

Reproductive biology of *Limnoria chilensis*: another boring peracarid species with extended parental care

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Several boring peracarid species engage in extended parental care with parents tolerating small juveniles in their burrows, but only anecdotal observations have been reported from boring isopods of the genus *Limnoria*. The isopod *Limnoria chilensis* Menzies is frequently found in holdfasts of the macroalgae *Macrocystis pyrifera* (L.) C. Agardh and *Durvillea antarctica* (Chamisso) Hariot. In the present study, holdfasts of *D. antarctica* that harboured *L. chilensis* were carefully dissected in order to examine the association pattern of reproductive females and small juveniles. In most infested holdfasts, *L. chilensis* reached very high densities of 43.7 ± 3.9 (mean \pm SE) individuals cm^{-2} (range: 0–90 individuals cm^{-2}). The overall sex ratio (females:males) was close to unity (1.2). Male size varied between 1.5 and 2.6 mm body length (BL) and female size between 1.5 and 3.6 mm BL. The percentage of reproductive females was low (19.7% of all females), and only the largest females (>2.6 mm BL) were reproductive. Embryo numbers ranged between six and 19 per female and a significant correlation between female BL and the number of embryos was found. Several females were found with small juveniles (0.8–1.2 mm BL) in the terminal end of their burrows. On several occasions, aggregations of similar-sized juveniles (1.0–1.5 mm BL) in their own burrows were found near a female burrow, indicating that these juveniles initiated their first individual burrows from within the maternal burrows. Some females with small juveniles in the terminal end of their burrows were either accompanied by males or they were ovigerous, indicating that they may have been in the process of producing a second brood. The fact that juveniles build their first burrows in the protection of female burrows suggests that such small juveniles have not yet developed full boring capacity. Extended parental care in this (and other boring) peracarid species represents a mechanism facilitating high juvenile survival rates. Given the highly local recruitment, it is suggested that the reproductive biology of this isopod has strong implications for its population biology.

KEYWORDS: Reproduction, Extended parental care, Isopoda, Peracarida, boring, kelp holdfasts.

Introduction

Animal homes that are constructed in hard substrata provide efficient shelter, but the costs of excavating may be very high. It is, thus, not surprising that many

species that bore into hard substrata co-operate with other individuals in order to improve boring efficiency. Linsenmair (1979, 1984) identified the short time period during which it is possible to excavate burrows in hard desert soil as one of the main driving forces in the evolution of monogamous mating behaviour in the desert isopod *Hemilepistus reaumuri* Audoin and Savigny. The evolution of eusocial behaviour in the naked mole rat has also been related to difficulties associated with efficient excavation of burrows (Brett, 1991). Similarly, the occurrence of extended parental care in species that construct burrows in hard substrata has been related to the fact that small juveniles have not yet achieved full boring capacity (Jarman and Reyes-Castillo, 1985; Thiel, 1999a, 2000). Apparently, many boring or burrowing organisms can only achieve efficient boring by joining forces with conspecifics. This need has resulted in the evolution of distinct intraspecific associations in these boring species, ranging from monogamous pairs to small family-groups and finally large colonies of genetically closely related individuals.

The presence of intraspecific associations is often revealed through direct observations of the inhabitants from a particular burrow or burrow system. In species that live at low densities, individual dwellings with all of their inhabitants can be relatively easily sampled (see, for example, Forbes, 1973; Thiel *et al.*, 1997; Murata and Wada, in press). Sampling of individual dwellings has allowed for recognition of interspecific associations (for example, Rasa and Endrödy-Younga, 1997; Sanver and Hawkins, 2000), male and female groups or pairs (Shuster, 1987), or parent–offspring associations (for example, Hamr and Richardson, 1994; Rasa, 1999; Murata and Wada, in press). However, when animal burrows occur at high densities, discovering individuals associated in the same dwelling is more difficult, since it is almost impossible to take a sample of an individual dwelling. In the amphipod *Corophium volutator* (Pallas), which can occur at densities exceeding 10 individuals cm⁻², Flach (1992) solved this problem by producing small-scale maps of the exact position of amphipod burrows. She could thereby show that reproductive females are often surrounded by groups of similar-sized juveniles. These results reconfirmed careful observations by Thamdrup (1935), who had revealed that juvenile *C. volutator* remain in the maternal burrow for several days and then start their own burrows from within their mothers' burrows. Similar forms of maternal care have also been suggested for other crustacean species (for example, *Callianassa kraussi* Stebbing—Forbes 1973; *Heterotanais oerstedii* Krøyer—Bückle-Ramirez, 1965), and have been postulated to occur in other species (Thiel, 1999b). However, observations of intraspecific associations in many potential species are impeded by the very high abundance of individuals in substrata that are difficult to sample.

