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RESEARCH ARTICLE

Dispersal mechanisms in amphipods: a case study of *Jassa herdmani* (Crustacea, Amphipoda) in the North Sea

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Abstract *Jassa herdmani* (Walker 1893), a tube-building amphipod typical of hard substrates, was found in large densities on shipwrecks from the Belgian part of the North Sea, in association with the hydrozoan *Tubularia indivisa*. In this area, shipwrecks only represent the source of hard substrates in an environment dominated by soft sediments. Nevertheless, the long-distance dispersal of *Jassa* species has never been investigated. Therefore, we tested the hypothesis of dispersal with currents, by investigating the behaviour of *J. herdmani* in the laboratory. Size distribution revealed that newly released juveniles (<1 mm) predominated throughout the year and the lower frequency of the size class 1–3 mm indicates a high mortality or a dispersal at this life stage. Individuals of *J. herdmani* may initiate actively the transport by tidal or surface currents by swimming to the surface of the water or by floating at the surface, as suggested by behaviours noted in the laboratory. The reaction of the amphipods to a current was investigated in the laboratory. We could not detect any sexual function associated with drifting and there was also no preponderance of a size class in the drifting individuals. When testing different substrates, we observed a significant influence of the substrate type on the frequency at which drifting occurred: *J. herdmani* showed a better adherence on *T. indivisa* compared to other substrates. Finally, the amphipod showed also a preference for its host compared to other substrates, which suggests a possible detection mechanism.

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Introduction

Amphipods lack a larval stage and their dispersal could be limited compared with taxa possessing planktonic larvae (Franz and Mohamed 1989). Nevertheless, there are many marine invertebrates with direct development that have a wide geographical distribution (Castilla and Guiñez 2000; Thiel 2003a). In certain cases, direct developers might even be more likely to establish populations at distant sites than species with planktonic development, but the dispersal mechanisms of benthic invertebrate species with a direct development have been poorly documented (Johannesson 1988).

Human constructions and shipwrecks are the most important components of the artificial hard substrates in the Belgian part of the North Sea and harbour species-rich epifaunal communities (Zintzen et al. 2006). More than 200 recent shipwrecks are recorded in the Belgian waters (Massin et al. 2002). The tube-building amphipod, *Jassa herdmani* (Walker 1893), was found on these shipwrecks, living in association with the hydroid *Tubularia indivisa* Linnaeus (1758), with densities up to 100,000 individuals m^{-2} (Zintzen et al. 2006). The presence of *J. herdmani* has also been noted at the Belgian coast on other unnatural hard substrates, such as breakwaters (d'Udekem d'Acoz 1993).

The largest part of the Belgian section of the North Sea is covered by soft sediments, which are an unsuitable habitat for *J. herdmani*. The distance between artificial hard substrates ranges from 1 to 10 km and, therefore, interaction among these populations may exist. Many authors have identified rafting on artificial and natural substrata as a highly efficient dispersal mechanism in organisms with direct development (e.g. Ingólffson 1995[U1]; Thiel 2003b). Peracarid crustaceans and other brooding marine invertebrates are typically abundant on floating macroalgae (Thiel 2003b). It is also hypothesized that the existence of suitable dispersal vectors, such as macroalgae or wood, can lead to an increase in dispersal distances when the rafting organisms reproduce and their offspring recruit within the parental raft (Thiel 2003b).

