

COMPARISON OF LIFE HISTORY PARAMETERS IN COEXISTING SPECIES OF THE GENUS *JASSA* (AMPHIPODA, ISCHYROCERIDAE)

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ABSTRACT

Species of the genus *Jassa* dominate marine fouling communities where they can reach remarkably high densities. Several species have often been found co-occurring in the same habitats, such as the three congeners *J. falcata* (Montagu, 1808), *J. marmorata* Holmes, 1903 and *J. herdmani* (Walker, 1893) in the hard bottom communities of the island of Helgoland (German Bight, North Sea). In ecological and physiological studies, these species have frequently not been distinguished. To get an idea of the extent of ecological differentiation among the species, some life history parameters were analyzed and compared. In a laboratory experiment, survival rates and moulting frequencies were studied in adults under two different temperature regimes. Field samples were analyzed with respect to brood size and body size. The results revealed clear differences among the three studied species with respect to life cycle and reproduction as well as adaptations to temperature: survival rates of adults, and how these are affected by temperature; intermoult periods of adult females and their dependence on age; adult body size; ova per brood; brood size/body size relationship. The total number of moults in females was not affected by temperature, which indicates an endogenously fixed maximal number of moults. The findings highlight the importance of a strict discrimination of *Jassa* spp. to properly understand patterns of distribution.

KEY WORDS: Amphipoda, body size, brood size, intermoult period, *Jassa falcata*, *Jassa herdmani*, *Jassa marmorata*, survival

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INTRODUCTION

Species of the amphipod genus *Jassa* Leach, 1814 (Ischyroceridae) are an important element of marine fouling communities. *Jassa* spp. often show local abundances of up to 800 000 individuals m⁻², thus exceeding all other types of macrozoobenthos in terms of abundance and sometimes even biomass (Franz, 1989; Scinto et al., 2007; Zintzen et al., 2008; Beermann and Franke, 2011; Krone et al., 2013). The ability to build tubes qualifies *Jassa* as excellent pioneering settlers on any kind of hard substratum, as each individual constructs its own microhabitat using ‘amphipod silk’ (Conlan, 1994; Dixon and Moore, 1997). Clean substrata have been found to become quickly colonized by high densities of *Jassa* spp. due to the settlement of drifting specimens (Franz and Mohamed, 1989; Havermans et al., 2007; Beermann and Franke, 2012). Several species of *Jassa* overlap in their geographical distributions, and even coexist on a small spatial scale. For example, three species are known to coexist in the fouling communities of Helgoland (German Bight, North Sea): *J. falcata* (Montagu, 1808), *J. marmorata* Holmes, 1903 and *J. herdmani* (Walker, 1893) (Conlan, 1990; Beermann and Franke, 2012; Fig. 1).

In spite of the high ecological importance of these species, information on species-specific biological/ecological traits is still scarce. This is mainly due to a former taxonomic confusion. Prior to a major revision of the genus by Conlan (1989, 1990), all individuals of *Jassa* were attributed to a

single species, ‘*Jassa falcata*’ (see Sexton and Reid, 1951); this was broadly accepted in most ecological and taxonomic studies performed over the subsequent decades. Therefore, ecological studies on *Jassa* published before 1990 have to be challenged, because they possibly dealt with a mixture of species.

The taxonomic confusion was caused by the high polymorphism in *Jassa*, which is linked mainly to their particular reproductive pattern. There is a marked sexual dimorphism, with males being bigger in size and showing several special characteristics (Fig. 1). The most conspicuous feature is the enlarged second gnathopod, which bears a thumb-like protuberance on the propodus. The ‘thumbs’ develop with a terminal moult that marks the beginning of successful sexual activity. After this moult, males leave their tubes, searching and attending receptive females for the rest of their lives (Borowsky, 1985; Conlan, 1989; Clark and Caudill, 2001). In addition to the sexual dimorphism, there is a distinct dimorphism within thumbed males: ‘major form’ males are bigger in size and exhibit large second gnathopods with big thumbs, whereas ‘minor form’ males show smaller body sizes with minute thumbs (Conlan, 1989). The two different male morphs probably represent conditional reproductive strategies, as their alternative realization depends on the quality of food available during preceding developmental stages (Kurdziel and Knowles, 2002).

