



## Active and passive migration in boring isopods *Limnoria* spp. (Crustacea, Peracarida) from kelp holdfasts

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### ABSTRACT

Many boring isopods inhabit positively buoyant substrata (wood and algae), which float after detachment, permitting passive migration of inhabitants. Based on observations from previous studies, it was hypothesized that juvenile, subadult and male isopods migrate actively, and will rapidly abandon substrata after detachment. In contrast, reproductive females and small offspring were predicted to remain in floating substrata and thus have a high probability to disperse passively via rafting. In order to test this hypothesis, a colonization and an emigration experiment were conducted with giant kelp (*Macrocystis integrifolia*), the holdfasts of which are inhabited by boring isopods from the genus *Limnoria*. A survey of benthic substrata in the kelp forest confirmed that limnoriids inhabited the holdfasts and did not occur in holdfast-free samples. Results of the colonization experiment showed that all life history stages of the boring isopods immigrated into young, largely uncolonized holdfasts, and after 16 weeks all holdfasts were densely colonized. In the emigration experiment, all life history stages of the isopods rapidly abandoned the detached holdfasts – already 5 min after detachment only few individuals remained in the floating holdfasts. After this initial rapid emigration of isopods, little changes in isopod abundance occurred during the following 24 h, and at the end of the experiment some individuals of all life history stages still remained in the holdfasts. These results indicate that all life history stages of *Limnoria* participate in both active migration and passive dispersal. It is discussed that storm-related dynamics within kelp forests may contribute to intense mixing of local populations of these burrow-dwelling isopods, and that most immigrants to young holdfasts probably are individuals emigrating from old holdfasts detached during storm events. The fact that some individuals of all life history stages and both sexes remain in floating holdfasts suggests that limnoriids could successfully reproduce during rafting journeys in floating kelp, facilitating long-distance dispersal. We propose that the coexistence of different modes of dispersal (short distance local migrations and long-distance regional dispersal) within these kelp-dwelling isopods might be advantageous in an environment where unpredictable El Niño events can cause extinction of local kelp forests.

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### 1. Introduction

Dispersal of marine invertebrates remains one of the least understood processes in the marine environment. During recent years this topic has received particular attention because reliable estimates of effective dispersal distances are considered important for the design of marine protected areas. Estimates of dispersal distances are often based on indirect measures, namely the duration of the planktonic life history stages (for most recent examples see e.g. Shanks et al., 2003; Carson and Hentschel, 2006). However, results from an ever increasing number of molecular studies on population connectivity in marine invertebrates indicate that dispersal distances are not directly related to the duration of

planktonic stages. For example, studies of species with indirect development increasingly suggested that long-lived planktonic larval stages may not necessarily result in long-distance dispersal (e.g. Baums et al., 2005; Johnson and Black, 2006; Levin, 2006). Recent studies on species with direct development confirmed a high potential for long-distance dispersal, most likely via passive migrations on rafts, i.e. on floating items (Waters and Roy, 2004; Donald et al., 2005). While molecular studies offer important insights about the outcome of successful dispersal, they provide relatively little information about the process itself.

Dispersal in the marine environment may be result of active or passive migration behaviour of organisms (e.g. Palmer, 1988). Active migration can involve walking or swimming from local source populations to nearby new habitats (Perry, 1988; Franz and Mohamed, 1989; Kumagai, 2006; Munguia et al., 2007). Passive movements of inquilines often occur when important ecosystem-engineering organisms (mussels, corals, mangroves, saltmarsh plants, algae) are detached from the primary substratum, thereafter being at the mercy of wind,

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waves and currents (e.g. Paine and Suchanek, 1983; Hobday, 2000; Norkko et al., 2000; Brooks and Bell, 2001a; Salovius et al., 2005).

Active migrations are often undertaken by particular ontogenetic life history stages, while all stages of a population may be susceptible to passive migrations. In directly developing species, active migrations are often undertaken by juvenile or subadult stages with adults (in particular reproductive females) leading a more sedentary life style. Interestingly, some of these organisms with direct development, when subjected to passive migrations on floating items, may become transported over extraordinarily long distances. These long-distance migrations can result in successful dispersal because all life-history stages, including reproductive females, are able to survive during these voyages (Thiel and Gutow, 2005).

Passive long-distance migrations can be expected for a number of organisms that live in and on floating substrata. Animals that excavate burrows into wood and macroalgae are most prone to be passively dispersed once these substrata are detached and float away with currents. Hill and Kofoed (1927) suggested that boring isopods *Limnoria lignorum* are transported to new habitats via floating driftwood. Davidson (2008) reported personal observations of rafting dispersal of *Sphaeroma quoianum* within an estuary. The worldwide distribution of *S. terebrans*, which bores into mangrove roots, was taken to infer long-distance dispersal via floating mangroves (Baratti et al., 2005). Rafting dispersal is frequently used to explain the wide distributional ranges of wood- or algae-dwelling isopods and amphipods (Johnson, 1935; Svararsson, 1982; Brooks, 2004).

Despite their high potential for passive rafting migrations, the behaviour of wood- or algae-boring isopods and amphipods upon detachment of their primary substratum from the bottom is not well known. Experimental studies indicated that many holdfast inhabitants disappear shortly after detachment (Kingsford and Choat, 1985; Edgar, 1987; Vásquez, 1993). During the first day after detachment, Edgar and Burton (2000) registered a strong decrease in numbers of *Limnoria carptora* from holdfasts of *Durvillaea antarctica*: benthic holdfasts often harboured more than 50 individuals, but detached holdfasts that were tethered for one day near the sea surface (i.e. mimicking floating plants) contained fewer than 5 individuals per holdfast. These data suggest that most individuals rapidly abandon holdfasts after detachment. Edgar (1987) also observed a decrease in the abundance of *Limnoria* spp., but substantial numbers of isopods also persisted in the holdfasts of *Macrocystis pyrifera* when these were suspended in the water column. Since subadults and males of boring isopods show a strong tendency for active migration (Eltringham and Hockley, 1961; Davidson et al., 2008) and subadults are the most active colonists of new substrata (Brooks and Bell, 2001b), it is hypothesized that the individuals that persist in the floating substrata are mainly reproductive females. This would favour maintenance of local demes in the floating holdfast during long-lasting rafting journeys and also increase the chance of successful colonization after returning to the shore, because ovigerous females release fully developed juveniles, which can immediately colonize adjacent habitats.

In the present study we examined the migration behaviour of a limnoriid isopod that excavates burrows in kelp holdfasts in order to reveal whether subadults (and males) show a higher tendency of active migration than reproductive females. In accordance with this hypothesis of stage-dependent migration behaviour, we expected that colonization of young holdfasts is mainly done by subadults and males. Furthermore, we hypothesized that detachment of kelp holdfasts induced active emigration in subadults and males, but that females persisted in their burrows in the holdfasts. In order to test these hypotheses we conducted a colonization and an emigration experiment.

