statistical tests.
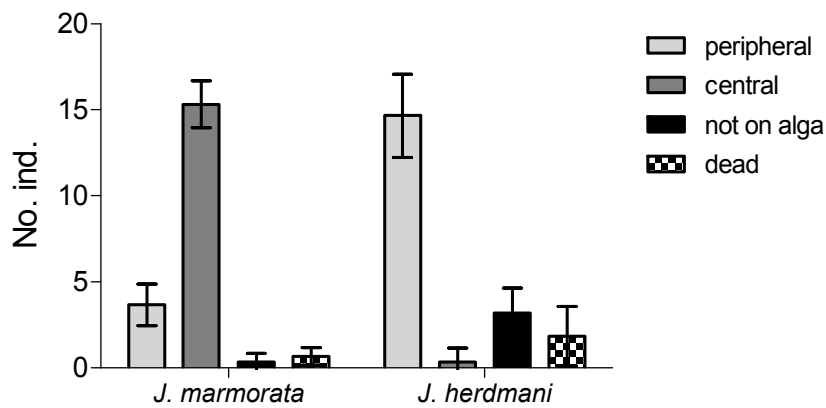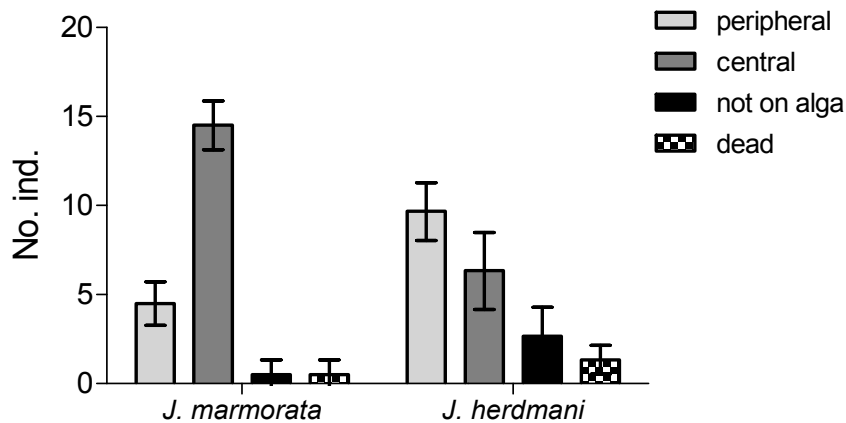

Figure 3.2.4 Spatial distribution of mixed-species groups consisting of 40 individuals (each 20 *J. marmorata* + 20 *J. herdmani*); means ± SD (N = 6).

Table 3.2.3 Results of two-way ANOVAs for the microhabitat selection in mixed-species groups (transformed data). The two species were each compared intraspecifically.

Factors & interactions	df	MS	F	P
J. marmorata				
Composition	1	0.1512	2.7926	0.1025
Area	3	21.3665	394.4014	**<0.0001**
Composition x Area	3	0.6042	11.1535	**<0.0001**
Error	40	0.0541		
J. herdmani				
Composition	1	0.0258	0.1183	0.7326
Area	3	20.1347	92.1643	**<0.0001**
Composition x Area	3	0.7187	3.2901	**<0.05**
Error	40	0.2184		

A comparison of the animals' behaviour in the reference experiment and in a medium which most probably contained "fish cues" of *T. bubalis* showed a significant interaction the factors 'water quality' and 'area' in both *J. marmorata* and *J. herdmani* ($P < 0.0001$ for both; Tab. 3.2.4). In direct comparison with the reference experiment, *J. marmorata* settled more often in the central parts of the thallus ($P < 0.0005$), and less often in the peripheral parts ($P < 0.005$; Fig. 3.2.5). The same pattern was found for *J. herdmani*, which was more frequent in the central parts and less frequent in the peripheral parts of the algal thallus (both $P < 0.0005$) than in the reference experiment. However, individuals of *J. herdmani* still preferred the peripheral parts over the central parts of the alga ($P < 0.01$).

Figure 3.2.5 Spatial distribution in single-species groups (20 ind.) of female *J. marmorata* and *J. herdmani* on a macroalga; seawater contained fish cues of the sea scorpion (*Taurulus bubalis*); means ± SD (N = 6).

Table 3.2.4 Results of two-way ANOVAs for the microhabitat selection in single-species groups (20 ind.) in seawater taken from a fish tank. The two species were each compared intraspecifically with the reference group.

| Factors & interactions	*df*	MS	F	*P*
J. marmorata				
Water quality	1	0.0001	0.0001	0.9999
Area	3	353.4443	158.2587	**<0.0001**
Water quality x Area	3	38.7778	17.3631	**<0.0001**
Error	40	2.2332		
J. herdmani				
Water quality	1	0.0001	0.0001	0.9999
Area	3	384.5556	168.4184	**<0.0001**
Water quality x Area	3	75.6667	33.1386	**<0.0001**
Error	40	2.2833		

3.3 Survival and moult intervals of adults

Under the constant laboratory conditions both sexes in all three species survived significantly longer at 8°C than at 18°C ($P < 0.05$; Table 3.3.1), except for male *J. marmorata* where no difference was found between the two temperature treatments ($\chi^2_1 = 0.1175$; $P = 0.7318$; Fig. 3.3.1). In all three *Jassa* species females lived longer than males at both temperatures ($P < 0.05$). The most long-lived individual was a *J. marmorata* female, which survived for a period of as long as 380 days at 8°C (Fig. 3.3.2).

Furthermore, there were also significant differences in survival rates between species at 8°C. Thumbed males of *J. falcata* survived significantly longer compared to males of *J. marmorata* ($\chi^2_1 = 13.24$; $P < 0.0005$) and *J. herdmani* ($\chi^2_1 = 11.31$; $P < 0.001$), whereas no difference was detected between males of the two latter species ($\chi^2_1 = 0.3245$; $P = 0.5689$). Female *J. falcata* lived significantly longer than females of *J. herdmani* ($\chi^2_1 = 5.244$; $P < 0.05$), but no further differences between species were found. At 18°C, however, differences between the species were statistically not significant, although both male and female *J. marmorata* tended to survive longer than the respective sexes of *J. falcata* and *J. herdmani*.

Table 3.3.1 Survival time (days) of *J. falcata*, *J. marmorata* and *J. herdmani* at two different temperatures; means ± SD, (N).

