Reproductive biology of a filter-feeding amphipod, *Leptocheirus pinguis*, with extended parental care

**Abstract** *Leptocheirus pinguis* (Stimpson, 1853) is a widely distributed, abundant, endobenthic amphipod that engages in extended parental care, i.e. females host their juveniles in their burrows for extended time periods. I examined reproduction and population biology of *L. pinguis* at mean low water (MLW) in muddy sediment in Lowes Cove, Maine, USA. Cores around individual burrows were taken monthly in 1994 and 1995, and four seasonal samples were taken at different tidal heights. During the major reproductive periods in spring/early summer and in the fall, females produced several consecutive broods and hosted growing offspring in their burrows. Juveniles remained in their mothers’ burrows until they reached a length of 5 mm (approximately one-third adult size) or more. At the study site, the majority of amphipods in individual burrows were adult females. Following the main reproductive periods, subadult individuals were found in their own burrows, but densities did not increase following the reproductive period in spring/early summer 1994, probably because large numbers of *L. pinguis* emigrated via the water column between June and December. *L. pinguis* is an annual species. Many members of the cohort born in spring/early summer start reproducing in the fall, and survive until the following spring when they produce several broods. Members of the cohort born in the fall start reproducing the following spring and also produce several consecutive broods. Both the spring/early summer and fall cohorts die off after the major reproductive period in the following spring/early summer. High standing stocks of microphytobenthos occur in soft-bottoms at MLW, and I conclude that *L. pinguis* can engage in extended parental care there because its food is abundant year-round. The limited expandability and low stability of burrows in soft-bottoms at MLW do not permit long persistence of parent–offspring groups in *L. pinguis*.

**Introduction**

Several peracarid crustaceans engage in extended parental care where parents care for their growing offspring. Parents can provide substrate, shelter, and improved feeding conditions for their juveniles. This subsocial behavior has been described primarily for benthic peracarids, but some pelagic hyperiid amphipods also provide a domicile and food for their offspring (Richter 1978a; Laval 1980). In most cases, the parent–offspring groups consist of an adult female and her offspring. Usually, juveniles leave the female before reaching sexual maturity, and thus, no overlap of generations occurs within one burrow. Growing juveniles may stay with their mother while she is starting to care for a second clutch (Thiel et al. 1997), but larger juveniles seem to leave shortly after the following clutch is released from the brood pouch. Larger juveniles provide no support to the parental females.

Two categories of peracarids with extended parental care have been distinguished, epibenthic and tube-/burrow-living species (Thiel et al. 1997). The latter include tanaids (Bückle-Ramirez 1965; Johnson and Attramadal 1982; Bird and Holdich 1985; Hassack and Holdich 1987), kelp-boring amphipods (Conlan and Chess 1992; Chess 1993), endobenthic amphipods (Thamdrup 1935; Goodhart 1939; Watkin 1947; Shillaker and Moore 1987; Thiel et al. 1997), and highly mobile species living in self-constructed or acquired domiciles, such as hyperiid amphipods (Richter 1978a; Laval 1980) and *Siphonoecetes della-vallei* (Richter 1978b).

*Leptocheirus pinguis* is an endobenthic amphipod which inhabits U-shaped burrows in muddy sediments.
from the low intertidal zone to depths greater than 250 m along the Atlantic coast of North America (Verrill and Smith 1873; Holmes 1905; Sumner et al. 1913; Blake 1933; Brunel 1956; Bousfield 1973). *L. pinguis* pumps water through its burrow, filtering out suspended particles with highly setose gnathopods (Barnard and Karaman 1991). *L. pinguis* is widely distributed along the northern American Atlantic coast, and is one of the most abundant amphipod species in some regions (e.g. Holmes 1905; Sumner et al. 1913). Its average densities, however, are only about 200 to 400 ind m$^{-2}$, with the highest density recorded being 3300 ind m$^{-2}$ (Dickinson et al. 1980; Wildish 1980; Dickinson and Wigley 1981; Michael 1987). Despite its importance as prey for commercially important fish (Wigley and Theroux 1965; Hacunda 1981; Mahon and Neilson 1987), little is known about the reproductive biology of *L. pinguis*. We found that it performs extended parental care, and two cohorts of juveniles can inhabit the burrow of an individual female (Thiel et al. 1997).