## 2. Materials and methods

### 2.1. Study organisms

The holdfasts of many large kelp are commonly inhabited by isopods from the genus *Limnoria* (Menzies, 1957; Edgar, 1987; Cookson, 1991).

Along the Pacific coast of S America, these algae-burrowing isopods had previously been identified as *Limnoria chilensis* (e.g. Elias, 1981; Thiel and Vasquez, 2000; Thiel, 2003), but a recent molecular study suggests the existence of divergent lineages within the genus *Limnoria* (Haye and Marchant, 2007). Since the taxonomic identification of these lineages has not yet been resolved, herein we refer to them as *Limnoria* spp. These isopods burrow in the holdfasts of different algae, including *Durvillaea antarctica*, *Lessonia trabeculata*, *L. nigrescens*, *Macrocystis integrifolia* and *M. pyrifera* (Thiel and Vasquez, 2000; Thiel, 2003). Large holdfasts may contain hundreds of individuals. The isopods excavate extensive burrows in the holdfasts and feed on the algal tissues, similar as described for wood-boring limnoriids (Cragg et al., 1999). Usually there is one individual per burrow, but adult females may occasionally share burrows with male partners or with their small offspring. Small juveniles start to build their own burrows from within their mother's burrow and based on this observation it had been inferred that they might recruit directly into their natal holdfast (Thiel, 2003). No observations on the migration behaviour of these isopods are available.

Three of the principal host algae of the isopods, *D. antarctica*, *M. pyrifera* and *M. integrifolia*, have gas-filled structures and float to the sea surface when detached from the bottom. These algae are also frequently found floating along the Chilean coast (Macaya et al., 2005; Hinojosa et al., 2006).

### 2.2. Study site and isopod population during the study period

The study was carried out during austral summer/fall (December 2005–May 2006) in a large kelp forest of *M. integrifolia* in Playa Blanca, Región de Atacama (28°11'18"S, 70°09'53"W) on the northern-central coast of Chile. The kelp forest, which also contains patches of *L. trabeculata*, has a long-shore length of approximately 1200 m. Common understory algae are *Halopteris* sp., *Dictyota kunthii*, and *Asparagopsis armata* (Buschmann et al., 2004).

The experiments and samplings were conducted by scuba-diving on the shoreward side of the kelp forest, which is sheltered against the predominant winds from the SE. Water depth in that part of the kelp forest ranged from 2–5 m. Between January and May 2006, the background population of *Limnoria* spp. at the study site was surveyed to reveal the strength of the association of *Limnoria* spp. with kelp holdfasts. During the same time period, a colonization experiment was conducted to find out which life history stages immigrate into young holdfasts. In December 2005, we conducted an emigration experiment to reveal which life history stages actively emigrate in response to detachment of giant kelp. In order to obtain all isopods from a holdfast, these had to be sampled in the field and thereafter carefully dissected in the laboratory. Consequently all samples taken herein were destructive samples.

For the survey of the background population of *Limnoria* spp., we took two types of benthic samples, (i) substratum containing a kelp holdfast and (ii) substratum without a holdfast. Samples were taken with a corer of 11 cm diameter (95 cm<sup>2</sup> surface area). At random places within the kelp bed, the corer was pushed into the algal substratum, which was quickly detached and immediately placed into plastic bags. Before taking substratum samples with holdfasts, we carefully cut off all stipes, which was necessary to place the corer over the substratum. At each sampling date (31 January, 4 April and 26 May 2006), ten replicates of each treatment (substratum with holdfast and substratum without holdfast) were taken. In the substratum samples with holdfasts, there were no significant differences in the wet weight of holdfasts between the three sampling dates (31 January: 50.8 ± 30.1 g, mean ± S.D.; 4 April: 49.0 ± 23.2 g; 26 May: 30.1 ± 9.3 g; 1-way ANOVA,  $F=2.563$ ,  $p=0.096$ ).

### 2.3. Colonization experiment (young holdfasts)

The colonization of young holdfasts by isopods was monitored over a time period of 16 weeks. At the beginning of the experiment

(31 January 2006), about 60 young holdfasts that appeared new (lively green colour) and largely uncolonized by isopods were marked with coloured cable ties. Immediately after marking the holdfasts, we collected 8 of them in order to reveal the initial stage of colonization. Nine weeks (4 April 2006) and 16 weeks (26 May 2006) after these holdfasts had been marked we sampled another 8 and 7 holdfasts, respectively (at week 6, when there should have been about 44 holdfasts left, we could only find 7 of the initially marked 60 holdfasts). After identifying a marked kelp individual for sampling we carefully removed all the stipes without disturbing the holdfast. We then placed a plastic bag over the remaining holdfast, and carefully detached it from the substratum, using a dive knife. Immediately after detachment the bag was closed over the holdfast and sealed tight with a rubberband in order to enclose all inhabitants of the holdfast. There were significant differences in the wet weight of holdfasts between the three sampling dates (31 January:  $70.6 \pm 15.6$  g, mean  $\pm$  S.D.; 4 April:  $123.2 \pm 33.0$  g; 26 May:  $72.7 \pm 22.4$  g; 1-way ANOVA,  $F=11.372$ ,  $p=0.001$ ; post-hoc Tukey: Jan < April > May); these differences were due to fast growth of holdfasts in February/March, and between April and May holdfasts were eroded substantially by the burrowing activity of isopods. Since the intensely burrowed holdfasts in May were partly hollow, the holdfast volumes (which included burrow volumes) showed no significant differences between the three sampling dates (31 January:  $69.6 \pm 29.7$  ml, mean  $\pm$  S.D.; 4 April:  $83.5 \pm 35.0$  ml; 26 May:  $58.1 \pm 22.7$  ml; 1-way ANOVA,  $F=1.357$ ,  $p=0.280$ ).

#### 2.4. Emigration experiment (detached algae)

The emigration of isopods in response to detachment of their host algae was estimated in an indirect way. On 21 December 2005, we detached holdfasts from adult algae and suspended them near the sea surface, mimicking the conditions during natural detachment events, i.e. when algae break off the bottom and rise to the sea surface due to the buoyancy produced by their pneumatocysts. We cut off all the stipes, then detached the holdfast with a dive knife, and slowly moved them to the sea surface where the holdfasts were attached to a surface buoy. This procedure is comparable to natural detachment events, where holdfasts are detached and pulled to the sea surface by the positively buoyant kelp parts. Kelp individuals used for this experiment came from water depths of 3–5 m and were suspended from the buoys at about 20 cm below the sea surface, similar as seen in naturally floating kelps. Holdfasts were sampled after intervals of 5, 15, 30, 60, 720 and 1440 min (5 replicates per time interval). Control holdfasts were collected directly from the bottom with all their original inhabitants. For sampling, a plastic bag was pulled over the holdfast, which was then detached from the bottom or cut off from the cable-tie, the plastic bag was quickly pulled over the entire holdfast and closed with a rubberband. This procedure was done very carefully and fast to avoid losses of isopods, but occasionally a few individuals might have escaped during sampling. Once on the shore, the seawater was carefully drained over a sieve to retain isopods that had left their burrows during manipulation in the plastic bag. The bag then was filled with 10% formalin for storage and later examination of the samples.