	J. falcata		*J. marmorata*		*J. herdmani*	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
8°C	59.4 ± 33.3; (20)	131.4 ± 90.7; (21)	26.9 ± 23.8; (20)	133.5 ± 122.5; (20)	35.5 ± 19.4; (21)	82.3 ± 62.6; (19)
18°C	22.0 ± 16.0; (19)	67.4 ± 31.1; (20)	29.7 ± 16.7; (21)	73.8 ± 39.5; (21)	23.1 ± 15.4; (19)	49.0 ± 38.2; (21)
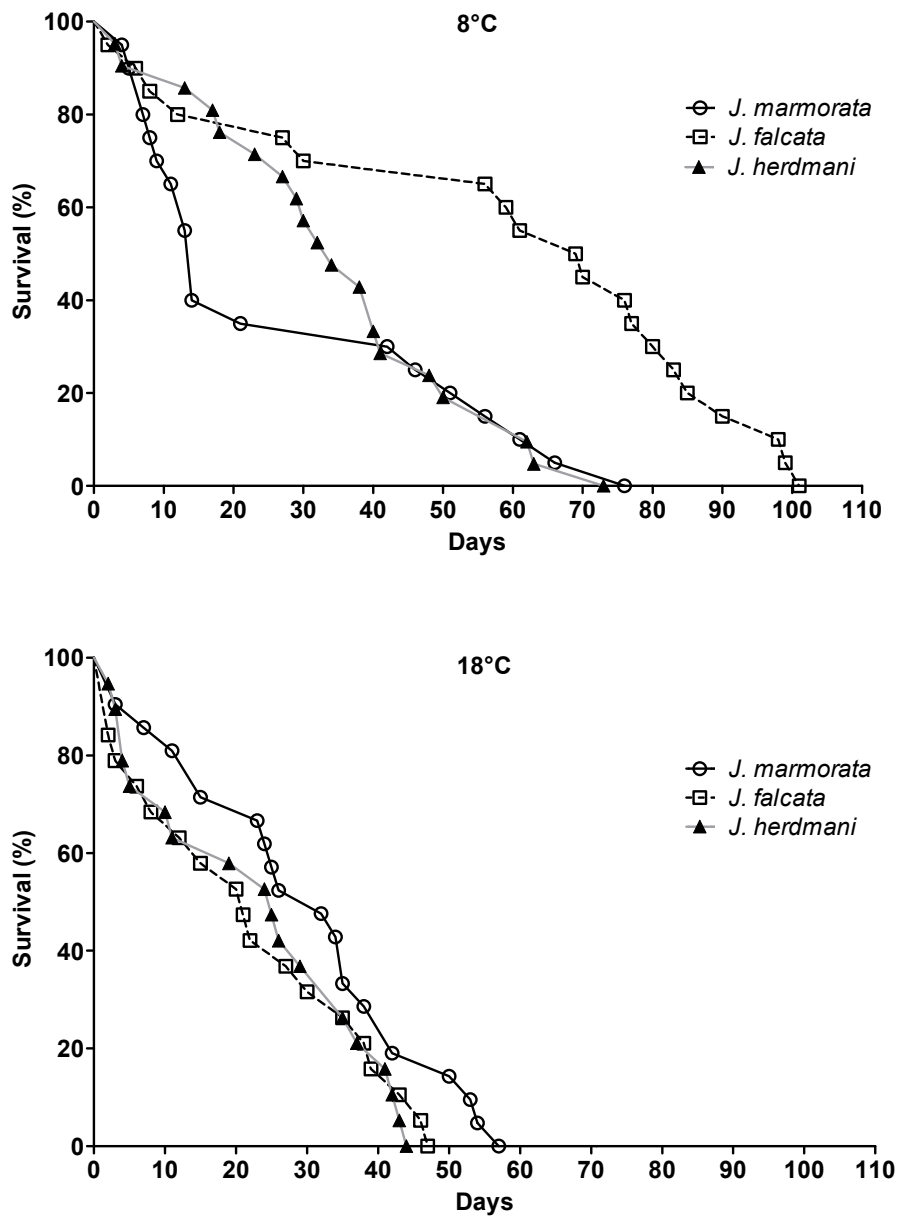
Figure 3.3.1 Survival rates of thumbed males ('major form') of *J. falcata*, *J. marmorata* and *J. herdmani* under two different temperature regimes (8°C and 18°C).
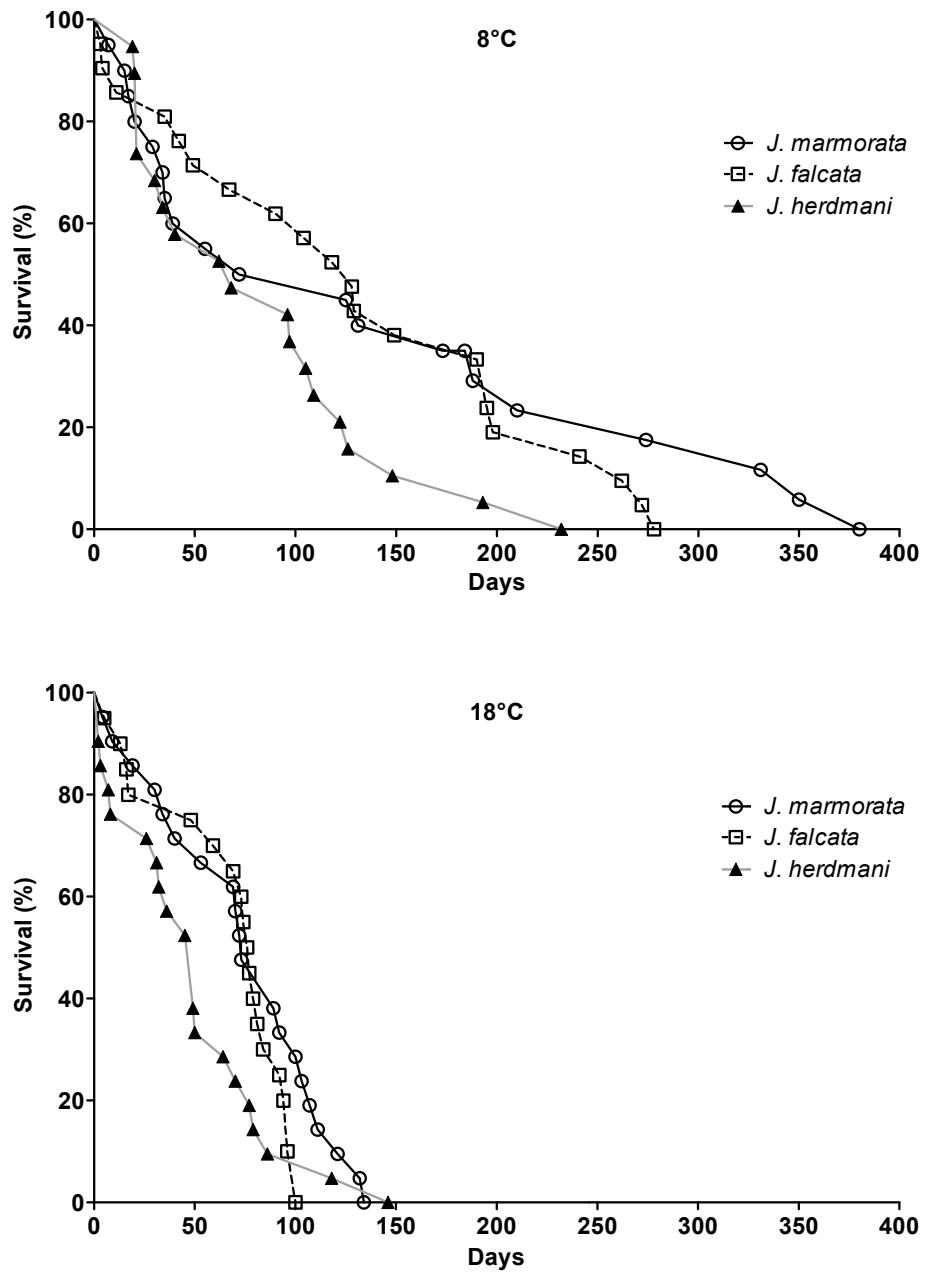
Figure 3.3.2 Survival rates of adult females of *J. falcata*, *J. marmorata* and *J. herdmani* under two different temperature regimes (8°C and 18°C).

During the experiment the females underwent several moults, whereas thumbed males did not moult any more. In all three species the factor 'temperature' had no significant effect on the total number of moults per individual ($P = 0.2672$.) In contrast, species affiliation had a clear effect on the total number of moults per individual ($P < 0.0005$; Tab. 3.3.2, 3.3.3). This was due to *J. herdmani* showing a lower number of moults than *J. marmorata* for both temperatures (8°C: P < 0.05; 18°C: $P < 0.05$).