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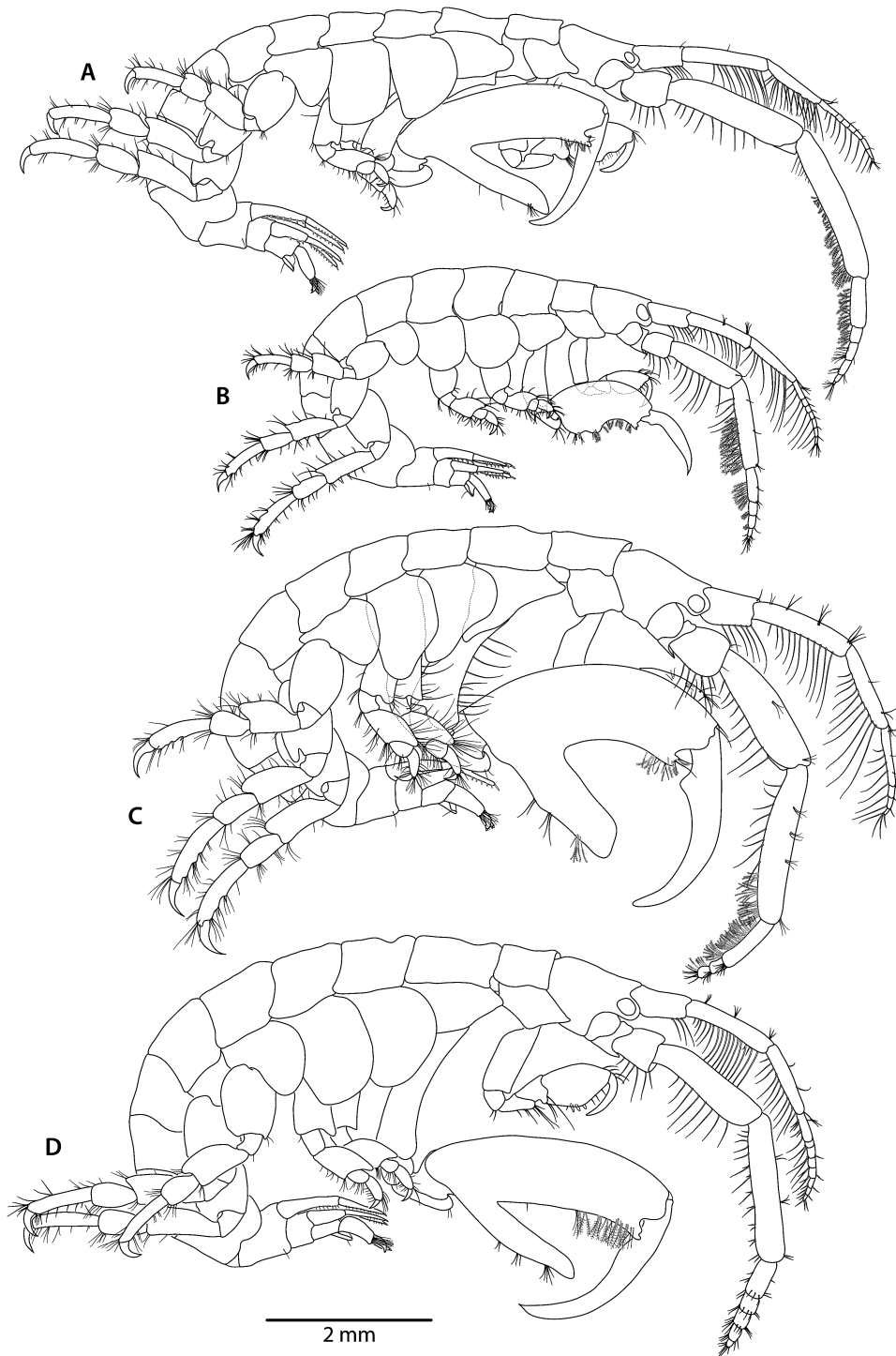


Fig. 1. Habitus of *Jassa* spp. from Helgoland, North Sea: A, thumbed male ('major form') of *J. falcata*; B, adult female of *J. falcata*; C, thumbed male ('major form') of *J. marmorata*; D, thumbed male ('major form') of *J. herdmani*.

Only few studies have focused on life history parameters of *Jassa*, and the available data were mostly assessed from field samples of *J. marmorata* and *J. slatteryi* Conlan, 1990 (Franz, 1989; Clancy, 1997; Jeong et al., 2007; Scinto et al., 2007). The only investigation upon life history parameters of *Jassa* under controlled laboratory conditions was carried

out by Nair and Anger (1979b) on '*Jassa falcata*' and most probably dealt with a mixture of species (Conlan, 1990).

The present paper reports on a comparative analysis of some life history parameters in coexisting species, and may contribute to a better understanding of the species' coexistence.