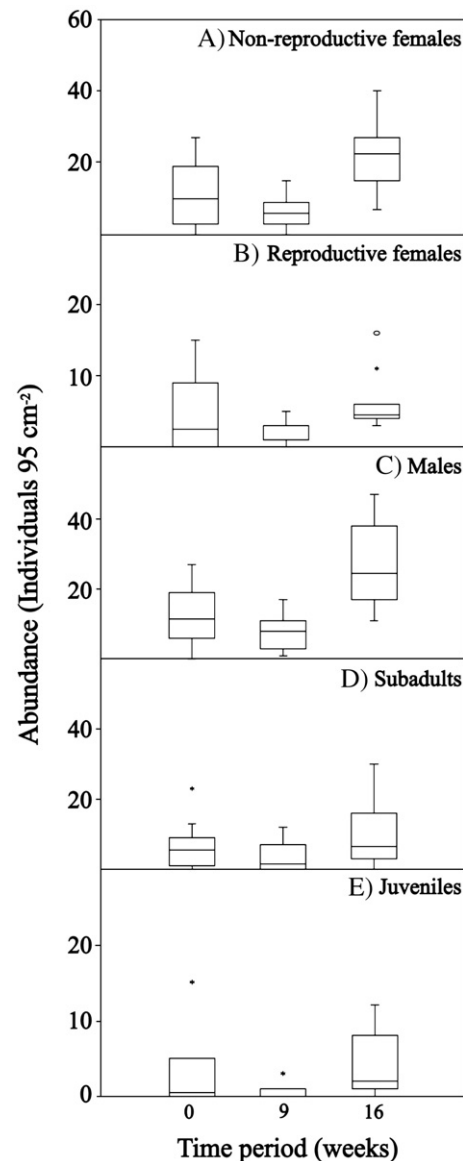
#### 2.5. Processing of samples in the laboratory

Preserved samples were washed over a sieve and left for 24 h in seawater. We measured the holdfast volume based on the displaced volume: a jar (1000 ml) was filled to the rim with water, the holdfast was placed in the jar, the displaced water was gathered in a tray and its volume determined. The holdfasts were then weighed (wet weight) and carefully dissected to extract the isopods from their burrows. All isopods were collected and stored in 70% EtOH. Isopods were sexed and their developmental stage determined. Males were identified based on

the presence of penis appendices and adult females were recognized from the oostegites. We distinguished reproductive females with a fully developed marsupium and embryos and non-reproductive females with tiny oostegite buds not forming a complete marsupium. Small juveniles (0.8–1.2 mm body length) and subadults (1.2–1.6 mm) were distinguished based on their total body length. For the measurements of the body length, the isopods were carefully stretched out with a forceps. We measured total body length from the anterior edge of the head segment to the posterior end of the pleotelson with a measurement ocular in a regular dissecting microscope.

#### 2.6. Data analysis

The results of the habitat survey (benthic samples with and without holdfasts) were presented as the number of isopods per area (95 cm<sup>2</sup>), while for the analyses of the colonization and of the



**Fig. 1.** Abundance (individuals 95 cm<sup>-2</sup>) of *Limnoria* spp. in holdfasts of fully developed individuals of *Macrocyctis integrifolia* during the three sampling dates (31 January, 4 April and 26 May 2006); box plots show median, 25% percentiles, and ranges;  $n=10$  holdfasts per sampling date; data for benthic samples not containing holdfasts never contained any isopods and are not shown.

emigration experiments total isopod abundance was expressed as individuals per 100 g algal tissue, thereby accounting for different holdfast sizes. For the samples of the habitat survey and the colonization experiment we conducted a one-way ANOVA to examine whether sampling date had a significant effect on the total abundance of isopods. Furthermore, we used contingency tables to examine whether the proportions of developmental stages in the colonization experiment differed significantly between the three sampling dates (0, 9, and 16 weeks). In order to reveal whether floating duration had an effect on the abundance of isopods during the emigration experiment, we conducted a one-way ANOVA for each life history stage with the factor floating period as independent variable (0, 5, 15, 30, 60, 720, 1440 min floating period).

All analyses were conducted with SIGMASTAT 3.0. Data were log ( $x + 0.5$ ) transformed to achieve homogeneity of variances if necessary. For habitat survey and the colonization experiment we used the Tukey-test to test for differences between sampling dates, and for the emigration experiment we used Dunnett's test to compare between controls and experimental treatments.

### 3. Results

#### 3.1. Abundance and distribution of *Limnoria* spp. in the kelp forest

Isopods *Limnoria* spp. were only found in the benthic samples with holdfasts. In the 30 samples of substratum without holdfasts (mainly containing understory algae such as *Asparagopsis armata* and *Dictyota kunthii*) that were taken between January and May 2006 we never found any limnoriids. In contrast, the substratum samples with holdfasts contained large numbers of limnoriids (Fig. 1). The total numbers of isopods per sample ranged from 1 individual 95 cm<sup>-2</sup> to 134 individuals 95 cm<sup>-2</sup> (see also Table 1). During the latter part of the study period the number of limnoriids in these samples increased, and in May we found significantly more individuals in these holdfasts than in January and April (31 January: 39.0±32.9 individuals 95 cm<sup>-2</sup>, mean±S.D.; 4 April: 21.4±14.1 individuals 95 cm<sup>-2</sup>; 26 May: 70.8±36.5 individuals 95 cm<sup>-2</sup>; one-