Table 3.3.2 Number of moults in adult females of *J. falcata*, *J. marmorata* and *J. herdmani* at two different temperatures; means ± SD, (N).

	J. falcata	J. marmorata	J. herdmani
8°C	4.55 ± 2.45; (18)	6.66 ± 4.35; (12)	2.72 ± 1.61; (11)
18°C	4.58 ± 1.90; (17)	6.64 ± 2.52; (17)	3.73 ± 2.28; (15)

Table 3.3.3 Results of two-way ANOVA for the number of moults in adult *Jassa* spp. females.

Factors & interactions	df	MS	F	P
Species	2	0.3989	8.8722	**<0.0005**
Temperature	1	0.0560	1.2475	0.2672
Species x Temperature	2	0.0114	0.2554	0.7751
Error	84	0.0449		

Temperature had a significant effect on the length of the intermoult period ($F_{1,84} = 1038.19$; $P < 0.0001$). In all three species moult intervals of females were significantly shorter at 18°C than at 8°C (each $P < 0.0005$; Fig. 3.3.3, Tab. 3.3.4). Additionally, significant differences were also found among species ($F_{2,84} = 29.84$; $P < 0.0001$). Female *J. marmorata* showed the shortest moult intervals at both temperatures, differing significantly from the intervals of *J. falcata* and *J. herdmani* at 18°C ($P < 0.005$) as well as from those of *J. herdmani* at 8°C ($P < 0.005$). No difference between *J. falcata* and *J. herdmani* was detected, neither at 8°C ($P = 0.1397$) nor at 18°C ($P = 0.8393$).

In all three species and at both temperature regimes the length of intermoult periods increased significantly over time ($P < 0.001$). This is reflected in the slopes of the linear regressions, differing significantly from zero (Fig. 3.3.3) with a single exception: At 18°C female *J. marmorata* did not show an increase in moult intervals over time ($F_{1,111} = 0.3728$; $P = 0.5427$). However, at 8°C the slopes of the linear regressions differed significantly from those at 18°C in all three species ($P < 0.005$). A comparison between species revealed that the regression lines of *J. marmorata* had always the lowest slopes: They differed at 8°C from *J. falcata* ($F_{1,158} = 11.925$; $P < 0.001$) as well as *J. herdmani* ($F_{1,106} = 10.067$; $P < 0.005$) and also did so at 18°C (*J. falcata*: $F_{1,187} = 9.9005$; $P < 0.005$; *J. herdmani*: $F_{1,165} = 10.116$; $P < 0.005$). No difference was found between *J. falcata* and *J. herdmani*, neither for 8°C ($F_{1,108} = 1.4713$; $P = 0.2278$) nor 18°C ($F_{1,130} = 0.0032$; $P = 0.9545$).

Table 3.3.4 Moult intervals (days) of adult females of *J. falcata*, *J. marmorata* and *J. herdmani* at two different temperatures; means ± SD, (N).

	J. falcata	*J. marmorata*	*J. herdmani*
8°C	28.2 ± 5.2; (83)	25.9 ± 3.5; (80)	31.1 ± 4.4; (30)
18°C	13.3 ± 2.2; (78)	11.0 ± 2.2; (113)	13.9 ± 2.0; (56)
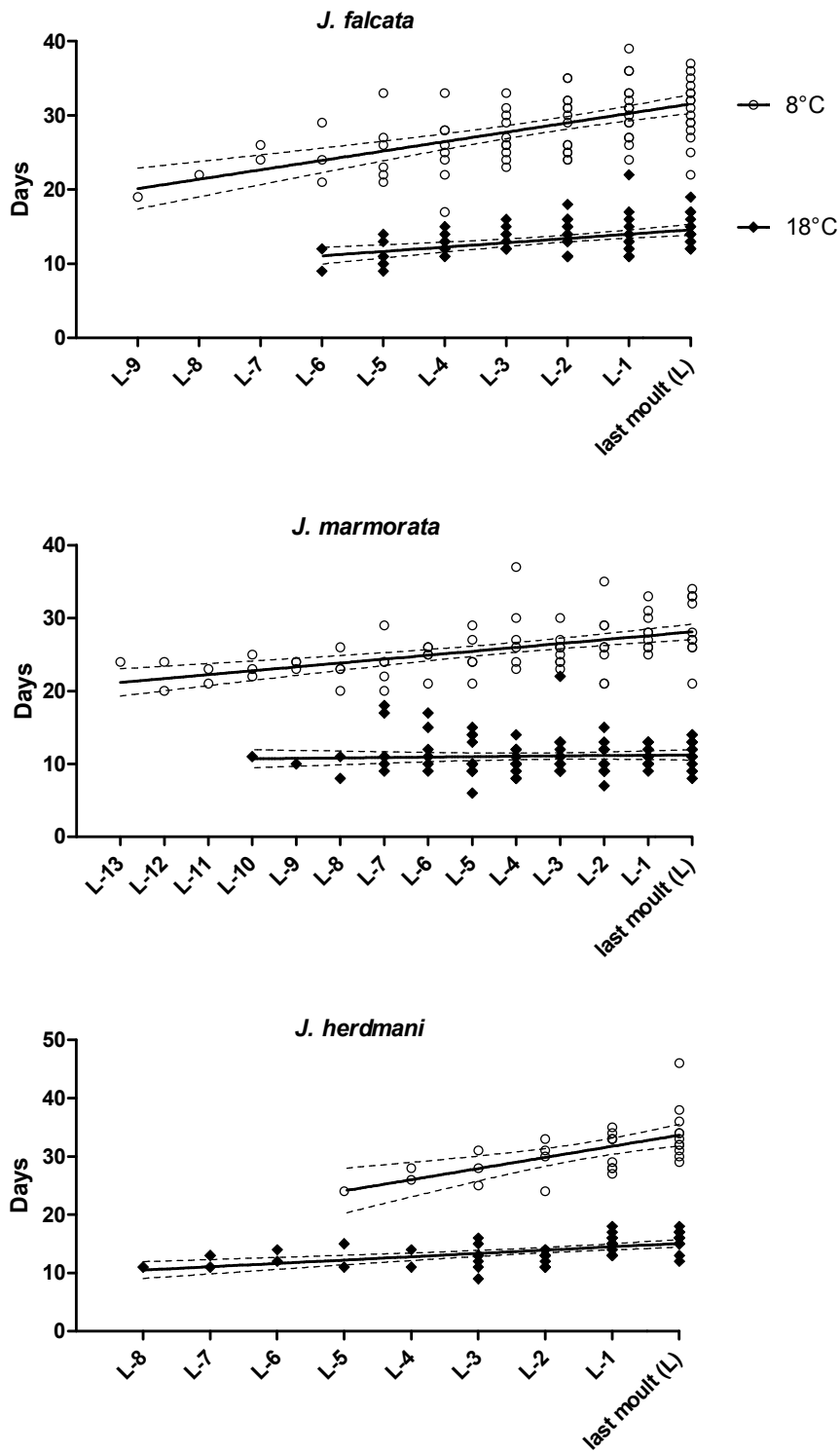
Figure 3.3.3 Linear regression for successive moult intervals per individual in adult females of *J. falcata*, *J. marmorata* and *J. herdmani* at two different temperatures (8°C and 18°C). Moults are denoted in retrograde order (with last moult as L, and previous moults as L-1, L-2 etc.).