A wide diversity of boring peracarid crustaceans reach very high densities in wood and algal tissues. For several species of boring isopods and amphipods, there is evidence of particular intraspecific associations. For example, males and females may cohabit as heterosexual pairs in one burrow (Menzies, 1957; Conlan and Chess, 1992). In addition, females (and males) were frequently found together with small offspring, indicating the existence of extended parental care in several boring species (Conlan and Chess, 1992; Messana *et al.*, 1994; Brearley and Walker, 1996; Thiel, 1999a; Murata and Wada, 2002).

Isopods from the genus *Limnoria* are highly diverse and occur in all major oceans (Cookson, 1991). Most species of this genus excavate burrows in tissues of algae or higher plants (Menzies, 1957). The association of parents (usually the females) together with small juveniles has been reported for the species *L. lignorum*

(Henderson, 1924) and *L. algarum* (Menzies, 1957). Since other *Limnoria* species excavate in similar substrata as *L. lignorum* and *L. algarum*, it could be hypothesised that they exhibit a similar form of extended parental care. The main objective of the present study was to examine the intraspecific association pattern of the algal-boring species *L. chilensis* with a particular emphasis on the association of females with small juveniles.

Material and methods

The isopod habitat

Limnoria chilensis has been found in holdfasts of the macroalgae *Durvillea antarctica* (personal observation), *Macrocyctis pyrifera* (Paternoster and Elias, 1980; Cookson, 1991), *Lessonia nigrescens* Bory and *L. trabeculata* Villouta and Santelices (Thiel and Vásquez, 2000). The macroalga *D. antarctica* has a circum-subantarctic distribution (Hoffmann and Santelices, 1997). Along the Pacific coast of Chile, it occurs from Cape Horn to Antofagasta, yet its main distribution is south of Los Vilos (approximately 32°S). While the algae *M. pyrifera* and *L. trabeculata* are commonly found in shallow subtidal waters, *L. nigrescens* and *D. antarctica* grow in the low intertidal zone of exposed rocky shores. Individuals of *D. antarctica* examined herein were sampled in March 2001 on the intertidal rocky shore near Pumillahue, Chiloé (41°55'S, 74°02'W).

Sampling of kelp holdfasts and processing of samples

During spring low tide, approximately 30 plants were detached from the natural substratum together with their holdfast, using an axe. Immediately following detachment, the holdfasts were examined for the presence of the isopod *Limnoria chilensis*. If dense assemblages of isopods were found, the percentage of the holdfasts colonised by *L. chilensis* was estimated to the nearest 5%. Small blocks of rectangular surface area (approximately 0.5 cm² surface area) of tissue were cut from holdfasts where >25% of the holdfast basis was colonised by isopods. These small blocks were immediately preserved in 10% formalin. In order to ensure that isopods did not leave their burrows, care was taken to preserve small tissue-blocks as soon as possible after collection (i.e. within 5 minutes after detachment from rock substratum). Preliminary observations had indicated that isopods did not leave their burrows once in contact with formalin, but slowly started to crawl out of their burrows if these were not preserved immediately.

In the laboratory, the blocks of plant tissue were removed from formalin and placed in freshwater for dissection. Before the dissection, the area of the basal surface of each tissue block (the side with the burrow openings) was estimated by drawing its surface area on millimetre-paper. The surface area estimated in this way was used to calculate the density of isopods. During dissection, careful attention was paid to animals that were found in the same burrow or in communicating burrows—these were kept together for further analysis. Individuals were classified as associated only when they were clearly identified as being associated with others in the same or in communicating burrows. All other individuals were considered as being of uncertain association status. The body length (BL) of the isopods was measured with the aid of a measurement ocular after stretching them out dorsoventrally with forceps. The sex of adult animals was determined based on the presence of penes appendages and modified pleopods (males) or oostegites (females). In

ovigerous females five developmental stages of embryos were distinguished—Stage A: embryos shortly after fertilisation, egg-like in appearance; Stage B: limb buds emerge, but still in egg membrane; Stage C: embryo hatched from egg, assuming a comma-like shape; Stage D: appendages developing, pereonal segmentation is increasingly visible; and Stage E: embryo resembles juvenile in appearance, ready to emerge from marsupium.