Several studies indicate that drifting by post-settlement juveniles or small adults may be an important dispersal mechanism for soft-sediment macrobenthic organisms (Cummings et al. 1995). In some amphipod taxa there is a pelagic (active or passive) dispersal at all life stages. Its range depends on the swimming capacities of the species, but even poor swimmers could be dispersed periodically by currents (Franz and Mohamed 1989). Records of planktonic capture exist for species of the genus *Jassa* (see Conlan 1989) and juvenile individuals of *J. falcata* occurred frequently in the plankton around the island of Helgoland (Nair and Anger 1979). Moreover, the transport by surface currents has been identified as an important factor in dispersal of some shoreline crustaceans such as isopods and amphipods (Locke and Corey 1989). A study on the short-distance dispersal of *Jassa marmorata* showed that it occurs mainly by small juveniles and is density-dependent. In these tube-building amphipods, short-distance dispersal might be a behavioural consequence promoting the search for a site for tube-building or mating (Franz and Mohamed 1989). Nevertheless the long-distance dispersal of *Jassa* species has never been investigated. Therefore, the present study aims at further investigating the dispersal mechanisms of *J. herdmani*, by testing the hypothesis of dispersal by currents. We focused on the function of dispersal (whether it has a sexual function, i.e., the search for a mate), as well as on the importance of the substrate type on drifting frequency. Dispersal could occur in juveniles, as well as in adult individuals, and therefore we will considerer some aspects of the population dynamics of the species. This could provide us more information on the timing and the life stage involved in dispersal events. We had also determined the preference of different substrates by the amphipod, in order to detect a possible recognition of its hydrozoan host *T. indivisa*. Finally, we conducted starvation experiments to learn more about the survival time of the amphipods, while dispersing by currents.

Materials and methods

Study sites

Samples were collected during S.C.U.B.A.-diving on two shipwrecks from the Belgian part of the North Sea: the Birkenfels (WGS-84 coordinates: N 51°38′, 989–E 02°32′, 268; depth: 37 m), and the Kilmore (WGS-84 coordinates: N 51°23′, 730–E 02°29′, 790; depth: 30 m), located at a distance of 29 and 17 nautical miles from the coast, respectively. These sites were known to harbour a large population of *J. herdmani* (Zintzen et al. 2006).

Size distribution

Size distribution of *J. herdmani* was investigated in order to determine the life stage involved in dispersal. During the year 2005 (18/03/2005, 15/06/2005, 17/08/2005, 27/10/2005), random samples were taken at the Kilmore, transferred to buffered formalin (final concentration 4%) and then stored in alcohol (70%) in the collections of the Royal Belgian Institute of Natural Sciences. Several difficulties during the collection precluded a monthly sampling. All the specimens larger than 1 mm were isolated under a binocular microscope and the fraction of juveniles from 1 to 3 mm has been calculated. Then, the remaining of the sample was sieved on a 1 mm and a 28 μm mesh size. The fraction retained on the 28 μm sieve was isolated and a subsample was extracted to count the (<1 mm) juveniles of *Jassa herdmani*. These data were used to reveal the peaks of <1 mm new recruits throughout the year. The body length was measured from the tip of the rostrum to the base of the telson, by stretching the body by pincers.

Behaviour and dispersal methods

In order to investigate their behaviour, living individuals of *J. herdmani* were collected during S.C.U.B.A.-diving on the Kilmore and the Birkenfels in the year 2006 (08/04/2006, 11/05/2006, 08/06/2006, 24/06/2006). Temperatures in the North Sea (Westhinder Sandbank) varied from 5°C (February) to 17°C (July) in this year. We scraped large amounts of *Tubularia indivisa* on the shipwreck surface and then transferred them to plastic bags. Once arrived in the laboratory, the individuals of *J. herdmani* were released in several aquaria filled with aerated natural seawater, at a temperature of 5(+/−0.5)°C. The amphipods were nourished with rotifers and with dried algae (*Ulva* sp., *Porphyra* sp.) that were crushed in small particles. It seems that this combination of aliments produced the best results for survival when Nair and Anger (1979) raised *Jassa falcata* in the laboratory. Amphipods' behaviour in the aquaria was observed and several experiments were realized (submission to a current, substrate choice and starvation experiments).