Discussion

4.1 Abundances and population structure in the field

In both experiments immersed PVC panels were quickly colonised by *Jassa* species. The panels became overgrown with *Jassa* tubes to a varying degree of coverage. Amphipods were the primary colonisers and dominated the fouling communities over the whole period of investigation. Tubiculous amphipods have repeatedly been reported to dominate marine biofouling systems (e.g. Barnard 1958; Norderhaug et al. 2002; Zintzen et al. 2008; Krone et al. 2013). The dynamics of the fouling process is probably affected by diverse environmental factors such as seasonal factors, water turbidity/wave exposure, substrate quality, and biogeographic constraints. According to Langhamer et al. (2009), a certain degree of sessile epifaunal colonization of a substrate is required before smaller vagile and hemi-sessile species such as *Jassa* can establish themselves. However, this does not seem to be a precondition for the colonization of PVC panels by *Jassa* species at Helgoland. Caspers (1952) reported that *Jassa* spp. (as '*J. pulchella*') can be the primary settlers on navigational aids, building multiple layers of tubes which form dense and thick fouling masses. This could be confirmed by observations of the author. The resulting mats largely prevent other animals such as the blue mussel *Mytilus edulis* Linnaeus, 1758 from settlement, and simply by overgrowing *Jassa* species can suppress any organisms (e.g. algae, barnacles), which may have arrived at about the same time (Caspers 1952; Barnard 1958). This is corroborated by the results of the first field experiment at the exposed location: With increasing coverage of the panels by *Jassa* mats over time, other sessile organisms became scarce. In contrast, panels at the sheltered location were mainly covered by solitary ascidians. This conforms to the results of Harms & Anger (1983). Nevertheless, thick mats of *Jassa* tubes partly covered the ascideans and also filled the gaps among individuals.

The amphipod species diversity recorded in the first field experiment showed distinct differences among the three locations. It was highest at the 10 m station, followed by the sheltered location. The fouling community at the exposed location exhibited the lowest amphipod species diversity which even decreased over the summer months. As the total number of species remained constant, this decrease in amphipod diversity (Simpson's diversity index) was due to the very high abundances of *Jassa* species in summer. De Kluijver (1991) identified two major parameters structuring the natural hard bottom communities of Helgoland: the amount of light, and the degree of hydrodynamics. Although this study mainly dealt with large epibenthic instead of smaller, vagile species, the findings may apply to Helgoland's amphipod fouling communities as well. Studies in the Mediterranean Sea also showed that the degree of water turbulence and the associated rate of sedimentation have a strong effect on both amphipod species diversity and species richness (Conradi et al. 1997).

Panels which had been exposed for one month only (second field experiment) exhibited fouling communities with lower amphipod species diversity. This underlines the importance of the duration of exposure to the diversity of the establishing amphipod community. Distinct differences in species diversity after a one-month exposure were recorded between summer and winter months. This reflects the well-known seasonality in colonization activity characteristic of higher geographic latitudes, with decreased settlement rates in winter (Meadows 1969).

Species of *Jassa* showed the highest abundances in the fouling communities of the present investigation, dominating all other amphipod species. In general, the highest abundances were detected at the exposed location followed by the sheltered location, whereas abundances at the 10 m station were by far the lowest. This is just the opposite of what was found for the diversity of amphipod species. Predation is probably a major factor for amphipod abundances and fouling communities in general (Stoner 1980; Greene & Grizzle 2007). The near-bottom panels at the 10 m station were probably much easier accessible to benthic

predators (crustaceans and fish) than the suspended installations at the exposed and the sheltered location. Thus, an increased predation rate may be the major cause of the reduced amphipod abundances values at the 10 m station. Similar observations were made by Greene & Grizzle (2007) for the abundances of *J. marmorata* and *Caprella* sp. in fouling communities on fish cages.

It is interesting to note that the location with the highest *Jassa* abundances (exposed location) exhibited the lowest amphipod species diversity. This may be a result of increased interspecific competition (Bengtsson 1989). High abundances of *Jassa* may prevent the establishment of other amphipod species in a direct and/or indirect way. *Jassa* individuals can prey directly on smaller sympatric amphipods which get within reach of their tubes (Armsby & Tisch 2006). They can also feed by filtering floating juveniles out of the water column, thus preventing their establishment in the fouling community (Highsmith & Coyle 1991). Furthermore, the thick layer of tubes may itself prevent further organisms to settle on the substrate (indirect prevention). All these factors may be responsible for the low amphipod species diversity at the exposed location, which was located directly above the 10 m station where the amphipod species diversity was higher, while *Jassa* abundances were lower. The observed patterns are in accordance to the 'inhibition model' suggested by Connell & Slatyer (1977) for alternative mechanisms of successional development. Accordingly, early colonisers can occupy space and/or other resources, thus preventing other species from settling. In such cases, the early arrival can be more important for a successful colonisation of a habitat than a species' competitive ability.

Abundances of *Jassa* species on the test panels clearly differed between months and with the length of time which the panels had been exposed in the field. Additionally, there were species-specific quantitative differences in the abundances of the three *Jassa* species at the different locations. *Jassa falcata* reached its highest abundance values at the 10 m station where it was the dominant *Jassa* species. In contrast, *J. marmorata* clearly dominated at both the exposed location, where it reached its highest abundances, and at the sheltered

location. *Jassa herdmani* was never dominant; the highest abundances of this species were found at the exposed location. The low abundances of *J. falcata* at the exposed and the sheltered location may result from a direct interference with *J. marmorata*. In July, both species were equally abundant at the exposed location, but when the densities of *J. marmorata* increased in August, *J. falcata* nearly vanished from this location. As adult *J. marmorata* can grow bigger than adults of *J. falcata* (Conlan 1990; Purz 2012), they are probably able to displace the smaller species from homogeneous habitats such as PVC test panels. This may occur by an optional retreat of the competitively inferior species or even by intraguild predation (Armsby & Tisch 2006).

Both *J. marmorata* and *J. herdmani* were significantly more abundant at the exposed than at the sheltered location. Similar results were obtained in a summer field experiment by Beermann & Franke (2012). This difference may be due to the stronger currents which provide for an increased supply of food and an increased rate of colonization. At all three locations, the *Jassa* populations clearly increased in August (*J. falcata* at the 10 m station, *J. marmorata* as well as *J. herdmani* at both the exposed and the sheltered location). In *J. marmorata* this increase in density was followed by a decrease at both the exposed and the sheltered location in the subsequent months towards November. Scinto et al. (2007) reported on a peak of abundances in spring (February to April) for Mediterranean *J. marmorata* populations, whereas a population sampled by Franz (1989) on floating wooden docks in New York had their highest abundances in summer (June to August). The latter author also reported on sharp declines in density followed by rapid recoveries. As many generations co-occur in a population, the declines could be an accidental effect of age-dependant disappearance of generations when recruitment of juveniles is low. At Helgoland, however, a seasonal factor was probably responsible for the decline in November, as abundances decreased at both the exposed and the sheltered location at the same time.

Dispersal in *Jassa* species is mainly restricted to juveniles and small adults (Franz & Mohamed 1989; Havermans et al. 2007). The panels which had been exposed in a year-round experiment for one month only (second field experiment), represent snapshots of the seasonal changes in recruitment intensity. One month of exposure is too short a period to allow arrived juveniles for growing to maturity (Nair & Anger 1979b). Therefore, the specimens collected from test panels after one month of exposure mainly consisted of juvenile colonizers and (much less frequently) of juveniles which had hatched from the pouches of recruited ovigerous females. The data showed marked changes in recruitment activity over the annual cycle. Recruitment occurred all-year-round, but was insignificant in winter. As the sheltered location was protected by the walls and boulders of the South Harbour, the delivery of potential colonisers was probably strongly constrained at this location. The disposition of juveniles to dispersal via currents is most likely a strategy which reduces intraspecific competition up to cannibalism in crowded populations (Franz & Mohamed 1989; Armsby & Tisch 2006), and also promotes a rapid colonisation of habitats. The high recruitment rate on test panels in summer may simply reflect a peak of density and reproductive activity of *Jassa* populations at that time of the year. This is corroborated by the results of the first field experiment and the experiment of Beermann & Franke (2012).