Results

The isopod *Limnoria chilensis* lives in very dense assemblages in the holdfasts of *Durvillea antarctica* (figure 1). Their burrows usually open towards the basal part of the holdfasts. Isopod burrows often occur in combination with those of other,

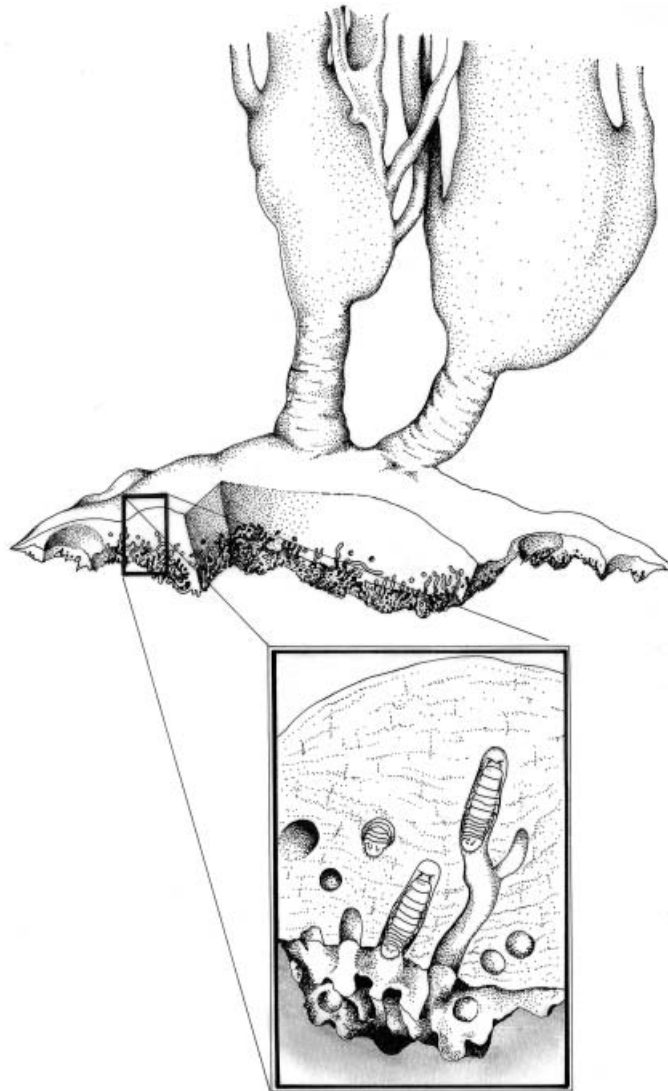


FIG. 1. Holdfast of *Durvillea antarctica* showing the burrows of *Limnoria chilensis* that are extending upwards within the holdfast tissue.

large, macroinvertebrates (e.g. the gastropod *Scurria scurra* Lesson, or the decapod crab *Acanthocyclus hassleri* Rathbun). Isopods reached very high abundances of 43.7 ± 3.9 (mean \pm SE) individuals per square centimetre (range: 0–90 individuals cm^{-2}) in the holdfasts of *D. antarctica*. At such high abundances, the burrows are densely intermingled, but are rarely connected with each other. In the terminal end of burrows, small amounts of decaying plant tissue could be found. Burrows of large females often reached deep into the healthy holdfast tissue. Occasionally, small juveniles occurred in the burrows of large females (figure 2a), and these burrows frequently contained decaying plant tissue at the terminal end. Large juveniles were also found in their own burrows, which, however, remained connected to the burrows of large females (figure 2b). Many similar-sized juveniles were found inhabiting neighbouring burrows around an adult burrow, suggesting that they represented offspring of a single female.

The embryos found in the female marsupium (stage E) were slightly smaller than juveniles found in the terminal end of the female burrow (figures 3a,b). Juveniles that remained in the female burrow ranged between 0.8 and 1.2 mm BL (figure 3b), while those found in small side-burrows originating from the female burrow varied between 1.0 and 1.5 mm BL (figure 3c). The size range of juveniles found in