MATERIAL AND METHODS

Survival Rates and Moults Intervals of Adults

We collected adult individuals of *J. falcata*, *J. marmorata* and *J. herdmani* (thumbed 'major' males and females with brood pouch) of the same size classes (approx. 9 mm for males and 7 mm for females) from artificial habitats (walls and navigational aids) of Helgoland harbor in June 2010. This was achieved by completely scraping off the epibiotic assemblages from the surfaces, using a specially designed hand net with a built-in blade-like rim. Quickly executed, this procedure allowed for capturing all animals with only minor risk of losing specimens and/or physical injury. In the laboratory, randomly selected individuals were then put separately in small bowls with 100 ml seawater and a piece of meshed gauze (2 × 1 cm; for details on species discrimination, see Conlan, 1990; Beermann and Franke, 2011). The animals were kept under a constant light regime (LD 12:12) and fed a mixed diet of the nauplii of *Artemia* and powder of dried *Ulva* thalli. A daily exchange of the seawater and cleaning of the bowls assured that no deterioration of relevant environmental conditions such as oxygen and/or ammonia concentration occurred. In the bowls, the animals acted quite naturally, building tubes or (in the case of thumbed males) clinging to the gauze. The experiments were performed at two different temperatures, 8°C (annual mean of sea water temperature at Helgoland) and 18°C (highest monthly mean of sea water temperature in summer), with 42 specimens (21 males + 21 females) of each of the three species (42 × 3 × 2 = 252 individuals in total). As only 42 thumbed males of *J. falcata* were available from 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 that died on the first day of observation, probably due to non-visible injuries suffered during the sampling process, were excluded from the analysis.

Body Length and Brood Size

Thumbed males ('major' and 'minor' forms) and adult females (with brood pouch) of *J. falcata*, *J. marmorata* and *J. herdmani* were collected as described above from navigational aids of Helgoland harbor in August 2012. A minimum number of 100 individuals per sex and species were randomly selected, comprising all size classes. The percentage of 'minor form' males never exceeded 10%, and this morph was therefore not considered separately. All individuals were fixed apart in 70% ethanol and photographed in lateral position. Because of the curved posture of the fixed amphipods, total body lengths were measured using the 'segmented line' function of the freeware ImageJ (Ver. 1.46). In addition, the number of eggs of egg-bearing individuals were counted and related to body size.

Statistical Analyses

The computer software packages GraphPad Prism (5.03) and STATISTICA (8.0) were used for calculations. All analyses were performed at a 95% confidence level. The data on the survival of adult specimens did not meet the condition for an analysis of variance (ANOVA). Therefore, mortality of adult specimens was plotted over time and survival rates were then compared with the non-parametric logrank test (Mantel-Cox) among the three species of *Jassa*, as well as between the 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 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 homogenous (Bartlett test). For more detailed analyses Tukey's post hoc test was used. Individual lengths of moult intervals over time were analyzed, comparing linear regression slopes (*F* test).

Because the data did not meet the assumptions of an ANOVA, total body lengths were compared between species and sexes, respectively, using the non-parametric Kruskal-Wallis test. Dunn's post hoc test was applied to look at differences in detail. The data on brood sizes of adult females also did not fulfill the prerequisite of an ANOVA, thus also not allowing for testing with an ANCOVA. Therefore the data were compared between the species with a Kruskal-Wallis test, followed by Dunn's post hoc test. Brood sizes were then plotted on body lengths of the respective females, and the slopes of linear regressions were compared to test for differences between the species with respect to their brood size/body size relationship (*F* test).

RESULTS

Survival Rates and Moults Intervals of Adults

Under the constant laboratory conditions both sexes in all three species survived significantly longer at 8°C than at 18°C (each $P < 0.05$; Fig. 2; Table 1), except for males of *J. marmorata* where no difference was found between the two temperature treatments ($\chi^2_1 = 0.1175$; $P = 0.7318$). In all three species of *Jassa*, females lived longer than males at both temperatures (each $P < 0.05$). The most long-lived individual was a female of *J. marmorata*, which survived for as long as 380 days at 8°C.

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 (each $P > 0.05$), although both male and female *J. marmorata* tended to survive longer than the respective sexes of *J. falcata* and *J. herdmani*.

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 ($P < 0.0005$; Tables 2 and 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: $P < 0.05$).

Temperature had a significant effect on the length of the intermoult period ($P < 0.0001$; Table 5). In all three species moult intervals of females were significantly shorter at 18°C than at 8°C (each $P < 0.0005$; Fig. 3, Table 4). Significant differences were also found among species ($P < 0.0001$). Female *J. marmorata* showed the shortest moult intervals at both temperatures, differing significantly from *J. falcata* and *J. herdmani* at 18°C ($P < 0.005$) as well as from *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) 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 from *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.*