The sex ratio in populations of all three species varied seasonally. Similar fluctuations were reported for *J. slatteryi* populations in Korea (Jeong et al. 2007). Nair & Anger (1980) found variations in the percentage of females in a *Jassa* spp. community at Helgoland. However, their findings related to a mixture of species (see Conlan 1990) and are thus hardly comparable to the present data. In addition, the sampling method only allowed for rough estimations and may not have been representative. Nevertheless, the authors found a surplus of females which corresponds with findings on Mediterranean populations of *J. marmorata* (Scinto et al. 2007). In the present investigation populations of *J. marmorata* at both the exposed and the sheltered location were weighted towards females in early

summer, while the sex ratio shifted in favour of males later in the year. In contrast, the *J. herdmani* population at the exposed location showed a balanced sex ratio nearly throughout the year. Potential factors which can produce seasonal changes in the sex ratio of a population are environmental sex determination (ESD) by factors such as temperature, photoperiod and other unknown environmental parameters as well as infections with parasites (Bulnheim 1967, 1977, 1978; Ginsburger-Vogel & Magniette-Mergault 1981; Watt & Adams 1993). But also differences between the sexes with respect to mortality and/or the time within which maturity is reached can result in temporal changes in the sex ratio. Juvenile *Jassa* spp. males grow and mature faster than females (Nair & Anger 1979b). Therefore, when specimens of *J. marmorata* are analysed which are bigger than 4 mm, this can result in a male biased sex ratio, due to sex-specific differences in the growth pattern.

Ovigerous females were found in all months of the year. This applied to all three species, although the low abundances in *J. falacta* did not allow for a proper statistical analysis. However, in both *J. marmorata* and *J. herdmani* the proportion of ovigerous females decreased in the winter months. This was particularly pronounced in *J. marmorata* at the sheltered location, where ovigerous females even disappeared completely in January. Year-round reproduction was also reported for other *J. marmorata* populations (Franz 1989; Scinto et al. 2007). Franz (1989) and also Nair & Anger (1980) for *Jassa* spp. at Helgoland, reported an increase in the proportion of ovigerous females in winter and early spring, which clearly contrasts with the results of the present investigation.

In a variable extent depending on season, thumbed (i.e. reproductively active) males were generally less common than non-thumbed males. Seasonal changes also occurred in the proportion of the two distinct male morphs: In winter 'minor form' males were more frequent than the alternative morph in both *J. marmorata* and *J. herdmani*. This is probably explained by the poorer food quality in winter, as the protein content of the food (and not the genetic make-up) sets an

individual's developmental pathway leading alternatively to the 'minor' or the 'major' male morph (Kurdziel & Knowles 2002).

The population structure of *J. marmorata* on panels after one month of exposure (second experiment) was surprisingly little different from that on panels which had been exposed for a longer time and were collected at the respective months. This is a further indication that the population structure on the test panels is determined by recruitment from the surrounding habitats rather than by successional development on the panels themselves.

4.2 Microhabitat selection on a macroalga

Isolated females of *J. marmorata* mostly took shelter in the central parts of the algae. This preference contrasts with the settlement behaviour of conspecific males as well as with that of both males and females of *J. herdmani*. Although isolated males of *J. marmorata* preferred the peripheral over the central algal parts, thumbed males in a natural community probably would not. The appearance of a thumb on gnathopod 2 marks the beginning of sexual activity. Males then abandon their tubes to spend the rest of their life roaming around and searching for receptive females (Borowsky 1985; Conlan 1989). This suggests that in the field thumbed males of *J. marmorata* would also be found preferentially in central parts of algal thalli where they can expect to encounter receptive females. Therefore, females were chosen as the primary object of the present study on habitat selection in *Jassa* species.

Amphipods usually show the highest diversity in marine benthic habitats among Crustacea. There are several examples of closely related species which co-occur on a small spatial scale (e.g. Fenchel & Kolding 1979; Skadsheim 1983; Lancelotti & Trucco 1993). A stable co-ocurrence requires physiological, morphological or/and behavioural trade-offs among competing species (Tilman 1987), which may result in differential distributions of species along environmental gradients such as salinity (Fenchel & Kolding 1979; Skadsheim 1983), wave exposure (Lancelotti & Trucco 1993), sediment depth (Hill & Elmgren 1987), and other factors. *Jassa* species are hemi-sessile filter feeders. In densely crowded fouling communities they compete primarily for space as a limited resource. Hence, spatial segregation may act as a form of resource partitioning, reducing interspecific competition and thus allowing for a stable coexistence (Connell 1983; Schoener 1983, 1985, 1986).

When tested in groups, female *J. marmorata* again used both the peripheral and the central parts of the algal thallus, whereas female *J. herdmani* were restricted to the peripheral parts. At an increased density, the pattern observed for *J. marmorata* slightly changed in favour of the central algal parts.

However, when specimens of *J. marmorata* encountered those of *J. herdmani*, they scarcely settled in peripheral parts, whereas *J. herdmani* showed the same pattern as for the single species set-ups. There is a clear interspecific effect, with individuals of *J. herdmani* having a stronger effect on the distribution of *J. marmorata* than conspecific individuals. A possible explanation for the observed patterns is provided by the differential escaping behaviours of *J. marmorata* and *J. herdmani* responding to disturbance. After a mechanical stimulus, *J. marmorata* takes shelter by hiding in an algal thallus, whereas *J. herdmani* swims away (Beermann & Franke 2012). In a direct encounter of individuals of *J. marmorata* with the congeneric *J. herdmani* in the peripheral parts of the thallus, *J. marmorata* mostly eludes to the central parts for settlement, whereas *J. herdmani* typically would swim away and settle again in the peripheral parts. In addition to the species' general microhabitat preference, these behavioural patterns would affect the spatial distributions of *J. marmorata* and *J. herdmani* in the field on small spatial scales even when animal densities were relatively low.

The microhabitat preference of *J. marmorata* and *J. herdmani* was also influenced by environmental parameters. In the presence of 'fish cues' in the seawater, *J. marmorata* strongly avoided peripheral algal parts. In contrast to their clear preference of the peripheral parts in filtered natural seawater, individuals of *J. herdmani* in 'fish cue' seawater also settled in central parts of the thallus. 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; Jacobson & Stabell 2004) and crustaceans (Main 1987; Holomuzki & Short 1988; Lindén et al. 2003). Also amphipods have been demonstrated to avoid potential predatory fish species by altering their behaviour in response to 'fish cues' (kairomones) in the water. However, most studies have dealt with fresh-water *Gammarus* species (e.g. Anderson et al. 1986; Holomuzki & Hoyle 1990; Wudkevich et al. 1997; Pennuto

& Keppler 2008) whereas only few investigations (e.g. Zamzow et al. 2010) have observed direct predator avoidance in amphipod species of marine environments.

The obtained results represent the first evidence of a predator avoidance behaviour in marine tube-building amphipod communities. This behaviour must be taken into account when assessing the spatial distribution of *Jassa* individuals in the field, as aggregation at 'safer' areas could come along with a reduced food supply (Scheffer 1997), especially in filter feeders. In addition, the result of predator avoidance behaviours may change competitive interactions among prey species (Holt 1984), for example among the co-occurring *Jassa* species at Helgoland. The mode of avoidance behaviours may depend on different environmental parameters (e.g. 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 (Wudkevich et al. 1997; Wisenden et al. 2001). All these possible influences on *Jassa*'s settlement behaviour must be considered thoroughly in future surveys.