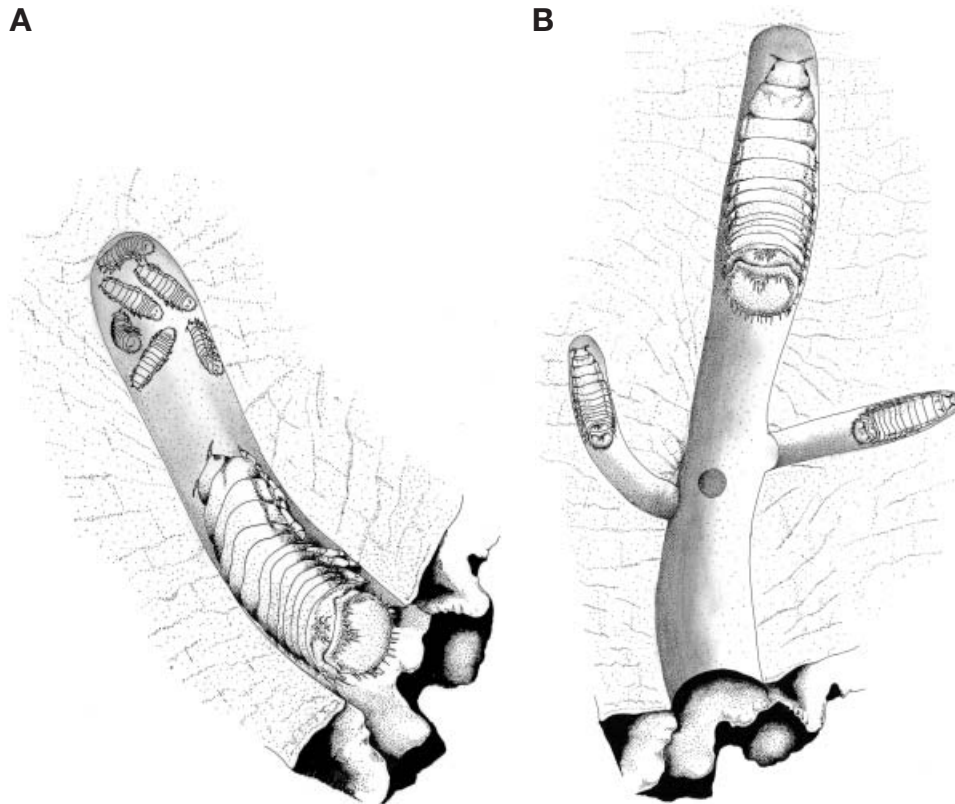


FIG. 2. Female *Limnoria chilensis* in burrow with (A) small juveniles in terminal end of maternal burrows and (B) larger juveniles in side-burrows originating from maternal burrow.