Laboratory experiment (1): submission to a unidirectional current

Since it is not known how *J. herdmani* disperses, the hypothesis of dispersal with sea currents has been investigated and hence, the reaction of *J. herdmani* to a unidirectional flow mimicking a current was tested. An aquarium was constructed, in order to obtain a laminar current (Fig. 1). It was composed of two basins, one on a table above the other, in contact with each other by means of pipes. Three pumps aspirated seawater from the lower basin which streamed through three pipes in the upper basin leading to a current flow of 3.5 cm sec^{-1} in this basin. The upper basin was separated in two parts by means of two plates which contained drinking straws cut in half and placed horizontally one above another in rows. This system created a current close to be laminar in the upper basin. The seawater flowed to the end of the upper basin, where two outflows took it to the lower basin.

Different types of substrates were placed in the current, in order to investigate the frequencies of individuals drifting away. Both artificial (hairs of brush) and natural substrates (parts of *T. indivisa*) were fixed on caps of plastic recipients with resin and used as substrates for *J. herdmani*. Three types of substrates were used: (1) natural substrates composed of *T. indivisa* and covered with *J. herdmani* individuals residing in their tubes, (2) natural substrates composed of *T. indivisa* covered by *J. herdmani* individuals without tubes and (3) the artificial substrates composed of brush hairs covered by *J. herdmani* individuals without tubes. When placing them in the seawater tank, the outflows of the tank were covered with a 1-mm-net in order to retain the amphipods drifting away with the current. The time at which amphipods left the substrates was recorded and the body length of the amphipods on the net was measured. The number of *J. herdmani* individuals drifting away was recorded after different time spans and for each substrate type the experiment was repeated five times. In order to obtain information about the sex of the individuals drifting away with the current, natural substrates covered by amphipods (without tubes) were placed in the current aquarium and the individuals retained by the net were measured and their sex was determined. This experiment was repeated ten times.

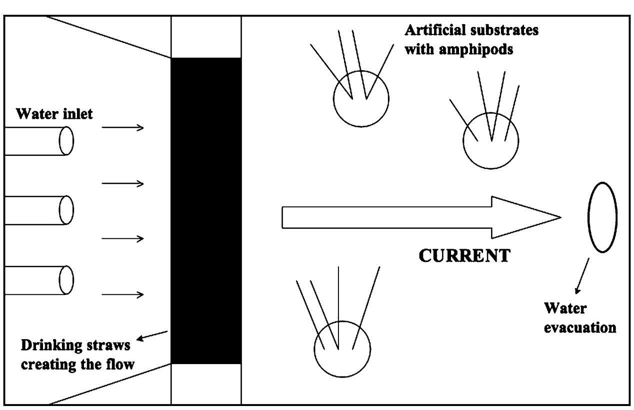

Fig. 1 The upper basin of the construction generating a unidirectional, close to laminar current

Laboratory experiment (2): substrate choice of J. herdmani

The choice of the substrate by *J. herdmani* was also investigated. Natural and artificial substrates were placed in an aquarium without a strong water circulation. The substrates used were: (1) natural substrates composed of *T. indivisa*, (2) artificial substrates composed of brush hairs and (3) artificial substrates composed of brush hairs soaked in *T. indivisa* for a few days in order to be covered by a possible secretion of the hydrozoan. The substrates were placed in the following two combinations: (1) three artificial non-impregnated substrata and three natural substrata and (2) three artificial impregnated substrata and three artificial non-impregnated substrata. All substrates were placed at the same distance from the air pump and the aquarium walls. A total of 25 adult amphipods (of unknown sex) were released in the middle of the aquarium and their position on the substrates was recorded after one hour, and then each day of the following week. The experiment was repeated twice for each substrate combination.

Laboratory experiment (3): survival time of J. herdmani

The survival time of *J. herdmani* was calculated in starvation experiments. This experiment could provide more information about survival time while dispersing by currents. These were started after each collecting date of *J. herdmani*, by submitting 50 amphipods to starvation at a water temperature of 5(+/−0.5)°C or 13(+/−1.0)°C, corresponding to winter and spring water temperature recorded in the North Sea. Each day, living individuals were counted and the body length and sex of dead individuals was recorded. Thus, the survival time is the time between the moment when the amphipods were placed in the aquarium until the moment of their death. During this experiment, cannibalism was observed. In order to avoid this, the experiment was repeated, separating each amphipod by using a compartmented box.