4.3 Survival and moult intervals of adults

Unsurprisingly, the laboratory experiments showed that temperature had an effect on the species' survival. At the higher temperature, all three species showed a reduced lifespan. This is a well-known pattern for marine invertebrates and has repeatedly been shown for amphipods (Nair & Anger 1979a, 1979b; Pöckl 1992). However, reliable information on potential life spans (in the absence of predation) of amphipods is still scarce, as most investigations relied on field samplings and therefore displayed life span in the presence of predation and other constraints.

Adult females of all three *Jassa* species survived longer than conspecific thumbed males in both temperature treatments. Similar observations were made in surveys on *Jassa* spp. (as '*J. falcata*' in Nair & Anger 1979b) as well as in starvation experiments with *J. herdmani* (Havermans et al. 2007) and may be explained by the unusual reproductive patterns in *Jassa* species. Males and females mature at about the same age (Nair & Anger 1979b). But in contrast to females, males get sexually active after a terminal moult which is accompanied by the appearance of a thumb-like protuberance on the second gnathopods. Thumbed males are sexually active for the rest of their lives, searching and attending receptive females all the time without building tubes anymore (Borowsky 1985; Conlan 1989). As a consequence, males certainly mate multiple times with different females in densely crowded *Jassa* communities, whereas females only produce a few broods linked to preceding moults. Thus, it is most likely the strategy of 'major' males to invest as much energy as possible in a rapid mating success, as they face a higher risk of predation (high exposition to predators due to their 'roaming behaviour'). The absence of energetically expensive moults once males have become sexually active, corroborates this assumption. Further studies need to show if this also applies to 'minor form' males of *Jassa*. However, in other amphipod genera such as *Gammarus*, males feature greater life spans than females, probably due to their physiologically less stressful mating patterns (Kinne 1953; Pöckl 1992).

At 8°C, males of the NE Atlantic *J. falcata* survived longer than males of *J. marmorata* and *J. herdmani*, probably reflecting differences in the species' geographical distributions. The low temperature of 8°C probably fits best *J. falcata*'s temperature optimum. Although no statistically significant differences among species were found for the 18°C treatment, *J. marmorata* tendentially showed the greater life span. As specimens of this cosmopolitan species have also been found in much warmer seas of the world, the demonstrated trend probably would become more evident at even higher temperature treatments. Reproduction of all three *Jassa* species at Helgoland seems to occur year-round (Nair & Anger 1980; unpublished Data). Therefore, it unlikely that the differences recorded among species relate to differences in the age structure of the sampled populations.

Although temperature clearly affected the intermoult period in all three species, the total number of moults proved to be largely independent of temperature. This suggests that similar to males, female *Jassa* may also be restricted to a fixed maximal number of moults per life time which are passed in more or less rapid succession depending on temperature.

Moult intervals are known to lengthen at decreasing temperatures in Crustacea (e.g. amphipods) as metabolism is slowed down (Kinne 1960, 1961; Hartnoll 1982; Conan 1985; Highsmith & Coyle 1991; Hartnoll 2001). Females of *J. marmorata* clearly exhibited the shortest moult intervals of the three species at both temperatures, whereas *J. falcata* and *J. herdmani* did not differ from each other. The process of moulting is essential for brood production in amphipods, as oviposition only can take place immediately after ecdysis. All other things being equal, a shorter intermoult period should result in a faster reproductive output of *J. marmorata*. This could explain field observations by Beermann & Franke (2012), indicating that *J. marmorata* is the more effective coloniser of clean substrate.

Under laboratory conditions, intermoult periods of adult crustaceans usually become longer over time, related to age and/or size of the individual

(Conan 1985). In *Jassa*, females of all three species showed an increase in intermoult periods over time in both temperature treatments (except for *J. marmorata* females at 18°C), which was even more obvious at 8°C than at 18°C. The increase of moult intervals with age does not necessarily be a response to decreasing growth rate, as growth and moulting rate in amphipod crustaceans can be decoupled (Highsmith & Coyle 1991). An alternative explanation might be provided by the findings of Kinne (1953, 1960) for different *Gammarus* species. When kept in isolation, females showed increasing moult intervals over time, whereas females which were accompanied by an adult male moulted at constant short intervals. Kinne (1953) demonstrated that this was caused by the praecopula, during which males grab and carry their mates. Although thumbed *Jassa* males ('major form') do not grab their females, but only attend them by sitting on their tubes without physical contact (Borowsky 1983, 1985; Conlan 1989; 1991; personal observation), the isolation of the animals from potential mates in the present experiment could be a possible explanation for the observed patterns. Again, *J. marmorata* also showed the lowest increase in the intermoult period of the three species and no increase at all at 18°C.

4.4 Concluding remarks

The taxonomic distinction of the three sympatric *Jassa* species is clearly substantiated by differences in their biological and ecological traits. This underlines the importance of an exact species determination in field and laboratory studies on amphipods. In the three *Jassa* species, ecological differences were found in quite different contexts: life history traits, spatial distribution in the field, and microhabitat selection. Differences in other contexts (e.g. feeding) may occur as well, but were not subject of the present investigation. Although the recorded differences in the biology and ecology of the species may primarily reflect adaptations to different environmental conditions, accomplished in the course of speciation, at least some of them also contribute to a partitioning of resources. This reduces the degree of interspecific competition among *Jassa* species, thus facilitating a short-term or even long-term coexistence on a small spatial scale.

5.1 Abstract

Amphipods are known to dominate marine fouling communities on a broad range of different substrates. In particular on artificial substrates, different species of the genus *Jassa* can occur sympatrically in remarkably high abundances, exceeding all other types of macrozoobenthos in terms of numerical abundance and even biomass. Considering the ever-increasing anthropogenic transformations of coastal areas and the scheduled introduction of offshore constructions, amphipods may increasingly influence the functioning of marine coastal ecosystems. Information on the biology and ecology of co-occurring *Jassa* species which would allow for an understanding of their coexistence, is largely missing.

In the present thesis field and laboratory experiments were conducted in order to analyse possible differences in both biological and ecological traits among three co-occurring *Jassa* species (*J. falcata*, *J. marmorata* and *J. herdmani*) at Helgoland (North Sea, German Bight). In the field, the *Jassa* communities which established on artificial panels, showed strong seasonal and spatial variations. General patterns were found to be in contrast to the amphipod species diversity in general: High abundances of *Jassa* species coincided with a low amphipod species diversity. *Jassa falcata* was the dominating species at a benthic station in 10 m water depth, whereas *J. marmorata* and *J. herdmani* were more abundant on panels which were positioned near the water surface (exposed and sheltered station). The two latter species showed higher abundances at the exposed than at the sheltered station, although *J. marmorata* was always clearly dominant over *J. herdmani*. The differences in the spatial distribution patterns of the three species may partly result from direct interspecific competition for space. Additionally, populations of all three *Jassa* species exhibited strong temporal changes in both abundances and population structure (sex ratio, proportions of reproductively active individuals, male morphs), probably caused by seasonal factors. Rapid colonisation of free artificial surfaces was observed nearly throughout the year; its intensity, however, followed a clear seasonal pattern with

a maximum in the summer months. Recruitment probably occurred via drifting juveniles which originated from amphipod communities in the surroundings.