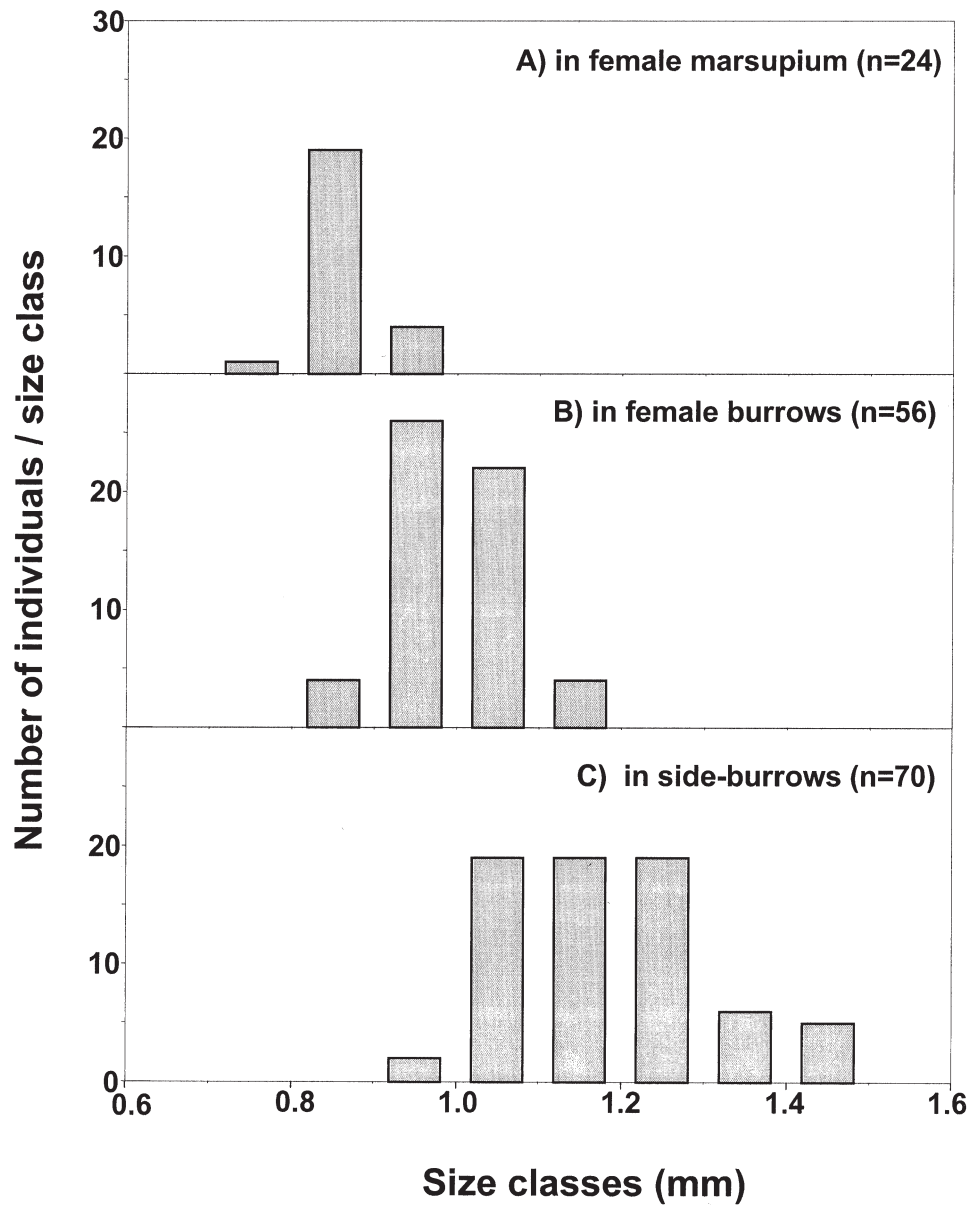


FIG. 3. Number of juvenile *Limnoria chilensis* from (A) female marsupium, (B) terminal end of maternal burrow and (C) side-burrows originating from maternal burrow in respective size classes; data from all holdfast samples collected in March 2001 are pooled.

side-burrows originating from female burrows (figure 3c) corresponds closely with the size range of other juveniles (compare figure 4c).

Adult females ranged between 1.4 and 3.6 mm BL, but only females >2.6 mm BL were found to be reproductive (figure 4a). The smallest individual with identifiable male appendages had a size of 1.4 mm BL, and the largest male found in this study was 2.6 mm BL (figure 4b). Based on these observations, all

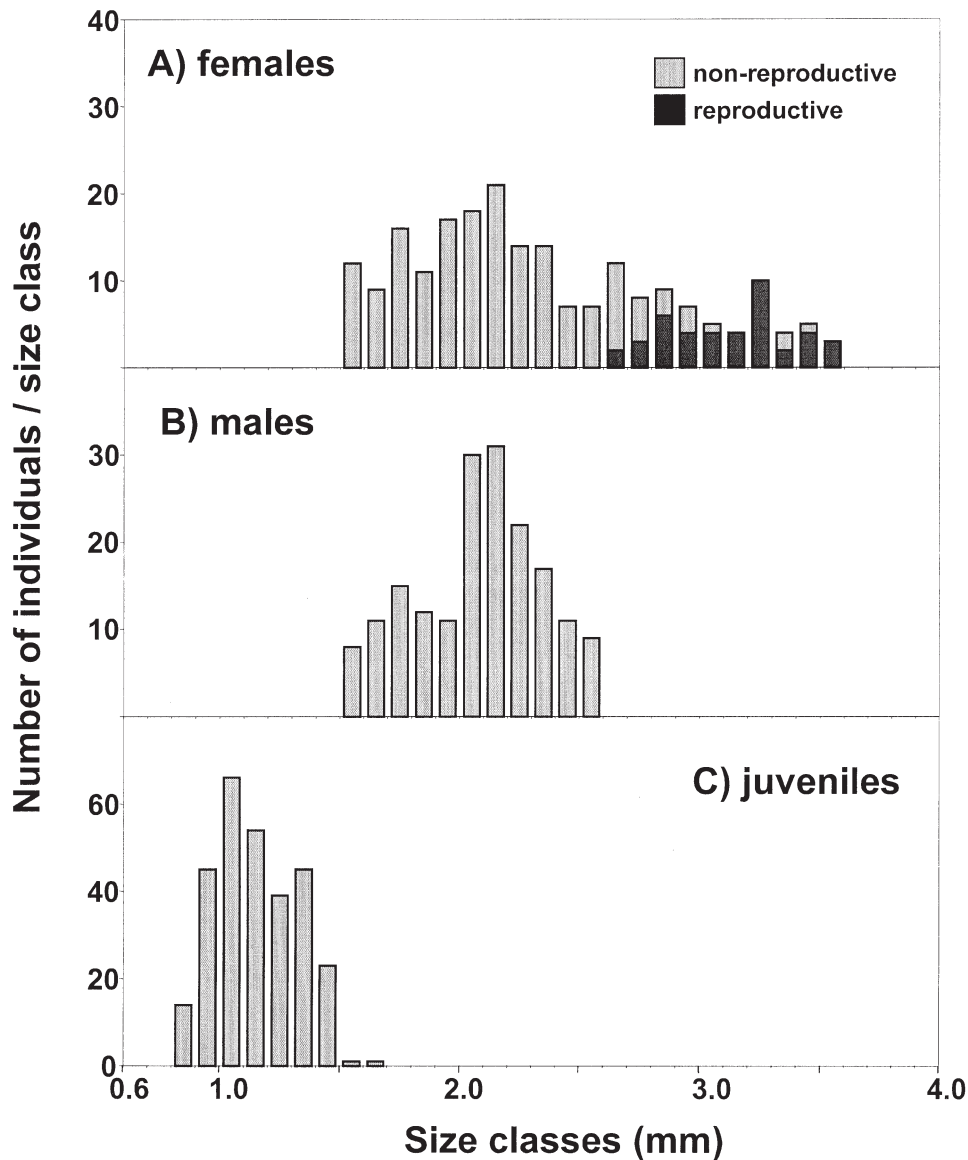


FIG. 4. Number of (A) female, (B) male and (C) juvenile *Linnoria chilensis* in respective size classes; data from all holdfast samples collected in March 2001 are pooled.