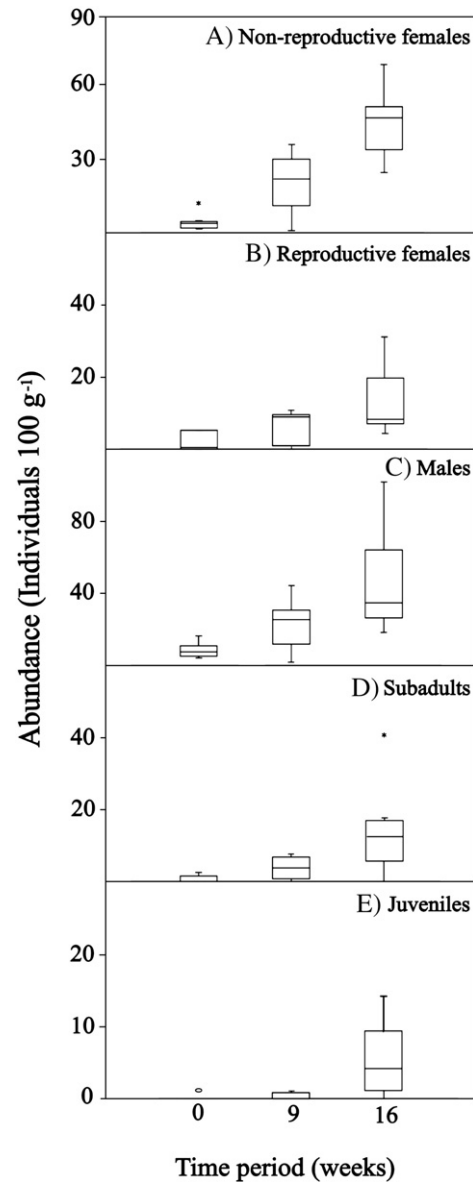


Fig. 2. Abundance (individuals 100 g<sup>-1</sup>) of *Limnoria* spp. in holdfasts of young individuals of *Macrocyctis integrifolia* during the three sampling dates; holdfasts were marked as young and uncolonized holdfasts on 31 January 2006; box plots show median, 25% percentiles, and ranges.

Table 1

Total abundances of *Limnoria* spp. (a) in substratum samples with holdfasts, (b) in young holdfast (marked 31 January 2006) during the colonization experiment, and (c) in benthic control and suspended experimental holdfasts at the respective time intervals after detachment

| Weeks               | n  | Min-max value | Individuals 95 cm <sup>-2</sup> |
|---------------------|----|---------------|---------------------------------|
| 0 (31 January 2006) | 10 | 1–91          | 39±32.9                         |
| 9 (4 April 2006)    | 10 | 4–48          | 21.4±14.1                       |
| 16 (26 May 2006)    | 10 | 22–134        | 70.8±25.9                       |

| Weeks               | n | Min-max value | Individuals 100 g <sup>-1</sup> |
|---------------------|---|---------------|---------------------------------|
| 0 (31 January 2006) | 8 | 9–35          | 16.4±9                          |
| 9 (4 April 2006)    | 8 | 3–101         | 54.7±33.7                       |
| 16 (26 May 2006)    | 7 | 57–224        | 130.2±55.5                      |

| Time intervals | n | Min-max value | Individuals 100 g <sup>-1</sup> |
|----------------|---|---------------|---------------------------------|
| 0 (control)    | 5 | 88–516        | 246.1±173.5                     |
| 5 min          | 5 | 0.3–21        | 11.2±7.4                        |
| 15 min         | 5 | 6–125         | 49.9±51.9                       |
| 30 min         | 5 | 13–54         | 35.5±15.3                       |
| 60 min         | 5 | 38–106        | 71.2±32                         |
| 720 min        | 5 | 1–45          | 11.2±19                         |
| 1440 min       | 5 | 7–87          | 44.5±35.2                       |

Sample size, minimum and maximum value in the samples, and average±std are given.

way ANOVA,  $F=5.233$ ,  $p=0.012$ ; post-hoc Tukey: Jan=April<May). The main increase registered was among adult individuals (Fig. 1), suggesting that immigration rather than reproduction may have contributed to this increase in abundance.

#### 3.2. Colonization experiment

All 8 holdfasts collected at the start of the experiment (0 week) harboured relatively few isopods (Fig. 2), ranging from a minimum of 6 individuals (5 of which were males) to a maximum of 22 isopods in one holdfast (corresponding to 35 individuals 100 g<sup>-1</sup>). The total number of isopods in the holdfasts increased during the experiment, from an initial value of 16.4±9.0 individuals 100 g<sup>-1</sup> (31 January) to 54.7±33.7 individuals 100 g<sup>-1</sup> (4 April) and reaching a value of 130.2±55.5 individuals 100 g<sup>-1</sup> at the end of the experiment (26 May) (Table 1; one-way ANOVA,  $F=12.832$ ,  $p=0.001$ ; post-hoc Tukey: Jan=April<May).

**Table 2**

Percentages of the different life history stages of *Limnoria* spp. during the colonization experiment in Playa Blanca, northern-central coast of Chile

| Weeks               | Non-reproductive female | Reproductive female | Males | Subadults | Juveniles |
|---------------------|-------------------------|---------------------|-------|-----------|-----------|
| 0 (31 January 2006) | 26.7                    | 18.0                | 50.7  | 3.7       | 0.9       |
| 9 (4 April 2006)    | 37.9                    | 12.6                | 41.5  | 7.4       | 0.6       |
| 16 (26 May 2006)    | 34.8                    | 11.5                | 36.8  | 10.8      | 6.0       |

The proportions of the different life history stages (Table 2) varied significantly between the three sampling dates ( $\chi^2=31.93$ ;  $p<0.001$ ). Post-hoc comparisons between the subsequent sampling dates showed that there were no significant differences between the first and second sampling date ( $\chi^2=6.76$ ;  $p>0.05$ ), but they were significant between the second and third sampling date ( $\chi^2=21.03$ ;  $p<0.001$ ). These differences are due to the increase in juveniles between weeks 9 and 16 ( $\chi^2=18.16$ ;  $p<0.001$ ).

Throughout the experiment, all size classes were found in these new holdfasts (Fig. 3). Between the start of the experiment and week 9 all size classes had increased in abundance, but juvenile and subadult individuals (<1.6 mm body length) and small adults showed the strongest increase. Between weeks 9 and 16, adults of the larger size classes (2.4–3.2 mm) increased in proportion, possibly due to growth. The growing number of juveniles in week 9 and in particular during

week 16 indicates increasing reproductive activity in these new holdfasts (see also above and Table 2) – this is supported by observations of reproductive females with small juveniles in their burrows, which we occasionally found during dissection of the holdfasts. The proportion of non-reproductive females increased over time, while that of males decreased (Table 2).

### 3.3. Emigration experiment

Very high abundances of isopods *Limnoria* spp. were found in the holdfasts that were collected directly from the bottom (Fig. 4). During detachment of holdfasts from the substratum, the divers immediately observed limnoriids crawling out of their burrows and rapidly swimming away from the holdfasts. Most isopods swam towards the bottom but some attached to nearby kelp plants or even to the diver. Experimental detachment had a significant effect on the total abundance of isopods in the holdfasts (one-way ANOVA,  $F=30.952$ ,  $p<0.001$ ). Already 5 min after being suspended at the sea surface, numbers of *Limnoria* spp. in the detached holdfasts were significantly lower than in the benthic control holdfasts. A large proportion of all developmental stages disappeared within the first 5 min. Thereafter, only minor changes in isopod abundance were observed (Fig. 4). The total abundances of isopods remaining in the experimental holdfasts represented about 5–20% of the abundances found in the control holdfasts (Table 1). In each of the six temporal treatments (5, 15, 30, 60, 720, and 1440 min