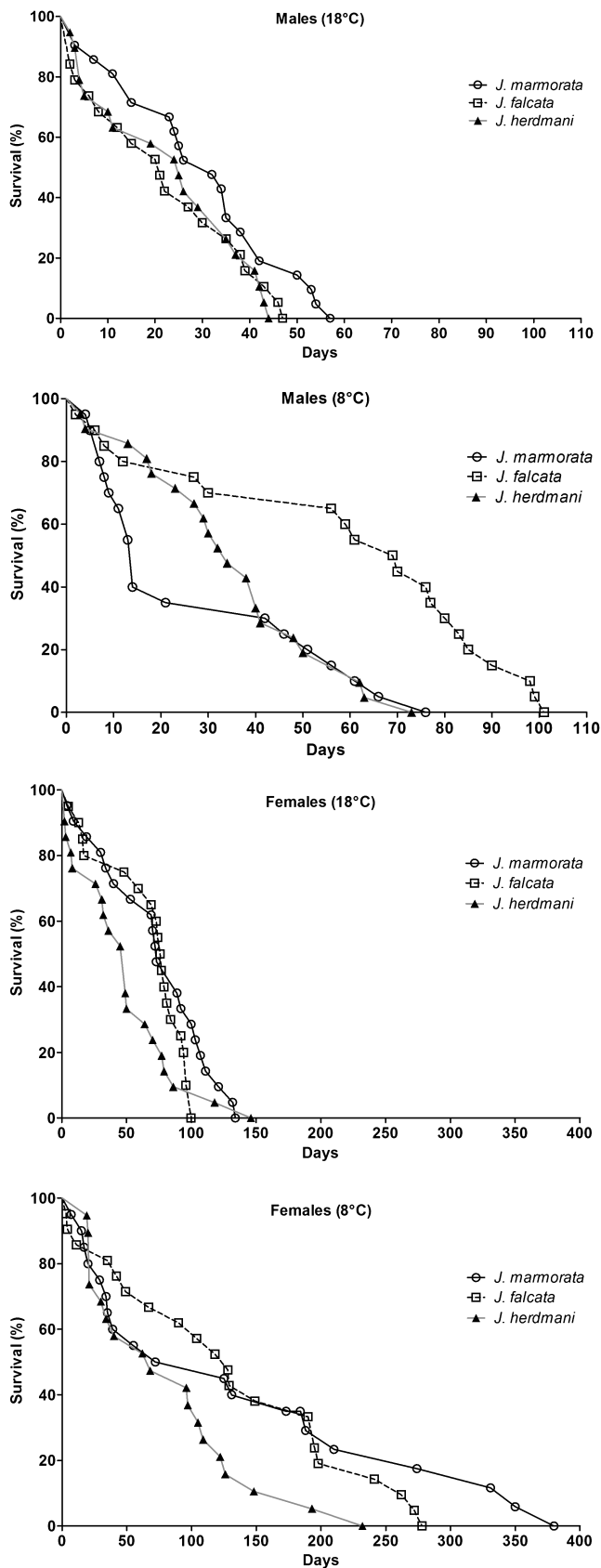


Fig. 2. Survival rates of thumbed males ('major form') and adult females of *J. falcata*, *J. marmorata* and *J. herdmani* at two different temperatures (8 and 18°C).

falcata and *J. herdmani*, neither for 8°C ($F_{1,108} = 1.4713$; $P = 0.2278$) nor for 18°C ($F_{1,130} = 0.0032$; $P = 0.9545$).

Body Length and Brood Size

In all three species of *Jassa* that we studied, thumbed males were significantly bigger in size than their respective females (each $P < 0.05$; Table 6). In direct comparison, significant differences between the species were detected for both males ($H_{K-W} = 65.14$; $P < 0.0001$) and females ($H_{K-W} = 30.67$; $P < 0.0001$; Fig. 4). *Jassa falcata* represented both the smallest males and females ($P < 0.05$). Male and female *J. marmorata* were usually bigger than those of *J. falcata* ($P < 0.05$), while individuals of *J. herdmani* were even larger in size. Males and females of *J. herdmani* were bigger compared to *J. falcata* and *J. marmorata* ($P < 0.05$), except for female *J. marmorata* ($P > 0.05$).

Brood sizes differed significantly among the species ($H_{K-W} = 50.01$; $P < 0.0001$). Females of *J. falcata* had the smallest number of eggs in their pouches, differing from *J. marmorata* and *J. herdmani* ($P < 0.05$; Table 7), whereas the two latter species did not differ from each other ($P > 0.05$). Body length/brood size relationship of *J. falcata* was significantly different from females of both *J. marmorata* ($F_{1,181} = 29.228$; $P < 0.0001$) and *J. herdmani* ($F_{1,184} = 32.655$; $P < 0.0001$; Fig. 5). No difference was found between the slopes of regression lines for *J. marmorata* and *J. herdmani* ($F_{1,197} = 0.028$; $P = 0.8671$).

DISCUSSION

Survival Rates and Moulting Intervals of Adults

Unsurprisingly, temperature had a significant 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 and Anger, 1979a, b; Pöckl, 1992). However, reliable information on potential life spans of amphipods is still scarce, as most investigations were based on field samplings and therefore calculated life spans in the presence of predation and other environmental constraints.