Data treatment

All statistical tests were performed with SAS 9.1 for Windows. Tests of analysis of variance, Chi2-tests and life table analysis (test for equality over strata: testing whether survival times differ with treatments) were used in this study. Shapiro-Wilks tests for normality of residuals and Bartlett's tests for homogeneity of variance were applied before each ANOVA. In all these ANOVA's, number and frequency of individuals as well as survival time were used as dependant factors and substrate type, month, day, time span, temperature and sex as classification variables.

Results

Size distribution

When considering the percentage of <1 mm juveniles in relation to the total number of individuals in the samples, this size class predominated in all samples (30–80% of all individuals). The recruits <1 mm were present in large densities throughout the year but their frequencies of occurrence did not differ significantly between the different months ($P = 0.27$). When comparing the percentage of <1 mm and 1–3 mm juveniles in relation to the total number of individuals in the samples (Fig. 2), the frequency of 1–3 mm was significantly lower and never exceeded 30%.

Behaviour

When introduced into the aquaria, *J. herdmani* became extremely active, swimming around and distributing themselves over the bottom and walls of the aquarium, laying often on their side. Most amphipods distributed themselves in the part of the aquarium having the highest current flow generated by the air pump. The amphipods often swam to the surface of the water and then they let themselves sink towards the bottom of the aquarium. Sometimes, a part of the individuals remained suspended at the water surface, beating their pleopods. A part of the amphipods submitted to starvation began to secrete threads of glandular tissue mixed with organic detritus present in the aquarium. The individuals still residing in their tubes on the hydroids, partially emerged with the first gnathopods, the antennae outstretched and the abdomen curled ventrally. When the current was high, a typical posture of partial emergence from the tube was observed, while in still water, the individuals emerged further from their tubes to the point where the pleopods and part of the ventrally curled abdomen were exposed.

Reaction of *J. herdmani* to a unidirectional current

In this part of the study, we investigated the influence of the substrate type and the time (5 min to 3 h) on the reaction of the amphipods when being submitted to a strong unidirectional flow. The frequency of individuals which drifted away with the current, differed significantly between the three different substrate types ($P = 0.002$) (Fig. 3). However, it did not differ between different time spans ($P = 0.18$). The highest frequency of individuals drifting away was observed for the artificial substrates but there was no interaction between different time spans and substrate types. Individuals of one sex did not drift away more frequently than those of the other sex. Moreover, larger individuals did not drift away more than small ones.

Substrate choice of *J. herdmani*

When we have to choose between natural, artificial and artificial impregnated substrates, *J. herdmani* significantly preferred the natural substrate ($P = 0.001$) (Fig. 4). The analysis revealed that the number of individuals colonizing a substrate differed significantly between the natural and artificial substrates ($P = 0.001$) but not between the different days ($P = 0.6$). There was no interaction between day and substrate type. The same analysis was applied for the second substrate combination (artificial versus impregnated artificial) and revealed that the number of individuals did not differ significantly between substrate types ($P = 0.13$), but differences appear between days ($P = 0.009$) (Fig. 5).

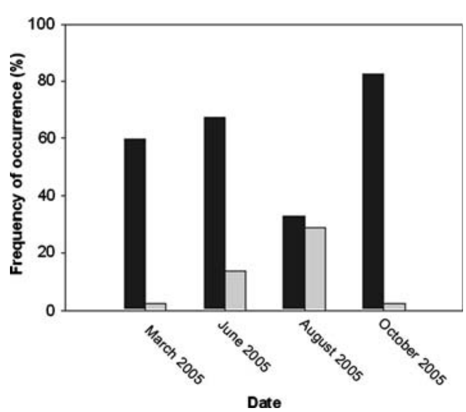

Fig. 2 Temporal evolution of the frequency of 1–3 mm juveniles (grey) and of <1 mm juveniles (black) for different months