individuals > 1.5 mm were sexed according to the presence/absence of male appendages. Of the total number of female isopods ($n = 213$), 42 females (19.7%) were reproductive (i.e. with embryos in marsupium, with juveniles in burrow, or with oostegites). Embryo numbers varied between six and 19 embryos per ovigerous female, and a significant correlation between body length and the number of embryos in the marsupium was found (figure 5). Females with small juveniles in their burrows hosted numbers that corresponded to their size (see quadrats in figure 5). Also, for one female the number of juveniles found in side-burrows corresponded to her size (see arrow in figure 5). The relationship between the number of juveniles in

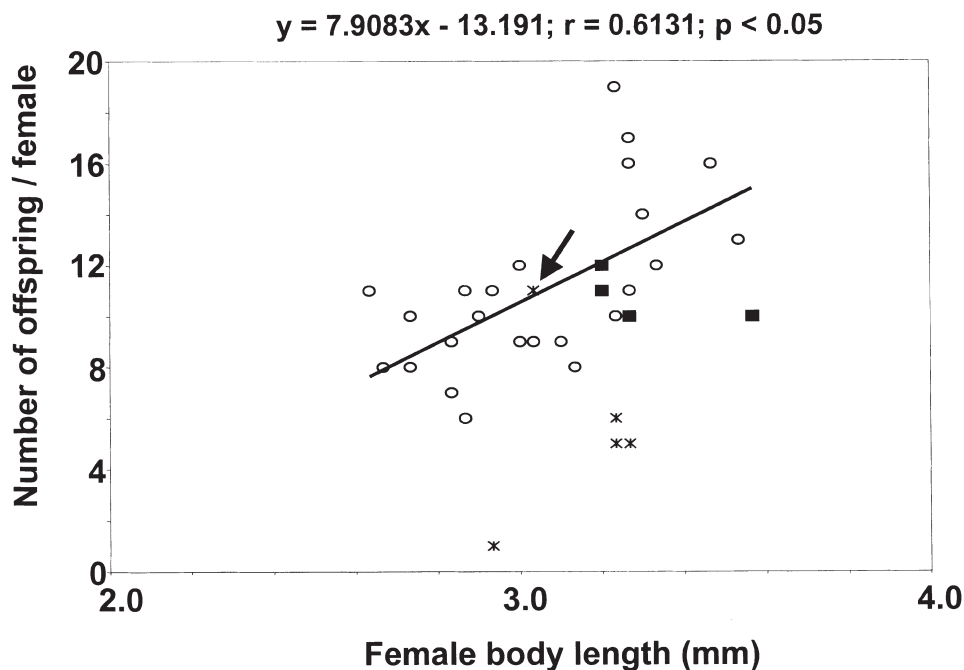


FIG. 5. Number of embryos/juveniles in relationship to body length of female *Limnoria chilensis*; embryos were taken from marsupium (dots), small juveniles from terminal end of maternal burrow (squares), and large juveniles from side-burrows (stars); equation refers to females with embryos in their marsupium (dots); data from all holdfast samples collected in March 2001 are pooled.

side-burrows and female size was not found for several other females (figure 5), which has several possible explanations. For example, juveniles may not have built their burrows originating from the burrow of their mother, or may have been lost during the sampling process (for example, the female with which only one juvenile was found in a side-burrow). Alternatively, the female may have moulted after releasing one brood, and thus its actual size does not correspond to the number of juveniles found in side-burrows (females with five or six juveniles in side-burrows).

Production of at least two broods by a single female is suggested by the fact that several females with juveniles in side-burrows also had embryos in their marsupium. In 15 cases, males could be clearly identified cohabiting with a female (table 1). Several of these males were found together with females that either had juveniles in their own burrows or in side-burrows. Males were never found with ovigerous females that contained embryos of intermediate developmental stages in their marsupium (table 1).