Adult females of all three 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 and Anger, 1979b) as well as in starvation experiments with *J. herdmani* (Havermans et al., 2007). These findings may be explained by the particular reproductive pattern in *Jassa* species. Males and females mature at about the same age (Nair and Anger, 1979b). In contrast to adult females, which continue to moult throughout their life building and living in tubes, males get sexually active with a terminal moult which is accompanied by the appearance of a thumb-like protuberance on the second gnathopods. Thumbed males spend the rest of their life by searching and attending receptive females without building tubes anymore (Borowsky, 1985; Conlan, 1989). In densely crowded communities of *Jassa*, males certainly will mate several times with different females in rapid succession, 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, while facing a high

Table 1. Survival time (days) of *J. falcata*, *J. marmorata* and *J. herdmani* at two different temperatures. Values are means \pm SD (*N*).

	<i>J. falcata</i>		<i>J. marmorata</i>		<i>J. herdmani</i>	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
8°C	59.4 \pm 33.3 (20)	131.4 \pm 90.7 (21)	26.9 \pm 23.8 (20)	133.5 \pm 122.5 (20)	35.5 \pm 19.4 (21)	82.3 \pm 62.6 (19)
18°C	22.0 \pm 16.0 (19)	67.4 \pm 31.1 (20)	29.7 \pm 16.7 (21)	73.8 \pm 39.5 (21)	23.1 \pm 15.4 (19)	49.0 \pm 38.2 (21)

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*. In other amphipod genera such as *Gammarus*, males feature greater life spans than females, probably due to their different mating strategies (Kinne, 1953; Pöckl, 1992). The long life spans of adult females under laboratory conditions may not be representative for the situation in the field. As the females were maintained in isolation, brood production and incubation were largely inhibited. Hence, saved costs of brooding may have resulted in an unnaturally long life span of females. Nevertheless, even without the option of fertilization some females in the chosen set-up produced eggs in irregular intervals and deposited them in their pouches. These eggs were extruded from the pouches after 2-3 days.

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 temperature conditions in the species' main geographical ranges. As a species which is restricted to the NE Atlantic, *J. falcata* seems to be better adapted to the low temperature of 8°C than its congeners. Although no statistically significant differences in survival rates were found among species for the 18°C treatment, there was a slight trend to a longer life span in *J. marmorata*. As this cosmopolitan species is also found in warmer waters, the demonstrated trend probably would become more evident at even higher temperatures. All three species at Helgoland reproduce year-round (Beermann, 2013). Therefore, it seems to be unlikely that the differences recorded among species relate to differences in the age structure of the sampled populations.

Although temperature in all three species clearly affected the intermoult period of females, 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.

Related to a slowdown in general metabolic activity, moult intervals in Crustacea (e.g., amphipods) are known

to lengthen at decreasing temperatures (Kinne, 1960, 1961; Hartnoll, 1982, 2001; Conan, 1985; Highsmith and Coyle, 1991). At both temperatures, females of *J. marmorata* had the shortest moult intervals of the three species, 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. Shorter intermoult periods thus result in a quicker succession of broods and should promote population growth. This may partly explain field observations by Beermann and Franke (2012), which indicated that *J. marmorata* is the more effective coloniser of clean substrata.

Under laboratory conditions, intermoult periods of adult crustaceans usually become longer over time, related to age and/or size of the individual (Conan, 1985). Females of all three species showed an increase in intermoult periods over time in both temperature treatments, which was even more obvious at 8°C than at 18°C. The lowest increase was recorded in *J. marmorata*, which (as the only exception) showed even no increase at all at 18°C. The increasing length of moult intervals with age is not an obligatory result of decreasing growth rates, as growth and moulting in amphipod crustaceans are not strictly coupled (Highsmith and Coyle, 1991). The findings of Kinne (1953, 1960) for different *Gammarus* species might provide an alternative explanation: While isolated females showed increasing moult intervals over time, females which were accompanied by an adult male moulted at constantly short intervals. Kinne (1953) demonstrated that this was induced by the precopula, during which males grab and carry their mates. Although thumbed 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; J.B., personal observation), the isolation of adult females from potential mates in the present experiment might be responsible for the observed increase in moult intervals over time. It remains thus to be studied whether this would also occur in the typical field situation where males are always present in excess.

Table 2. Number of moults in adult females of *J. falcata*, *J. marmorata* and *J. herdmani* at two different temperatures. Values are means \pm SD (*N*).

	<i>J. falcata</i>	<i>J. marmorata</i>	<i>J. herdmani</i>
8°C	4.55 \pm 2.45 (18)	6.66 \pm 4.35 (12)	2.72 \pm 1.61 (11)
18°C	4.58 \pm 1.90 (17)	6.64 \pm 2.52 (17)	3.73 \pm 2.28 (15)

Table 3. Results of two-way ANOVA for the number of moults in adult females of *Jassa* spp.