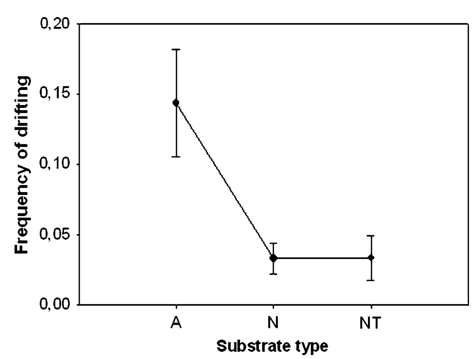

Fig. 3 Average frequencies with SE of drifting individuals of *J. herdmani* for each substrate type (A = artificial substrate; N = natural substrate; NT = natural substrates with individuals residing in their tubes)

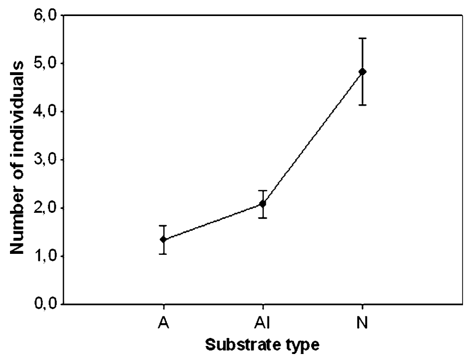

Fig. 4 Average number with SE of individuals of *J. herdmani* residing on each substrate type (A = artificial substrate, AI = artificial impregnated substrate, N = natural substrate)

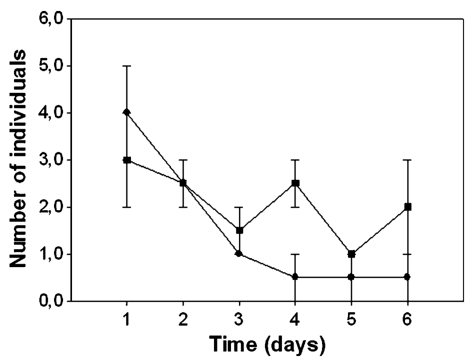

Fig. 5 Average number with SE of *J. herdmani* individuals residing on the artificial substrates (filled squares) and on the artificial impregnated substrates (filled circles) for each different day

Survival time of *J. herdmani*

The life table analysis produced with the data of the starvation experiments showed a significant difference between the survival times at 5°C and 13°C water temperature. The maximal survival time at 5°C was 39 days and 26 days at 13°C. The test for equality over strata indicated that there was a significant difference between temperatures ($P = 0.01$ for the Log-Rank test and $P = 0.03$ for the Wilcoxon test), with individuals placed at 5°C living longer than individuals placed at 13°C. Sex and temperature had an influence on the survival time, but not the body size. The survival time differed significantly between sexes ($P = 0.0005$), being higher for females and juveniles than for males.

Discussion and conclusions

Size distribution

The presence of <1 mm juveniles in the samples indicates a brood release by gravid females. The percentage of <1 mm varied from 30 to 80% of the total individuals in all size classes and thus, this size class predominated in each month. A high mortality after this developmental stage certainly occurred because the percentage of 1–3 mm in relation to the total number of individuals never exceeded 30%. It could also be possible that a part of the <1 mm recruits dispersed at this life stage and thus disappeared from the population. Indeed, in the study of Franz and Mohamed (1989) on the short-distance dispersal of *J. marmorata*, the movement was carried out mostly by juveniles, and particularly the smallest individuals (<1.5 mm). Thus, this could also be the case for *J. herdmani*.

