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

Leonardo Miranda [a], Martin Thiel [a,b,*]

[a] Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile
[b] Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile

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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.

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,

* Corresponding author. Facultad de Ciencias de Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile.
E-mail address: thiel@ucn.cl (M. Thiel).

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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 Kofoid (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; Svavarsson, 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^2 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