Factors and interactions	df	MS	<i>F</i>	<i>P</i>
Species	2	0.3989	8.8722	0.0003
Temperature	1	0.0560	1.2475	0.2672
Species \times Temperature	2	0.0114	0.2554	0.7751
Error	84	0.0449		

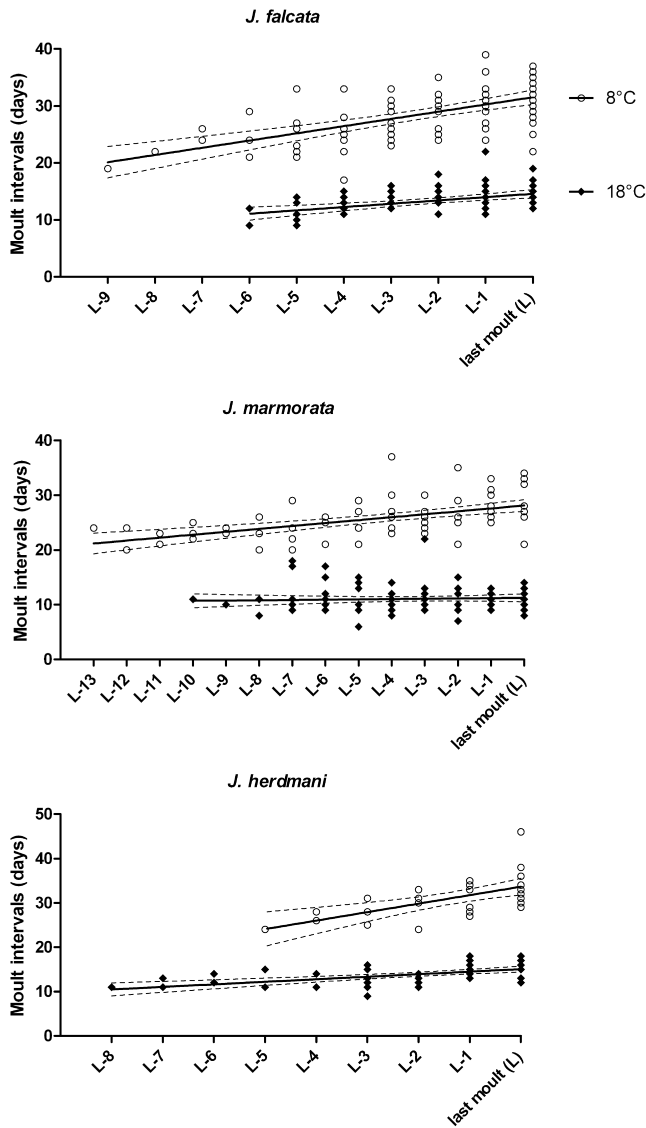


Fig. 3. Linear regression for successive moult intervals per individual in adult females of *J. falcata*, *J. marmorata* and *J. herdmani* at two different temperatures (8 and 18°C). Moults are denoted in retrograde order (with last moult as L, and previous moults as L-1, L-2, etc.).

Body Length and Brood Size

Thumbed males were usually bigger than females, reflecting the marked sexual dimorphism in the genus *Jassa* (Fig. 1). Although thumbed males show no precopulatory grabbing behavior (unlike amphipod genera such as *Gammarus*), they are exposed to strong interference competition with other males. Therefore, large body size increases a male's ability to win direct fights for mates. 'Minor form' males fol-

Table 4. Moult intervals (days) of adult females of *J. falcata*, *J. marmorata* and *J. herdmani* at two different temperatures. Values are means \pm SD (*N*).

	<i>J. falcata</i>	<i>J. marmorata</i>	<i>J. herdmani</i>
8°C	28.2 \pm 5.2 (83)	25.9 \pm 3.5 (80)	31.1 \pm 4.4 (30)
18°C	13.3 \pm 2.2 (78)	11.0 \pm 2.2 (113)	13.9 \pm 2.0 (56)

Table 5. Results of two-way ANOVA for the length of intermolt periods in adult females of *Jassa* spp.

Factors and interactions	df	MS	<i>F</i>	<i>P</i>
Species	2	0.0732	29.8396	<0.0001
Temperature	1	2.5474	1038.1888	<0.0001
Species \times Temperature	2	0.0078	3.2106	0.0453
Error	84	0.0024		

low a different strategy: Avoiding fights with bigger males, they aim at being reproductively successful by 'sneaking' copulations. These two different male morphs do not represent different evolutionary stable mating strategies, but conditional strategies which are realized alternatively depending on the food quality available during preceding developmental stages (Borowsky, 1985; Clark, 1997; Kurdziel and Knowles, 2002).