The swimming behaviour and the reaction to a flow: hypotheses for the dispersal mechanisms of *J. herdmani*

The amphipods often swam to the surface of the water, remaining at the surface and drifting away with the flow generated by the small air pump. After a while, they let themselves sink to the bottom of the aquarium. The behaviour of swimming from the bottom towards the surface may be a widespread habit, and presumably and adaptive trait to seek vegetation or to increase dispersal (Ingólfsson 1998[U2]). In a study on the phototaxis of gammaridean amphipods, Hunte and Myers (1984) found that phototaxis changed during the life time of an amphipod, triggering a migration to surface waters at a particular life stage. The transport by surface currents has been identified as an important factor in the dispersal of some shoreline crustaceans such as isopods and amphipods (Locke and Corey 1989). If the behaviour of swimming in the direction of the sun's bearing also occurs in the field, the probability of dispersal by surface and tidal currents can be real due to the presence of strong currents at the shipwreck sites.

In our flow experiments, no differences in the sex ratio of drifting individuals occurred. The 1:1 sex ratio suggests that there is no obvious function of drift in reproduction. Nevertheless, in tube-building amphipods, males are known to swim around in the search of receptive females, showing a 'cruising' behaviour (Borowsky 1983). This could increase the probability of males being drifted away by water currents. However, the 1:1 sex ratio of drifting individuals has also been observed in the study on haustoriid amphipods, in which drifting probably has no reproductive function, but it is rather an induced phenomenon increasing the dispersal. Food limitation could also be a factor that causes haustoriids to leave the substrate in which they reside (Grant 1980).

In the study of Franz and Mohamed (1989) on the short-distance dispersal (<1 cm) of *J. marmorata*, the movement was carried out mostly by juveniles (<1.5 mm). Our results did not confirm this, because there was no preponderance of a size class in the experiments with a current and there was no relation between time after placement in the current and the body size of drifting individuals. However, the 1 mm-nets at the outflows of the upper basin were not suitable for receiving small individuals (<1 mm) and no gravid females were recorded on the substrates used in the experiments. Nevertheless, not only juveniles are the dispersal agent in amphipods since Franz and Mohamed (1989) also recorded dispersal by adults, but with a lower frequency than that of juveniles. In a study on dispersal between different sites in a kelp forest, juveniles as well as adults were the dispersal vectors (Waage-Nielsen et al. 2003). Often, dispersal is density-dependent, as observed for *J. marmorata* (Franz and Mohamed 1989) and therefore, this hypothesis should be tested for *J. herdmani*.

The substrate type had a significant influence on the frequency at which drifting occured: our results indicated that drifting was highest when the artificial substrates were used. This could be due to the difficulties of adherence on these substrates. *J. herdmani* showed a better adherence on its host *Tubularia indivisa*, suggesting a possible adaptation to the strong currents near the shipwrecks. In the case of the natural substrates covered by amphipods without tubes, the frequencies of drifting individuals were higher than when the amphipods resided in tubes. Therefore, when mature males go cruising for receptive females, by leaving their tube and visiting other tubes on *Tubularia indivisa*, they are more susceptible to be washed away by currents.

Some individuals of *J. herdmani* remained suspended on the water surface for a relatively long time. Highsmith (1985) observed by floating experiments the same behaviour for many invertebrates, such as bivalves and amphipods, suggesting that floating may be a potential dispersal mechanism for these species. Floating can increase the probability of dispersal by rafting, because organisms floating at the surface are more likely to contact algae on which they can attach (Highsmith 1985). In a study on floating seaweed in the Belgian coastal waters, individuals of the genus *Jassa* were found in a part of the seaweed samples. Gravid females (females bearing eggs) were also observed and, therefore, rafting can be considered as a potential dispersal mechanism of *Jassa* species (Vandendriessche, personal communication). Moreover, individuals of *J. herdmani* have also been observed on floating substrata and floating seaweed at the Dutch coast (Stock 1993). Therefore, the hypotheses of floating, rafting and drifting with tidal or surface currents may all be suitable for *J. herdmani*.

The substrate choice of *J. herdmani*: a possible detection of the presence of its host *Tubularia indivisa*?