Discussion

Juvenile *Limnoria chilensis* remain in the burrow of their mother after emerging from the female's marsupium. Upon growing, these juveniles excavate their first individual burrows originating from the maternal burrow. This behaviour is similar to that found in other boring peracarid species and in some wood-boring terrestrial arthropods (e.g. Schuster and Schuster, 1985; Kent and Simpson, 1992). In the

Table 1. Numbers and percentages of female *Limnoria chilensis* that were found paired and unpaired with males; all females collected during this study were pooled.

Female stage	Paired		Unpaired or unknown		Total	
	number	per cent	number	per cent	number	per cent
without anything	8	53.3	193	82.5	201	80.7
oocytes in gonads	1	6.7	3	1.3	4	1.6
embryoA in marsupium	1	6.7	9	3.8	10	4.0
embryoB in marsupium			3	1.3	3	1.2
embryoC in marsupium			9	3.8	9	3.6
embryoD in marsupium			2	0.9	2	0.8
embryoE in marsupium	1	6.7	4	1.7	5	2.0
marsupium empty			3	1.3	3	1.2
juveniles in maternal burrow	1	6.7	3	1.3	4	1.6
juveniles in side burrows	3	20.0	5	2.1	8	3.2
All females	15	100	234	100	249	100

following section, the possible reasons for and consequences of this maternal tolerance towards small juveniles is discussed.

Boring into hard substrata requires time and energy (see, for example, Lovegrove, 1989). For example, female ambrosia beetles apparently require several months to burrow a tunnel of 50 mm length (Kent and Simpson, 1992). Jarman and Reyes-Castillo (1985) demonstrated that the mandibular force of larvae from wood-boring passalid beetles is substantially lower than that of adult beetles. In accordance with these results it has recently been shown that small juveniles of the wood-boring isopod *Sphaeroma terebrans* Bate require substantially more time to excavate a burrow than do subadults of this species (Thiel, 2000). Adults of *S. terebrans* require several hours for excavating burrows that accommodate the whole animal (John, 1970), while small juveniles need several days to construct adequate burrows (Thiel, 2000). Thus, juveniles that leave the parental burrow will be exposed on the surface of the burrowing substratum for relatively long time periods while excavating a new burrow. During this time period, juveniles will be without the protection of a burrow and consequently susceptible to physical (e.g. salinity, temperature) as well as ecological factors (e.g. predation). Prolonged cohabitation of juveniles in the parental burrow can, therefore, be considered advantageous in species that are likely to require a significant amount of time to excavate a new burrow, i.e. those that inhabit very hard substrata. Boring crustaceans can be found in a wide variety of substrata with different degrees of hardness, ranging from algal tissue to soft rock and biogenic calcareous substratum (e.g. Murata and Wada, 2000). Given that small juveniles have limited boring efficiency, extended parental care might primarily be expected in species that inhabit very hard substrata. Yet, extended parental care has been reported in species that dwell in hard (*Sphaeroma wadai* Nunomura in rock) as well as in relatively soft substrata (e.g. *Peramphithoe stypotrurpetes* Conlan and Chess, *L. chilensis* in algal tissue). Thus, boring peracarids, regardless of the substrata, apparently engage in a similar form of extended parental care where juveniles cohabit with female parents after emerging from the female's brood pouch. The idea that most boring peracarids engage in extended parental care is supported by the fact

that this behaviour has been reported in species that feed on their boring substratum (*P. stypotrufetes*, *L. algarum* Menzies, *L. chilensis*, *L. lignorum* (Rathke), *Lynseia annae* Cookson and Poore) and those that do not (*S. wadai*, *S. terebrans*). Thus, for the entire range of substrata inhabited by boring peracarids, extended parental care may be advantageous.

In many species that feed on plant substratum in their burrows, endo- or ectosymbionts have been reported. Offspring may be physiologically naive and may depend on vertical transmission of these symbionts. This is important in wood-feeding cockroaches and termites (Nalepa and Bell, 1997), and apparently also in passalid beetles (Schuster and Schuster, 1985). Whether vertical symbiont transmission is necessary in boring marine arthropods is not known at present. However, observations on ectosymbionts that are common in plant-boring peracarid crustaceans (El-Shanshoury *et al.*, 1994) suggest that it may be advantageous to establish burrows in the vicinity of adult burrows with a rich flora of such ectosymbionts. Knowledge of the role of ectosymbionts in *Limnoria* spp. is very limited at present, not permitting discussion of their importance in the evolution of extended parental care (see also Cragg *et al.* 1999).