Although *Leptocheirus pinguis* had been sampled extensively in previous studies, the occurrence of female–offspring groups had not been described, and little is known about this reproductive strategy. For a thorough understanding of extended parental care in marine amphipods, it is essential to have detailed knowledge about their reproductive biology. In the present study, the general life history of *L. pinguis* was studied with a major emphasis on its reproduction and population biology. Throughout the study, individual burrows with their inhabitants were collected to reveal the details of extended parental care in *L. pinguis*.

**Materials and methods**

Study area and sampling

The study was conducted in Lowes Cove, Maine, USA (43°56′N; 69°35′W; for a description of the site see Thiel 1997a, b). Sampling of *Leptocheirus pinguis* (Stimpson, 1853) was done monthly at a station at mean low water (MLW) during spring low tides, when the area was exposed. To collect individual burrows and their inhabitants, a 10-cm diameter core was placed over a burrow, gently pushed into the sediment to a depth of about 15 cm, closed at top and bottom, and immediately transferred to the laboratory where the burrow was carefully dissected and its inhabitants collected. In this way, the inhabitants of only one burrow were sampled. In cases where amphipods could not be assigned to individual burrows with certainty, the samples were discarded. All amphipods were preserved in 4% formalin, later transferred to 70% ethanol, and measured with a computer-based video-image analysis system along their dorsal surface from the rostrum to the base of the telson. All adult amphipods were sexed, and the reproductive stage of females (parental, ovigerous, or non-reproductive) was determined. In the following, I use the term “parental female” exclusively for females that were caring for juveniles in their burrows, and “non-parental female” for those without juveniles in their burrows.

To examine amphipod density, sediment samples of 176 cm$^2$ surface area were taken to a depth of 15 cm, sieved over a 500 μm mesh, preserved in 4% formalin, transferred to 70% ethanol, and sorted under a dissecting microscope. Six replicate samples were taken at each of four stations in spring, summer, fall and winter (May, August, November 1994 and February/March 1995, respectively). The sediments at all stations consisted of fine mud with high water content (Thiel 1997b). The four stations lie along a transect from 0.3 m above MLW, MLW, 0.3 m below MLW, to about 2 m below MLW.

Data from a previous long-term study on drifting macrozooplankton were evaluated to examine whether *Leptocheirus pinguis* move among different habitats via the water column. Plankton nets (750 μm mesh size) were deployed overnight for about 6 h at ebbing tide and 6 h at flooding tide at three depths (about 1.4 and 14 m below the surface). Each net had a flow meter attached in the center of the net opening to determine the volume of water filtered. Data were collected monthly from August 1970 to April 1973 and January 1975 to May 1979 in the Sheepscot River Estuary (43°59′N; 69°39′W) (McAlice and Jaeger unpublished data) which is about 10 km west of the Damariscotta River Estuary where Lowes Cove is located.

**Results**

Population structure of *Leptocheirus pinguis* in monthly burrow samples

Adult females dominated in monthly burrow samples from the study site in Lowes Cove (Fig. 1). Over the course of the year, 56 to 96% (October 1994) of individuals inhabiting their own burrows were adult females. The proportion of adult males collected in their own, or in female burrows, varied between 2 and 24%. Up to 34% of amphipods found in their own burrows were subadults (Fig. 1). Often, 10 to 20% of the adult females were found paired with males in their burrows (Fig. 2A). Following months with no or few paired females (e.g. June, October, November), the proportion of ovigerous females dropped (e.g. in July, August and December). The percentage of parental females (those caring for juveniles in their burrows) usually followed the percentage of ovigerous females (Fig. 2B).