Although adults of all three species covered a broad spectrum of body lengths, males and females of *J. falcata* were the smallest in the present investigation, followed by *J. marmorata* and the largest species, *J. herdmani*. This finding confirms the assessment of Conlan (1990), that *J. falcata* matures at smaller size than its congeners. Comparing closely related *Gammarus* species, Steele and Steele (1975) noted that smaller body size at maturity is characteristic of more 'southern' species, as it allows for quick reproduction with multiple generations per year, resulting in an overall increase in reproductive output. In contrast, 'northern' species of *Gammarus* tend to be bigger, producing a single large brood per year at the restricted seasonal period when the environmental conditions are favorable for the growth of juveniles. Nevertheless, this does not apply to *Jassa* as the two larger species, *J. marmorata* and *J. herdmani*, have a more southern geographic distribution than *J. falcata*, which is restricted to the north-eastern Atlantic. *Jassa marmorata*, in particular, is a cosmopolitan species, also occurring in warm-temperate waters such as the Mediterranean Sea and even the Caribbean Sea (Conlan, 1990).

Related to their small body size, *J. falcata* also showed the smallest brood sizes. Brood size of amphipods is positively correlated with female body length, usually following a linear relationship (Myers, 1971; Steele and Steele, 1975, 1991; Highsmith and Coyle, 1991). This is probably due to the position and shape of the ovaries, which form two slender elongated tubes on both sides of the intestinal caeca (Bruzelius, 1859; Charniaux-Cotton, 1957; Ford et al., 2005). Thus, ovaries only grow linearly with body size (Sheader and Chia, 1970). *Jassa falcata* showed the lowest increase in brood size with body length, whereas no difference was found between *J. marmorata* and *J. herdmani*. At a constant volume of the brood pouch, egg size is negatively correlated with brood size (Steele and Steele, 1975, 1991).

Table 6. Body length of adults of *Jassa* spp. Values are means \pm SD (*N*).

	♂♂	♀♀
<i>J. falcata</i>	8.04 \pm 1.33 (111)	7.33 \pm 1.13 (121)
<i>J. marmorata</i>	9.00 \pm 1.66 (109)	8.16 \pm 1.45 (122)
<i>J. herdmani</i>	10.13 \pm 1.94 (103)	8.30 \pm 1.43 (133)