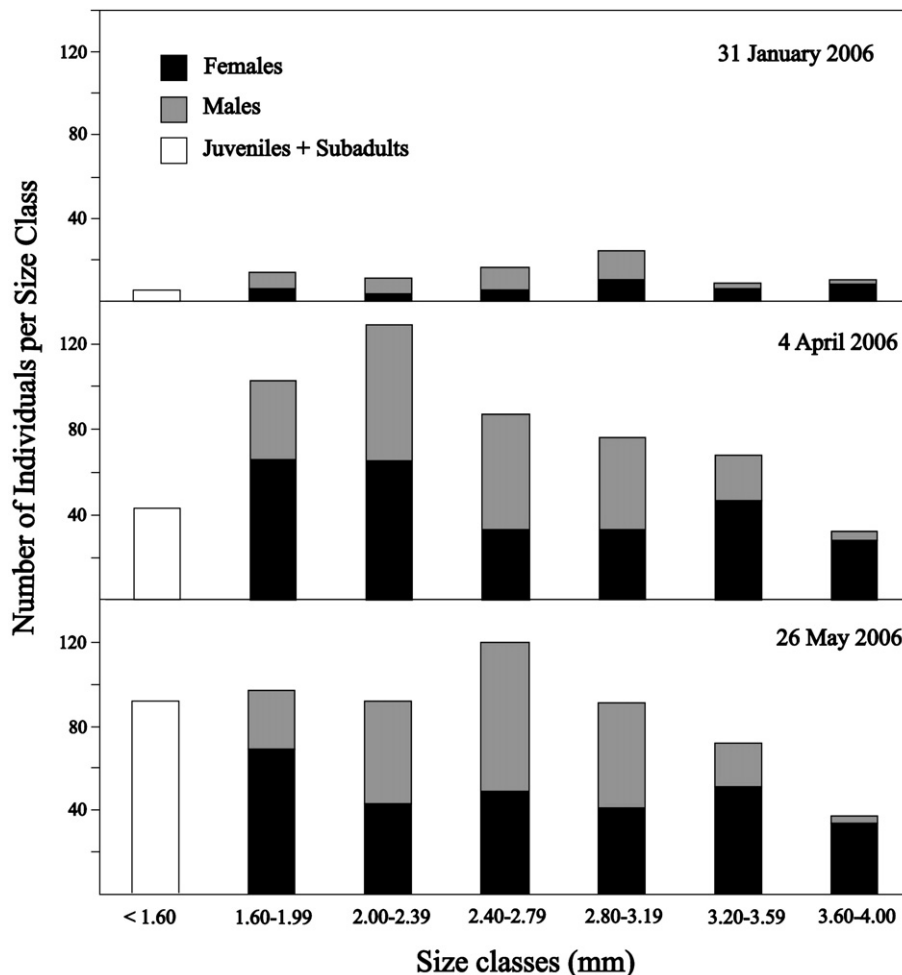
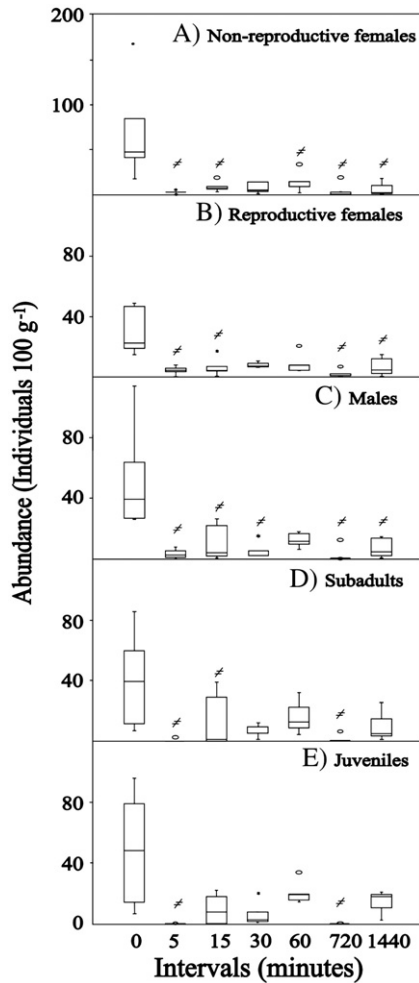


Fig. 3. Size frequency distribution of *Limnoria* spp. in holdfasts of young individuals of *Macrocystis integrifolia* during the three sampling dates; holdfasts were marked as young and uncolonized holdfasts on 31 January 2006.



**Fig. 4.** Abundance (individuals  $100\text{ g}^{-1}$ ) of *Limnoria* spp. in benthic and suspended holdfasts of *Macrocystis integrifolia* at the respective time intervals after detachment and installation at the sea surface; box plots show median, 25% percentiles, and ranges. Dunnett's test was used as a post-hoc test to compare abundances between the control with the experimental treatments; \* indicates significant difference between control and treatment.

after detachment) at least 4 of the 5 replicate holdfasts contained ovigerous females.

#### 4. Discussion

The boring isopods *Limnoria* spp. are very abundant in kelp forests along the Chilean coast, where they excavate extensive burrows in kelp holdfasts. All life history stages of these isopods were found to immigrate into young holdfasts. Similarly, upon detachment, members of all stages rapidly emigrated from holdfasts, most of which will be driven out of local kelp forests by currents and/or become stranded on nearby beaches. The high migration activity in response to holdfast detachment suggests highly dynamic movements of *Limnoria* spp. within a local kelp forest. While the majority of the inhabitants quickly abandoned their burrows when holdfasts were detached, some individuals of all life history stages persisted in the holdfasts for at least 24 h, possibly because they were unable to emigrate and excavate new burrows in other holdfasts. During this time, currents might carry some kelp rafts away from local kelp forests, and consequently these residents of holdfasts might embark on long-distance journeys.

##### 4.1. Active migrations of boring isopods

Migration of wood-boring isopods is thought to be induced by intrinsic factors such as life history stage, sex, reproductive status (e.g.,

Henderson, 1924; Kofoid and Miller, 1927; Johnson and Menzies, 1956; Eltringham and Hockley, 1961). Our data indicate that extrinsic factors (here detachment) also can induce active migrations in boring isopods. After holdfast detachment individuals of all life history stages quickly left their burrows. Interestingly, many of the reproductive females (incubating embryos in their marsupium or juveniles in their burrows) also emigrated actively from detached holdfasts. This appears to be in sharp contrast with previous studies and with our hypothesis, which suggested that ovigerous limnoriid females never or only rarely migrate actively (Johnson 1935, Johnson and Menzies, 1956; Eltringham and Hockley, 1961). Active migration and colonization of new habitats is mainly carried out by subadults, non-ovigerous females and males in boring isopods, but usually not by small juveniles or ovigerous females (Eltringham and Hockley, 1961; Brooks and Bell, 2001b; Davidson et al., 2008).