Reproductive potential of female *Leptocheirus pinguis*

The number of eggs per female and the number of juveniles per female were correlated with female size (Fig. 3) (eggs: $y = 7.569x - 66.896$, $r^2 = 0.205$, $p < 0.05$; juveniles: $y = 8.86x - 100.639$, $r^2 = 0.166$, $p < 0.05$). The smallest ovigerous female was 11.1 mm long (12 July 1995), and the longest parental female was 23.2 mm (17 April 1995). The mean length of females varied between 15 and 18 mm during most of the year, but dropped to 13.2 mm in September 1994 (Fig. 4A). In summer 1994, the mean length of male *Leptocheirus pinguis* varied between 11 and 15.5 mm, during the winter months it increased to 15.5–18 mm, but then dropped again to an average of 13 mm towards the following summer (Fig. 4A). The average number of eggs per female dropped substantially during summer 1994 and then steadily increased during the following fall and winter, but dropped again in the summer of 1995 (Fig. 4B). In May and June 1994 and...
1995, the average number of juveniles per female exceeded the average number of eggs per female, whereas for most of the year the numbers of juveniles were usually substantially lower than the numbers of eggs per female (Fig. 4B). Up to 167 juveniles were found in the burrow of one female *L. pinguis* (26 June 1994), but there were also two females that had only one juvenile each at the time of sampling (30/31 December 1994, 12 July 1995).

Size of juveniles in female burrows and of adults and subadults in their own burrows

The length of juveniles found in their mother’s burrow varied between 1.4 and 13.9 mm with the majority of juveniles between 2 and 5 mm in length (Fig. 5). Even after pooling the juveniles from all females collected at each sampling date, distinct cohorts could be recognized (Fig. 5). The clear distinction of three cohorts in May 1994 and May 1995 indicates that during these times many juveniles undergo at least two molts in the burrow of their mother. The low number of small juveniles...
(<4 mm) compared to medium-sized juveniles (4 to 6 mm) in June 1994 indicates a decrease in the production of juveniles. In July 1994, only a few medium-sized juveniles were found in the burrow of three females and in August and September 1994 no juveniles were found in the burrows of females. Following the summer, the first juveniles were found in the burrows of their mothers again in October 1994, but the total number of juveniles collected during the fall remained low. The lack of small juveniles on 30/31 December 1994 indicates that no more small juveniles were born into the burrows of reproductive females, despite the fact that about 40% of the females were ovigerous in November and early December (compare Fig. 2B) carrying on average 70 eggs per female (compare Fig. 4B). Beginning in February 1995, small juveniles were found in the burrows of parental females again. During spring 1995, parental females cared for large numbers of juveniles, most of which reached lengths of about 5 mm in their mothers’ burrows (Fig. 5). In May 1994 most of the burrow occupants (= subadults + adult females + adult males) were >14 mm in length (Fig. 6), but the first subadults had already established their own burrows at this time. During summer 1994, other subadults established their own burrows, while the actively reproducing adults remained at the study site. Between August and September 1994, many of the large individuals disappeared, and the newly recruited subadults dominated the local population (Fig. 6). This spring-1994 cohort grew and produced eggs quickly during the fall, and females started to care for juveniles in their burrows in October 1994. Beginning in November 1994, the first subadults from the fall-1994 cohort started to build their own burrows. During the winter months, the fall-1994 cohort continuously recruited at the study site. In February 1995, this fall-1994 cohort started to merge with the spring-1994 cohort, and by April 1995 they were indistinguishable. The spring cohort from 1994 persisted together with the fall cohort from 1994 until the spring of 1995 (Fig. 6).

Seasonal abundance of *Leptocheirus pinguis* in sediments and drifting in the water column

The highest densities of *Leptocheirus pinguis* were found in sediments at and just below MLW where they were most abundant in the spring and summer (Fig. 7). Between August and November 1994, the densities of *L. pinguis* decreased at all four tidal levels. The highest numbers of drifting amphipods, *L. pinguis*, were caught in the Sheepscot River Estuary during the months June to December; few individuals were found drifting between January and May (Fig. 8).

Discussion

Female *Leptocheirus pinguis* produced and cared for large numbers of juveniles in the spring/early summer every year, but overall densities of *L. pinguis* in the study area did not increase during this period. In the fall, females born in the spring started to reproduce, but the numbers of juveniles they cared for were relatively low. Nevertheless, many juveniles seemed to recruit immediately at the study site, particularly in December and January, when the numbers of drifting amphipods in a nearby estuary decreased substantially. Extended parental care is an important component in the reproductive biology of *L. pinguis*, and two aspects will be discussed: the life history of *L. pinguis* and advantages and costs of extended parental care in this filter-feeding amphipod.