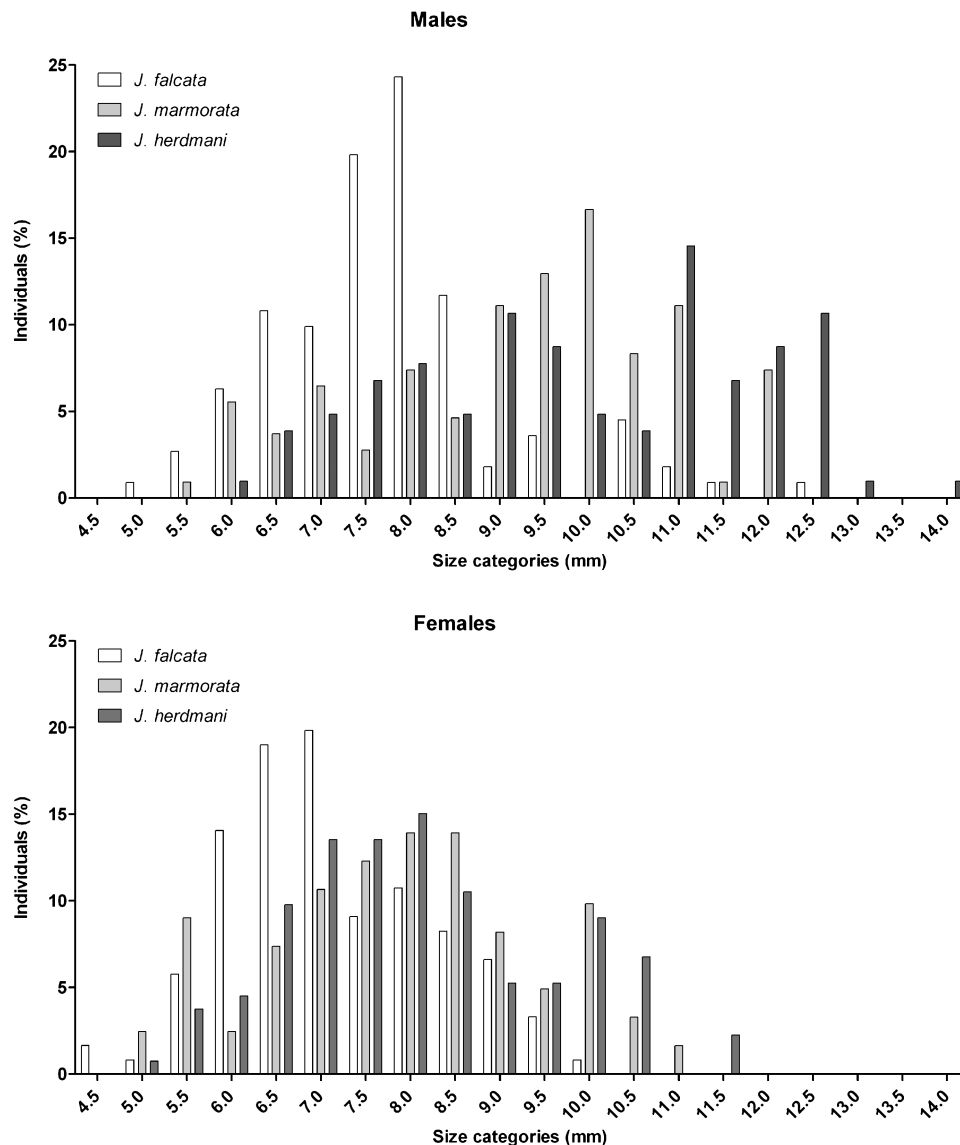


Fig. 4. Size frequencies (class interval = 0.5 mm) of thumbed males and adult females of *J. falcata*, *J. marmorata* and *J. herdmani*.

In accordance with that, the eggs of *J. falcata* are bigger in size than those of its two sympatric congeners of comparable size (unpublished data). The obtained results support the assumption, that Nair and Anger's (1980) investigation on '*J. falcata*' (in fact: *Jassa* spp. according to Conlan, 1990) dealt mainly with *J. marmorata* and/or *J. herdmani*. However, the present study only provides a snapshot in time and space of populations sampled at a single location in summer. Therefore, it cannot be excluded that brood and body size

patterns may change with season or/and some non-seasonal environmental factors, as shown for populations of *J. marmorata* on the eastern coast of North America (Franz, 1989; Clancy, 1997) and of *J. slatteryi* in southern Korea (Jeong et al., 2007).

The taxonomic distinction of the three species based on morphological criteria is clearly substantiated by the demonstration of differences in a number of life history parameters. In the present survey, *J. falcata* was smaller than the other two congeneric species and may therefore be able to explore other sources of food. This species also seems to be better adapted to lower temperatures and showed a lower dependence of brood size on body size. Lower number of ova per brood may be a trade-off for larger egg size and hence higher offspring survival. Besides its potentially longer life span, a major advantage of *J. marmorata* could be a higher potential reproductive output due to the larger brood size along with the higher number and quicker sequence of

Table 7. Brood size of *J. falcata*, *J. marmorata* and *J. herdmani*. Values are means \pm SD (*N*).

	No. of eggs
<i>J. falcata</i>	31.1 \pm 16.9 (86)
<i>J. marmorata</i>	65.1 \pm 40.8 (99)
<i>J. herdmani</i>	65.5 \pm 40.7 (102)

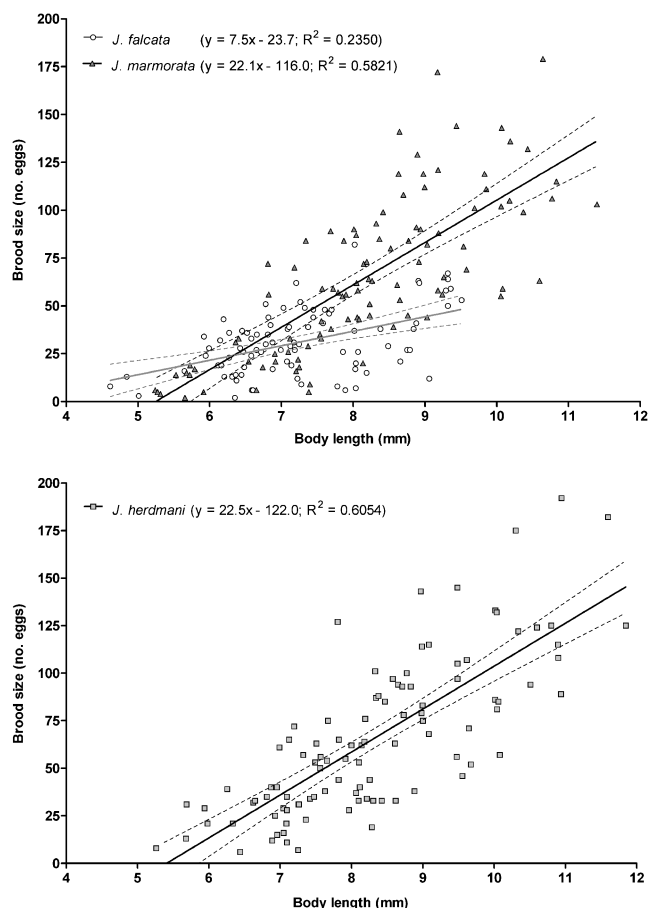


Fig. 5. Linear regressions for the brood size/body length relationships in (top panel) *J. falcata* and *J. marmorata* and (bottom panel) *J. herdmani*.

moult. Further differences with respect to things such as food utilization, dispersal potential, and/or depth distribution could also occur and contribute to the three species' ability to coexist.

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