The immediate reaction of all life history stages to detachment suggests that it might be advantageous for isopods to abandon detached holdfasts. Due to the rapid reaction of the isopods, this active emigration usually occurs within the kelp forest. *Limnoria* spp. are very agile swimmers (Henderson, 2000) and the individuals emerging from detached holdfasts quickly returned to the bottom (personal observations), where they are able to find new holdfasts as habitat. This strategy might be advantageous because the majority of detached holdfasts are typically deposited on nearby beaches (ZoBell, 1971), meaning certain death for holdfast inhabitants. Rapid emigration and return to the bottom may thus enhance the survival chances of isopods. The fact that we never found *Limnoria* spp. in substratum samples without holdfasts suggests that most isopod migrants quickly re-associated with holdfasts.

A few members of all life history stages remained in the holdfasts (5–20% of the total holdfast population). The apparent advantages of rapid emigration and return to benthic habitats suggest that those isopods that remain in the holdfasts might have been unable to leave at the moment of detachment. Possibly, these are individuals that have recently molted and have not yet fully recovered their boring activity. They might have a higher survival probability in their burrows (even when holdfasts are detached) than on the outside.

Many burrow-dwelling isopods and amphipods are highly susceptible to predators outside of their burrows (e.g. Perry, 1988). Consequently, active migration is a risky enterprise and it usually occurs during favourable time periods. For example, Saigusa et al. (2003) revealed high swimming activity of *Limnoria* sp. (most likely *L. lignorum* according to the authors) during night high tides. A study by Menzies (1961) also indicated high nocturnal migration activity of *L. tripunctata*. Our data confirm that at least during calm weather (when samples were taken) there is little active migration during the day. Interestingly, turbid conditions during storms may diminish the predation risk of small organisms (such as limnoriid isopods) swimming in the water column (see e.g. De Robertis et al., 2003). Thus, isopods that migrate during detachment events might experience low predation risk, even during the day.

##### 4.2. Detachment induced migrations and limnoriid population in kelp forests

Our results on active emigration from detached kelp plants suggest that colonization of new holdfasts is linked to major detachment events. The large numbers of limnoriids colonizing the young (marked) holdfasts can not be explained by local reproduction within these holdfasts. Most likely many of the colonizers emigrated from older holdfasts that were detached during the time period of the colonization experiment, when frequent coastal storms caused multiple detachment events. Notorious losses of kelp plants were observed in April and May 2006 (L. Miranda and I. Hinojosa, personal observations), possibly resulting in the significant increase of limnoriid abundance in the remaining holdfasts observed during that time period (see Figs. 1 and 2).

Due to the extremely rapid emigration response we infer that these migrations occur over distances of meters or tens of meters, i.e. within the kelp forest. For the wood-dwelling species *L. lignorum*, Johnson (1935) expressed that he “believed that the principal means of dispersal within an infected area is by regular seasonal migration. .... These migrations must not be understood as occurring over any considerable distances but rather as a matter of only a few meters or less.”

Studies on kelp dynamics have revealed infrequent but intense events of detachment of kelps (Jones, 1971). Based on our observations, we propose that detachment events provoke migration pulses and a high turnover of *Limnoria* spp. within local kelp forests, similar as reported for local populations of other peracarid crustaceans (e.g. Edgar, 1992; Taylor, 1998; Poore, 2005). For an amphipod associated with gorgonians, Kumagai (2006) also observed an increase in local migration rates over distances of 8–70 m shortly after storm events. It can be expected that these active migrations, whether induced by intrinsic or extrinsic factors, result in an efficient homogenization of local populations (i.e. within a kelp forest). Consequently, there is a relatively limited potential for high population differentiation and the development of local demes (within holdfasts) in a kelp forest.

#### 4.3. Passive long-distance dispersal of boring isopods

If detached kelps float away from the shore, their inhabitants can be passively transported to new habitats, which had also been suggested for boring isopods (Hill and Kofoid, 1927; Johnson, 1935; Svavarsson, 1982; Brooks, 2004; Davidson, 2008). Various authors reported boring isopods in driftwood and floating algae (Edgar, 1987; Edgar and Burton, 2000; Bushing, 1994; Si et al., 2000; Davidson, 2008), but the life history stages predominating in floating substrata were not known. This information, nevertheless, is very important, because the presence of reproductive females in floating substrata will increase the possibility of persistence and successful colonization after landfall. Ovigerous females are considered highly efficient colonizers because they will release offspring that recruit directly into the new habitats (Poore and Steinberg, 1999; Kumagai, 2006; Munguia et al., 2007). In the present study we found only low numbers of reproductive females remaining in the holdfasts. However, there were a few ovigerous females in all holdfasts, and in addition to these there were adult females and males. During long-lasting journeys, these may produce offspring that recruit within the natal holdfast, ensuring persistence of temporary demes within rafts (see also Hobday, 2000). Furthermore, reproductive females will then also facilitate successful colonization in new habitats.

The fact that only few individuals remain in the holdfast after detachment could even be advantageous for long-distance migrations. Boring isopods consume their substratum, and high numbers of grazers can accelerate the destruction of floating substrata (e.g. Gutow, 2003; Vandendriessche et al., 2007). The decrease in isopods abundance at the start of rafting journeys (i.e. immediately after detachment) leads to an increase in the availability of food resources for the remaining rafters, thereby facilitating successful long-distance dispersal.

#### 4.4. Active local migrations and passive long-distance dispersal

Storm events and the temporal variability of the environment (e.g. seasonal growth periods) have important effects on dispersal in many organisms (e.g. Dobbs and Vozarik, 1983; Johst and Brandl, 1997). Our results suggest that storm-related kelp detachment induces high local migration activity within kelp forests. While most isopods apparently participated in these local migration events, a small fraction of individuals also persisted within detached holdfasts, opening the possibility for long-distance dispersal. Depending on weather and oceanic conditions, floating objects can be transported over large distances in the Humboldt Current System (e.g. Marín and Delgado, 2007). If floating kelp rafts reach other kelp forests, there is a high likelihood that some of the reproductive females can become successful

founders of new populations or contribute significantly to existing populations (see e.g. Munguia et al., 2007).

Thus, within holdfast-dwelling *Limnoria* studied herein, there seem to coexist two different dispersal modes, namely (i) active short distance migrations, and (ii) passive long-distance dispersal. This might be advantageous under highly variable environmental scenarios as prevailing along the coasts of northern Chile and Peru. This area of the Humboldt Current System is exposed to highly unpredictable environmental conditions caused by El Niño Southern Oscillation (ENSO), which can result in extinctions of kelp beds over large spatial extensions (Castilla and Camus, 1992; Camus et al., 1994; Vega et al., 2005). Under such conditions, mixed dispersal distances (short and long) as suggested by our results might be advantageous, ensuring both population persistence in local kelp forests (via short distance migrations induced by detachment and habitat destruction) and recolonization of regrowing kelp patches (via long-distance rafting dispersal) (see also Johst and Drechsler, 2003).