In the laboratory, females of *J. marmorata* and *J. herdmani* preferred different microhabitats of a macroalga. Whereas *J. marmorata* was equally distributed over the algal thallus, *J. herdmani* preferred to settle in its peripheral parts. In the presence of *J. herdmani*, however, *J. marmorata* favoured the central over the peripheral parts of the alga. These differences in microhabitat selection may result in some partitioning of resources (space) and thus facilitate the species' long-term coexistence on a small spatial scale. Furthermore, the two species showed a clear predator avoidance behaviour in response to the presence of 'fish cues' in the seawater.

Survival rates and moulting frequencies of adults of the three species were compared under two different temperature regimes. Females had a much longer average life span than their respective males. Males of *J. falcata* survived much longer under the low-temperature regime than *J. marmorata* and *J. herdmani*. However, individuals of *J. marmorata* tendentially featured the longer life span at the high temperature. These differences in the response to temperature probably reflect differences in the species' geographic distribution.

In all three species, the total number of moults in females was not affected by temperature which indicates an endogenously fixed maximal number of moults. Furthermore, species differed in the lengths of intermoult periods. Females of *J. marmorata* exhibited the shortest intervals between moults which allows females for a closer succession of oviposition.

Ecological differentiation among the three species is evident on different levels: spatial distribution in the field, life history traits, and microhabitat selection. In the first place, species-specific differentiation in ecological traits may reflect adaptations to different environmental conditions. A least some of them may also contribute to a partitioning of resources, thus reducing interspecific competition and allowing for a stable coexistence.

5.2 Zusammenfassung

An vielen marinen Substraten dominieren Flohkrebsarten die Aufwuchs-
gemeinschaften deutlich in Bezug auf Artenvielfalt. Insbesondere die
röhrenbauenden Arten der Gattung *Jassa* treten hierbei in teils extrem hohen
Tierdichten häufig sympatrisch an sublitoralen künstlichen Hartsubstraten auf.
Jassa-Arten können teilweise alle anderen Tierarten in Abundanz und sogar
Biomasse weit übertreffen. In Anbetracht der zunehmenden anthropogenen
Küstenveränderung könnten diese Amphipoden somit eine wachsende Rolle in
küstennahen marinen Ökosystemen spielen. Über die Biologie und Ökologie von
gemeinsam auftretenden *Jassa*-Arten und die Mechanismen einer möglichen
Koexistenz war aber bislang nur sehr wenig bekannt.

In der vorliegenden Arbeit wurden Feld- und Laborversuche durchgeführt
um mögliche Unterschiede in der Biologie und Ökologie der drei vor Helgoland
(Nordsee, Deutsche Bucht) heimischen *Jassa*-Arten (*J. falcata*, *J. marmorata*,
J. herdmani) zu untersuchen. An im Freiland ausgebrachten künstlichen
Versuchsplatten entwickelten sich *Jassa*-Gemeinschaften, deren genaue
Zusammensetzung starke saisonale und örtliche Schwankungen aufwies. Hohe
Abundanzen von *Jassa* Arten gingen dabei einher mit einer verringerten
Amphipodendiversität insgesamt. *Jassa falcata* war die häufigste Art an einer
benthischen Station in zehn Metern Tiefe, während *J. marmorata* und *J. herdmani*
an Platten knapp unterhalb der Wasseroberfläche dominierten. Im direkten
Vergleich zeigten diese beiden Arten deutlich höhere Tierdichten an einem
strömungsexponierten als an einem geschützten Standort. *Jassa marmorata* war
aber die zahlenmäßig deutlich häufigere Art. Diese unterschiedliche räumliche
Verteilung der Arten im Feld könnte teilweise das Ergebnis ihrer direkten
interspezifischen Konkurrenz um Siedlungsraum sein. Die betrachteten *Jassa*-
Populationen aller drei Arten schwankten zusätzlich saisonal hinsichtlich ihrer
Gesamtabundanz sowie Populationsstruktur (Geschlechterverhältnis, Anteil
reproduktiver Tiere, Männchenmorphen). Aufwuchsfreie Platten wurden das
ganze Jahr über schnell von *Jassa* besiedelt, wobei die Besiedlungsdynamik

jedoch saisonale Schwankungen aufwies und in den Sommermonaten am stärksten war. Die Neubesiedlung erfolgte vermutlich durch Jungtiere, die von benachbarten Amphipodengemeinschaften stammten und im Wasserkörper verdriftet wurden.

Unter Laborbedingungen zeigten weibliche *J. marmorata* und *J. herdmani* unterschiedliche Mikrohabitatspräferenzen an einer Makroalge. Während *J. marmorata* alle Teile der Alge nutzte, waren Tiere von *J. herdmani* hauptsächlich auf die peripheren Teile des Thallus beschränkt. In Anwesenheit von *J. herdmani* bevorzugten Weibchen von *J. marmorata* sogar die zentralen Teile der Alge deutlich gegenüber den peripheren Teilen. Die Unterschiede in der Mikrohabitatpräferenz stellen eine Form der Aufteilung der Ressource „Raum" dar, was eine Koexistenz beider Arten begünstigen könnte. Zusätzlich konnte gezeigt werden, dass in Anwesenheit von Stoffen im Seewasser, die auf potentielle Fischräuber hinwiesen, beide Arten bei der Mikrohabitat-Wahl eine deutliche Reaktion im Sinne einer Predatorenvermeidung aufwiesen.

Die Überlebensraten und Häutungsintervalle von adulten Tieren aller drei Arten wurden vergleichend bei zwei verschiedenen Temperaturen untersucht. Weibchen aller drei Arten lebten hierbei im Mittel deutlich länger als ihre Männchen. Bei der niedrigen Versuchstemperatur überlebten Männchen von *J. falcata* deutlich länger als jene von *J. marmorata* und *J. herdmani*. Individuen von *J. marmorata* wiederum hatten längere Überlebensraten bei der höheren Versuchstemperatur. Die unterschiedliche Temperaturabhängigkeit der Lebens-dauer der Arten spiegelt wahrscheinlich artspezifische Unterschiede in der geographischen Verbreitung wider.

Bei den Weibchen aller drei Arten hatte die Temperatur keinen Einfluß auf die Gesamtanzahl der Häutungen, was auf eine endogen begrenzte Maximalanzahl von Häutungen hinweist. Unterschiede zwischen den Arten zeigten sich hingegen in der Länge der Häutungsintervalle. Weibchen von *J. marmorata* wiesen die kürzesten Abstände zwischen den Häutungen auf. Dadurch könnten die Tiere in einer schnelleren Abfolge ihre Bruten produzieren.

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Die beschriebene ökologische Differenzierung zwischen den *Jassa*-Arten betrifft unterschiedliche Ebenen: die räumliche Verteilung im Freiland, verschiedene Parameter des Lebenszyklus sowie die Mikrohabitatwahl. Die ökologischen Artunterschiede spiegeln in erster Linie wahrscheinlich artspezifische Anpassungen an verschiedene Umweltbedingungen wider. Zumindest einige dieser Unterschiede könnten aber auch zu einer Aufteilung von Ressourcen beitragen, wodurch eine interspezifische Konkurrenz reduziert und eine Koexistenz auf engem Raum erleichtert würde.