During their time in the maternal burrow, small juveniles grow in size. This is indicated by the fact that juvenile *L. chilensis* in the terminal end of the female burrow are slightly larger than the largest juveniles in the female marsupium. Similarly, juveniles in side-burrows are even larger than those in the terminal end of the female burrow. Survival of juveniles may be relatively high because they have no need to come to the substratum surface. Throughout the duration of juvenile–female cohabitation, juveniles are protected by the females, which remain in the opening of the burrow. Females may be visited by males during this time period but they are always in the inner regions of the burrow (e.g. Thiel, 1999a), thereby inhibiting direct contact of any male with their juveniles. Eltringham and Hockley (1961) also reported for *L. quadripunctata* Holthuis, *L. tripunctata* Menzies and *L. lignorum* that females are usually at the head of the burrow, and they suggested that this position might have some significance in the copulatory behaviour of these isopods. Based on the above considerations, however, I suspect that females of these species remain in the inner regions of the burrows to protect their offspring. Juveniles of boring peracarids are thus well sheltered from any adverse outside influences and may substantially benefit from this form of extended parental care. The duration of this juvenile–female cohabitation for *L. chilensis* is currently not well known.

The observations made in the present study for *L. chilensis* suggest that females do not feed during the first phase of extended parental care, since the terminal end of their burrow is occupied by the small juveniles. Similarly, feeding may be restricted in other boring isopods such as *S. terebrans* and *S. wadai*, where juveniles in the terminal end of the maternal burrow may impede efficient filter-feeding by the female. Females of several sphaeromatid isopods are known not to feed during their reproductive period, as is indicated by the reduction of their mouthparts (Holdich, 1968; Shuster, 1991). This has not yet been reported for limnoriid females but the above considerations suggest that female *L. chilensis* are at least partly restricted in their feeding activity during extended parental care.

While female *L. chilensis* apparently start to reproduce late in life, they nevertheless appear capable of producing at least two consecutive broods. Two observations support this idea: (a) females continue to excavate their burrows after their juveniles have established their side burrows, and (b) several females that had already

produced one brood are attended again by males. Male *L. chilensis* only appear to associate with females near the time of the reproductive moult, similar to what has been observed in *S. terebrans* (Thiel, 1999a). *Limnoria chilensis* appears to be an exception among the boring isopods that feed on their substratum—most of these species apparently live in heterosexual pairs (*Limnoria lignorum*—Henderson, 1924; *L. algarum*—Menzies, 1957; *Peramphithoe stypotruripes*—Conlan and Chess, 1992; *Lynseia annae*—Brearley and Walker, 1995). The large percentage of small females that have not yet reproduced may affect the disposition of male *L. chilensis* to remain with a single female. Instead of waiting until one particular female becomes receptive, males may continuously scout for receptive females in dense assemblages of isopods as reported herein. Protection of small juveniles may thus be entirely the task of females, similar to what has been reported for the filter-feeding *S. terebrans* (Thiel, 1999a).

In this study, only relatively few (and only the largest) females were found to be reproductive. Several factors could be responsible for the low percentage of reproductive females. Samples were taken towards the end of the austral summer (March), and the females found with offspring may only represent the ‘tail-end’ of the annual reproductive season. However, the fact that females were found in all stages of development suggests that seasonal effects may be of minor importance. Since herein I examined burrows of *L. chilensis* from dense assemblages, it is also possible that density-dependent effects may play a role (see e.g. Berryman *et al.*, 1985). In wood-boring bark beetles, individual female reproductive success decreases dramatically with increasing beetle densities (Robins and Reid, 1997). Future studies examining the population parameters of *L. chilensis* based on sampling at different times and densities are required in order to answer this question.

The observations made herein suggest that many juvenile *L. chilensis* remain in the kelp holdfast of their mother. Following spatial separation from the burrow of their mother, these juveniles may continue to grow and reproduce in the maternal holdfast. In another study, we had reported on observations that suggest similar small-scale recruitment patterns for many non-boring peracarid species inhabiting kelp holdfasts (Thiel and Vásquez, 2000). Thus, the combination of extended parental care and of ‘neighbourhood-recruitment’ in boring (and other) peracarids may result in the rapid build-up of dense local populations within relatively short time periods. Consequently, the dense assemblages reported from boring peracarids in microhabitats such as pieces of wood, mangrove roots, soft rock, and algal tissue (Kühne and Becker, 1964; Perry and Brusca, 1989; Murata and Wada, 2002; this study) may consist of individuals that are closely related to each other. The existence of such local ‘neighbourhoods’, consisting of closely related individuals (from the same age-class), has been reported for terrestrial arthropods with extended parental care (Ingvarsson, 1998; Johannesen and Lubin, 1999). The recruitment of offspring within the neighbourhood of parents may also affect the genetic diversity in populations of marine invertebrates with extended parental care, as demonstrated or suggested by several authors (e.g. Johannesson and Tatarenkov, 1997; Marty and Retière, 1999). Future genetic studies are necessary to examine this hypothesis for marine peracarids that display subsocial behaviour and occur in dense assemblages.

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