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#### References

- Baratti, M., Goti, E., Messina, G., 2005. High level of genetic differentiation in the marine isopod *Sphaeroma terebrans* (Crustacea, Isopoda, Sphaeromatidae) as inferred by mitochondrial DNA analysis. *J. Exp. Mar. Biol. Ecol.* 315, 225–234.
- Baums, I.B., Miller, M.W., Hellberg, M.E., 2005. Regionally isolated populations of an imperilled Caribbean coral, *Acropora palmata*. *Mol. Ecol.* 14, 1377–1390.
- Brooks, R.A., 2004. Discovery of *Sphaeroma terebrans*, a wood-boring isopod, in the red mangrove, *Rhizophora mangle*, habitat of northern Florida Bay. *Ambio* 33, 171–173.
- Brooks, R.A., Bell, S.S., 2001a. Mobile corridors in marine landscapes: enhancement of faunal exchange at seagrass/sand ecotones. *J. Exp. Mar. Biol. Ecol.* 264, 67–84.
- Brooks, R.A., Bell, S.S., 2001b. Colonization of a dynamic substrate: factors influencing recruitment of the wood-boring isopod, *Sphaeroma terebrans*, onto red mangrove (*Rhizophora mangle*) prop roots. *Oecologia* 127, 522–532.
- Buschmann, A.H., Vásquez, J.A., Osorio, P., Reyes, E., Filán, L., Hernández-González, C., Vega, A., 2004. The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp. (Phaeophyta) at different latitudes in Chile. *Mar. Biol.* 145, 849–862.
- Bushing, W.W., 1994. Biogeographic and ecological implications of kelp rafting as a dispersal vector for marine invertebrates. In: Halvorson, W.L., Maender, G.J. (Eds.), *Proceedings of the Fourth California Islands Symposium: Update on the Status of Resources*, March 22–25, 1994. Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 103–110.
- Camus, P.A., Vásquez, J.A., González, E.O., Galáz, L.E., 1994. Fenología espacial de la diversidad comunitaria intermareal en el norte de Chile: patrones comunitarios de variación geográfica e impacto de los procesos de extinción–recolonización post El Niño 82/83. *Medio Ambiente (Chile)* 12, 129–163.
- Carson, H.S., Hentschel, B.T., 2006. Estimating the dispersal potential of polychaete species in the Southern California Bight: implications for designing marine reserves. *Mar. Ecol. Prog. Ser.* 316, 105–113.
- Castilla, J.C., Camus, P.A., 1992. The Humboldt-El Niño scenario — coastal benthic resources and anthropogenic influences, with particular reference to the 1982/83 ENSO. *S. Afr. J. Mar. Sci.* 12, 703–712.
- Cookson, L.J., 1991. Australasian species of Limnoriidae (Crustacea: Isopoda). *Mem. Mus. Vic.* 52, 137–262.
- Cragg, S.M., Pitman, A.J., Henderson, S.M., 1999. Developments in the understanding of the biology of marine wood boring crustaceans and in methods of controlling them. *Int. Biodeterior. Biodegrad.* 43, 197–205.
- Davidson, T.M., 2008. Prevalence and distribution of the introduced burrowing isopod, *Sphaeroma quoianum*, in the intertidal zone of a temperate Northeast Pacific estuary (Isopoda, Flabellifera). *Crustaceana* 81, 155–167.
- Davidson, T.M., Rumrill, S.S., Shanks, A.L., 2008. Colonization and substratum preference of an introduced burrowing crustacean in a temperate estuary. *J. Exp. Mar. Biol. Ecol.* 354, 144–149.
- De Robertis, A., Ryer, C.H., Veloza, A., Brodeur, R.D., 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Can. J. Fish. Aquat. Sci.* 60, 1517–1526.
- Dobbs, F.C., Vozarik, J.M., 1983. Immediate effects of a storm on coastal infauna. *Mar. Ecol. Prog. Ser.* 11, 273–279.