We investigated the substrate preference of *J. herdmani*. The amphipods preferred to reside on the natural substrates made of *T. indivisa*. This could be due to a possible recognition of their host. The amphipods have also a better adherence on these natural substrates, as demonstrated with the drifting experiment. We also observed a higher number of amphipods residing on the artificial impregnated substrates than on the non-impregnated substrates, but this difference was not significant. There could be a possible recognition of a secretion of *T. indivisa* on the brush hairs and this secretion could be detected by sensory organs. In some amphipods, a specialized sensory organ, the callynophore, situated on the first antennae, possibly bears chemoreceptors for detection of pheromones, food or hosts. However, this organ is not present in amphipods belonging to the *Corophioidea* (Lowry 1986). Probably, these amphipods possess other chemoreceptors responsible for the chemodetection. The detection of hosts exists in hyperiideans, because they often are parasitoids (Lowry 1986). However, it might be possible that amphipods, particularly host-associated amphipods, have developed chemoreceptors for secretions from their hosts. In a study on an ascidian-dwelling amphipod of the genus *Leucothoe*, Thiel (2000) observed that the amphipod was most abundant in the ascidian host during the reproductive periods (in spring and autumn), but in the summer months they left their hosts. This indicates that a mechanism for detection of the hosts by the amphipods should exist, otherwise they would not be able to return in autumn to reproduce inside the host. In the experiments of substrate choice between impregnated and non impregnated artificial substrates, we observed that there was an influence of the day. We noted that the number of amphipods residing on the impregnated substrata was higher the first days than in the following days. This could indicate that the possible secretion of the hydrozoan disappeared after a few days, leading to a decreased attraction of *J. herdmani*.

The survival time of *J. herdmani*

Starvation experiments were conducted at a water temperature of 5(+/−0.5)°C or 13(+/−1.0)°C, matching with winter and spring water temperatures recorded in the North Sea. At a lower temperature, the average survival time as well as the maximal survival time are higher and it increases the dispersal duration. We do not know whether or not the amphipods can nourish while drifting away by sea currents, but even if they are not able to nourish, the survival time recorded in our starvation experiments is still important. Females had a longer survival time than males; this could be explained by their higher lipid reserves, because they have to produce yolk mass for the eggs (Nair and Anger 1979). Almost 25% of the females submitted to starvation were bearing eggs. They might have increased their survival time by a partial ingestion of their brood, which has been cited as being a possible cause of egg loss during brooding (Kevrekidis 2005).

In conclusion, the dispersal by juveniles might be highest during the breeding periods, when the frequency of new recruits (<1 mm) is highest. These juveniles predominated throughout the sampling year and the much lower frequency of 1–3 mm juveniles could indicate a high mortality after this life stage or that a part of the <1 mm recruits could disappear from the population due to dispersal by water currents. Adults could also be dispersed by strong currents but no sexual function of the drifting with a current was observed in our results. Individuals of *J. herdmani* may initiate actively the transport by tidal or surface currents, since we observed a behaviour which consisted in swimming to the surface of the water and then floating. The substrate type has a significant influence on the frequency at which drifting occurs: *J. herdmani* shows a better adherence on its usual host on shipwrecks, *Tubularia indivisa*. This could be an adaptation to the strong currents in the area. The amphipod also prefers this substrate when having to choose between different substrates. A possible detection mechanism could exist to search for the presence of the hydrozoan host, but this needs a further research. In our current experiments, the use of a smaller mesh size was impossible because it stopped the flow, but it could be interesting to investigate the reaction of gravid females and juveniles to a flow. In this way, the results of Franz and Mohamed (1989) for *Jassa marmorata*, in which newly released juveniles were the primary agents of short-distance dispersal, could be tested for *J. herdmani*. Since the survival time during starvation is important, dispersal by drifting between different shipwrecks might be possible and this could explain the occurrence in very large densities of *J. herdmani* on these shipwrecks on the Belgian Continental Shelf.

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