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7. Acknowledgements / Danksagung

8. Appendix
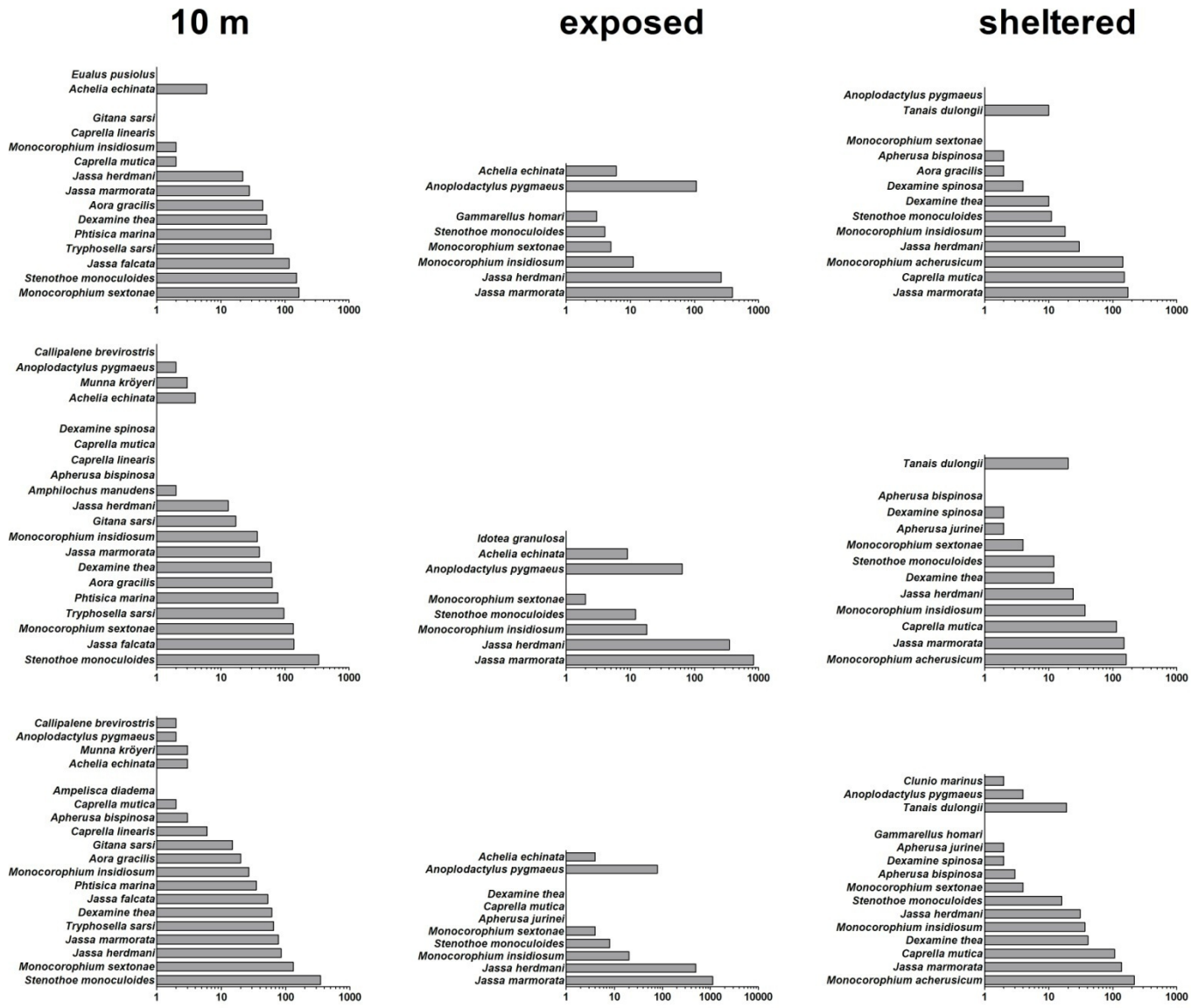

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Appendix I Seasonal changes (May 2010 - March 2011) in the abundances of amphipod species and further vagile arthropods found on the panels at the different locations (pooled replicates on a logarithmic scale).
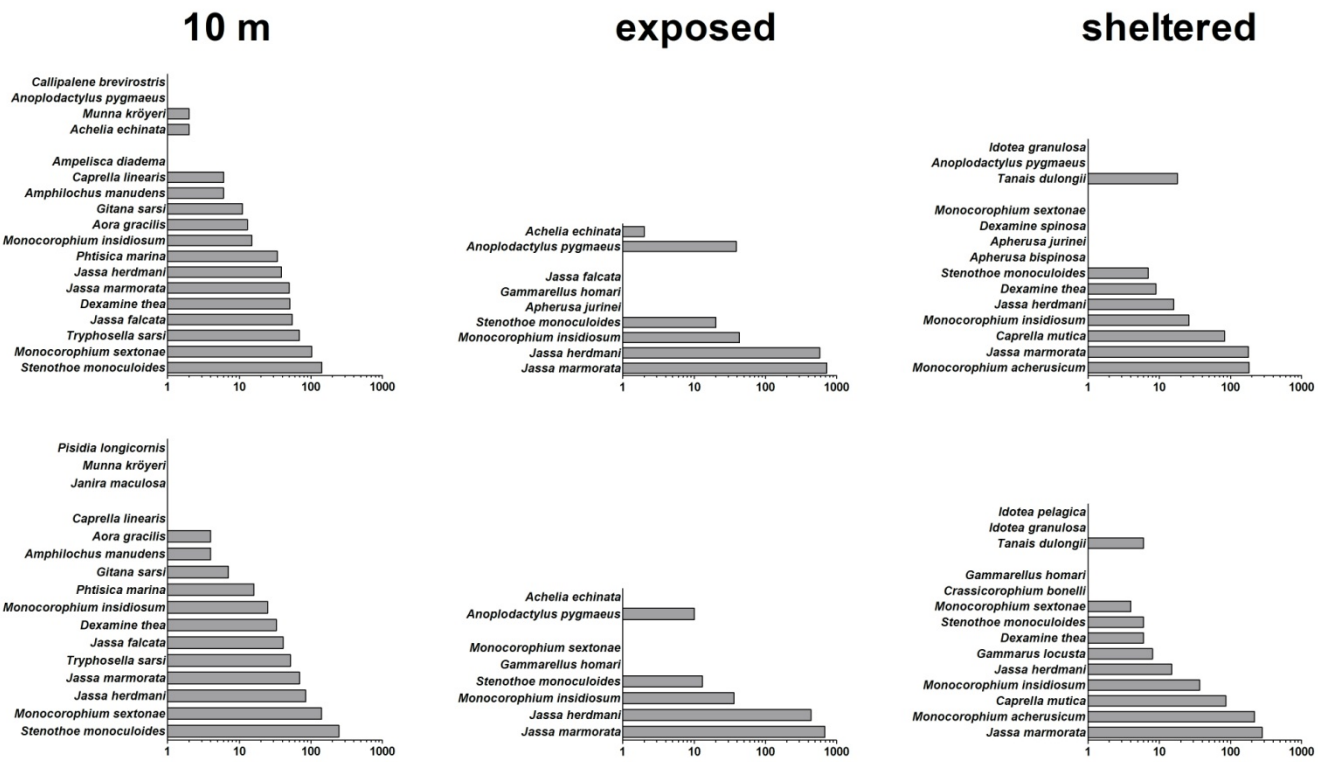
Appendix I (continued) Seasonal changes (May 2010 - March 2011) in the abundances of amphipod species and further vagile arthropods found on the panels at the different locations (pooled replicates on a logarithmic scale).

Appendix I (continued) Seasonal changes (May 2010 - March 2011) in the abundances of amphipod species and further vagile arthropods found on the panels at the different locations (pooled replicates on a logarithmic scale).

Appendix I (continued) Seasonal changes (May 2010 - March 2011) in the abundances of amphipod species and further vagile arthropods found on the panels at the different locations (pooled replicates on a logarithmic scale).