- Donald, K.M., Kennedy, M., Spencer, H.S., 2005. Cladogenesis as the result of long-distance rafting events in South Pacific topshells (Gastropoda: Trochidae). *Evolution* 59, 1701–1711.
- Edgar, G.J., 1987. Dispersal of faunal and floral propagules associated with drifting *Macrocystis pyrifera* plants. *Mar. Biol.* 95, 599–610.
- Edgar, G.J., 1992. Patterns of colonization of mobile epifauna in a Western Australian seagrass bed. *J. Exp. Mar. Biol. Ecol.* 157, 225–246.
- Edgar, G.J., Burton, H.R., 2000. The biogeography of shallow-water macrofauna at Heard Island. *Pap. Proc. R. Soc. Tasman.* 133, 23–26.
- Elias, I., 1981. Estudios sobre la poblacion del isopodo *Limnoria (Phycolimnoria) chilensis* Menzies asociada al grampon de *Macrocystis pyrifera*. *Physis, Secc. A.* 40, 33–42.
- Eltringham, S., Hockley, A., 1961. Migration and reproduction of the wood-boring isopod, *Limnoria*, in Southampton waters. *Limnol. Oceanogr.* 6, 467–482.
- Franz, D.R., Mohamed, Y., 1989. Short-distance dispersal in a fouling community amphipod crustacean, *Jassa marmorata* Holmes. *J. Exp. Mar. Biol. Ecol.* 133, 1–13.
- Gutow, L., 2003. Local population persistence as a pre-condition for large scale dispersal of *Idotea metallica* (Crustacea: Isopoda) on drifting habitat patches. *Hydrobiologia* 503, 45–48.
- Haye, P.A., Marchant, S., 2007. Newly developed PCR primers for polymorphic microsatellite loci from the marine isopod *Limnoria* sp. *Mol. Ecol. Notes* 7, 1245–1247.
- Henderson, J.T., 1924. The gribble: a study of the distribution factors and life-history of *Limnoria lignorum* at St. Andrews. *N.B. Contr. Can. Biol.* 2, 309–327 part 1 (14).
- Henderson, S.M., 2000. The swimming behavior of the marine wood borer *Limnoria quadripunctata* (Isopoda: Limnoriidae). *Crustac. Issues* 12, 227–238.
- Hill, C.L., Kofoid, C.A., 1927. Marine borers and their relation to marine construction on the Pacific coast. Final report of the San Francisco Bay Marine Piling Committee. 351 pp.
- Hinojosa, I., Boltana, S., Lancellotti, D., Macaya, E., Ugalde, P., Valdivia, N., Vásquez, N., Newman, W.A., Thiel, M., 2006. Zoogeography of four pelagic barnacles along the SE-Pacific coast of Chile. *Rev. Chil. Hist. Nat.* 79, 13–27.
- Hobday, A., 2000. Persistence and transport of fauna on drifting kelp (*Macrocystis pyrifera* (L.) C. Agardh) rafts in the Southern California Bight. *J. Exp. Mar. Biol. Ecol.* 253, 75–96.
- Johst, K., Brandl, R., 1997. Evolution of dispersal: the importance of the temporal order of reproduction and dispersal. *Proc. R. Soc. Lond., B* 264, 23–30.
- Johst, K., Drechsler, M., 2003. Are spatially correlated or uncorrelated disturbance regimes better for the survival of species? *Oikos* 103, 449–456.
- Johnson, M.W., 1935. Seasonal migration of the wood-borer *Limnoria lignorum* (Rathke) at Friday Harbor, Washington. *Biol. Bull.* 69, 427–438.
- Johnson, M.W., Menzies, R.J., 1956. The migratory habits of the marine gribble *Limnoria tripunctata* Menzies in San Diego Harbor, California. *Biol. Bull.* 110, 54–68.
- Johnson, M.S., Black, R., 2006. Islands increase genetic subdivision and disrupt patterns of connectivity of intertidal snails in a complex archipelago. *Evolution* 60, 2498–2506.
- Jones, L.G., 1971. Studies on selected small herbivorous invertebrates inhabiting *Macrocystis* canopies and holdfasts in Southern California kelp beds. *Beih. Nova Hedwig.* 32, 343–367.
- Kingsford, M.J., Choat, J.H., 1985. The fauna associated with drift algae captured with a plankton-mesh purse seine net. *Limnol. Oceanogr.* 30, 618–630.
- Kofoid, C.A., Miller, R.C., 1927. Biological section. Marine Borers and their relation to marine construction on the Pacific Coast. Report of the San Francisco Bay Marine Piling Committee. San Francisco, pp. 188–343.
- Kumagai, N.H., 2006. Distance effects on patterns and processes of dispersal in an octocoral-associated amphipod. *Mar. Ecol. Prog. Ser.* 321, 203–214.
- Levin, L.A., 2006. Recent progress in understanding larval dispersal: new directions and digressions. *Integr. Comp. Biol.* 46, 282–297.
- Macaya, E., Boltaña, S., Hinojosa, I., Macchiavello, J., Valdivia, N., Vásquez, N., Buschmann, A., Vásquez, J., Vega, A., Thiel, M., 2005. Presence of sporophylls in floating kelp rafts of *Macrocystis* spp. (Phaeophyceae) along the Chilean Pacific coast. *J. Phycol.* 41, 913–922.
- Marín, V.H., Delgado, L.E., 2007. Lagrangian observations of surface coastal flows north of 30°S in the Humboldt Current System. *Cont. Shelf Res.* 27, 731–743.
- Menzies, R.J., 1957. The marine borer family Limnoriidae (Crustacea, Isopoda). *Bull. Mar. Sci. Gulf Caribb.* 7, 101–200.
- Menzies, R.J., 1961. Suggestion of night-time migration by the wood-borer *Limnoria*. *Oikos* 12, 170–172.
- Munguia, P., Mackie, C., Levitan, D.R., 2007. The influence of stage-dependent dispersal on the population dynamics of three amphipod species. *Oecologia* 153, 533–541.
- Norkko, J., Bonsdorff, E., Norkko, A., 2000. Drifting algal mats as an alternative habitat for benthic invertebrates: species specific responses to a transient resource. *J. Exp. Mar. Biol. Ecol.* 248, 79–104.
- Paine, R.T., Suchanek, T.H., 1983. Convergence of ecological processes between independently evolved competitive dominants: a tunicate-mussel comparison. *Evolution* 37, 821–831.
- Palmer, M.A., 1988. Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Mar. Ecol. Prog. Ser.* 48, 81–91.
- Perry, D.M., 1988. Effects of associated fauna on growth and productivity in the red mangrove. *Ecology* 69, 1064–1075.
- Poore, A.G.B., 2005. Scales of dispersal among hosts in a herbivorous marine amphipod. *Aust. Ecol.* 30, 219–228.
- Poore, A.G.B., Steinberg, P.D., 1999. Preference–performance relationships and effects of host plant choice in a herbivorous marine amphipod. *Ecol. Monogr.* 69, 443–464.
- Saigusa, M., Okochi, T., Ikei, S., 2003. Nocturnal occurrence, and synchrony with tidal and lunar cycles, in the invertebrate assemblage of a subtropical estuary. *Acta Oecol.* 24, S191–S204.
- Salovius, S., Nyqvist, M., Bonsdorff, E., 2005. Life in the fast lane: macrobenthos use temporary drifting algal habitats. *J. Sea Res.* 53, 168–180.
- Shanks, A.L., Grantham, B.A., Carr, M.H., 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.* 13, 159–169.
- Si, A., Alexander, C.G., Bellwood, O., 2000. Habitat partitioning by two wood-boring invertebrates in a mangrove system in tropical Australia. *J. Mar. Biol. Assoc. U.K.* 80, 1131–1132.
- Svavarsson, J., 1982. *Limnoria borealis* (Isopoda, Flabellifera) and its commensal, *Caecijaera borealis* (Isopoda, Asellota), found in Icelandic waters. *Sarsia* 67, 223–226.
- Taylor, R.B., 1998. Short dynamics of a seaweed epifaunal assemblage. *J. Exp. Mar. Biol. Ecol.* 227, 67–82.
- Thiel, M., 2003. Reproductive biology of *Limnoria chilensis*: another boring peracarid species with extended parental care. *J. Nat. Hist.* 37, 1713–1726.
- Thiel, M., Vasquez, J., 2000. Are kelp holdfasts islands on the ocean floor? Indication for temporally closed aggregations of peracarid crustacean. *Hydrobiologia* 440, 45–54.
- Thiel, M., Gutow, L., 2005. The ecology of rafting in the marine environment – II. the rafting organisms. *Oceanogr. Mar. Biol. Annu. Rev.* 43, 281–420.
- Vandendriessche, S., Vincx, M., Degraer, S., 2007. Floating seaweed and the influences of temperature, grazing and clump size on raft longevity – a microcosm study. *J. Exp. Mar. Biol. Ecol.* 343, 64–71.
- Vásquez, J.A., 1993. Effects on the animal community of dislodgment of holdfasts of *Macrocystis pyrifera*. *Pac. Sci.* 47, 180–184.
- Vega, J.M.A., Vásquez, J.A., Buschmann, A.H., 2005. Population biology of the subtidal kelps *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales, Phaeophyceae) in an upwelling ecosystem of northern Chile: interannual variability and El Niño 1997–1998. *Rev. Chil. Hist. Nat.* 78, 33–50.
- Waters, J.M., Roy, M.S., 2004. Out of Africa: the slow train to Australasia. *Syst. Biol.* 53, 18–24.
- ZoBell, C.E., 1971. Drift seaweeds on San Diego County beaches. *Nova Hedwig.* 32 (Suppl.), 269–314.