Life history of *Leptocheirus pinguis*

Two reproductive periods were discernible for *Leptocheirus pinguis*, one major reproductive event in the spring/early summer and a second, smaller one in the fall. This is typical for some endobenthic, coastal, shallow-water amphipods, such as *Corophium volutator* (Wilson and Parker 1996) and *Unciola inermis* (Morrisson 1993), but others such as *Ampelisca vadorum*, *A. abdita* (Mills 1967), and *A. agassizi* (Bethune 1995) only have one reproductive event each year. In most of these other species, however, substantial increases in amphipod densities are discernible, following the major reproductive events. This is not true for *L. pinguis* in Lowes Cove. Despite the large number of juveniles produced in the spring/early summer, densities of
Fig. 5 *Leptocheirus pinguis*. Numbers of juveniles in respective size classes found in burrows of parental females between May 1994 and August 1995; all juveniles from each sampling date were pooled.
Fig. 6 Leptocheirus pinguis. Numbers of amphipods in respective size classes collected in their own individual burrows; some adult males and females shared burrows.
of individuals <10 mm in length inhabiting their own burrows in May to September 1994 and May to August 1995 (see Fig. 6). The large adults (≥17 mm) most likely died at the end of the summer as they disappeared by September 1994. The juveniles born in the spring 1994 (the spring generation S94) grew quickly over the summer and started to reproduce in the fall. Some juveniles born during the fall of 1994 (the fall generation F94) recruited immediately into the study area, and by April 1995 the F94 generation was indistinguishable from the spring generation, S94. Both S94 and F94 reproduced in spring of 1995, producing the next spring generation, S95, which recruited in low numbers to the sediments at MLW beginning in May 1995 (Fig. 6). Thus, members of the spring generation persist for about 15 months and participate in two reproductive events (fall and the following spring) during their lifetime. Members of the fall generation persist for about 10 months and only participate in one reproductive event. This interpretation does not agree with that of Wildish (1980) who concluded that *L. pinguis* would be a typical biannual species with a longevity of up to 30 months. The data presented in this study demonstrate that *L. pinguis* does not grow much older than 15 months and can already reproduce at the age of about 5 months.

In Lowes Cove, *Leptocheirus pinguis* in burrows were dominated by adult females reaching very high proportions during reproductive events in the spring and fall (Fig. 1). In burrow-dwelling amphipods, breeding females usually reside in their burrows, and mature males search for burrows with receptive females (Borowsky 1983). In the present study, amphipod burrows were sampled at low tide, when males would not be searching for mates but rather residing in female burrows or in their own. Thus, it is unlikely that the low percentage of males at MLW is a sampling artifact. Interestingly, Wildish (1980) reported more or less equal sex ratios for his subtidal (about 10 m depth) study population. At present, there is no reason to believe that the sex ratio of juveniles is biased towards females or that sex-change
occurs in these amphipods, and thus other reasons must be responsible for the female-biased sex ratio at the study site. *L. pinguis* is one of the most important prey items of shallow-water demersal fish (Wigley and Theroux 1965; Tyler 1971; Hacunda 1981; Mahon and Neilson 1987), and many males probably fall victim to these predators while searching for receptive females. Boates and Smith (1989) concluded that a decrease in the proportion of male Corophium volutator from about 20 to 10% was due to their crawling activity and subsequent losses to epibenthic predators. Higher mortality of mature males as the major reason for a female-biased sex ratio is also assumed in other studies (Mendoza 1982; Wildish 1982, 1984; Sudo and Azeta 1996). An alternative explanation for the strongly female-biased sex ratio of *L. pinguis* in sediments at MLW could be that mature females actively migrate towards this zone where food conditions are favorable for suspension- and filter-feeding species (Thiel 1997b).

The relatively high numbers of drifting *Leptocheirus pinguis* in the Sheepscot Estuary suggest that many individuals drift out of the estuaries into deeper waters during the summer and fall. The time period when many *L. pinguis* were found in the water column indicates that it is primarily individuals born in spring/early summer that migrate by drifting. The fate of these drifters is unclear, as there is little indication that large numbers of drifters return to the estuaries in the winter and spring. The factors causing these individuals to enter the water column also remain unclear. The densities of *L. pinguis* in Lowes Cove and other sites in the Damariscotta River Estuary (unpublished data) are relatively low (about 100 ind m$^{-2}$), so that intraspecific competition appears unlikely. The large numbers of drifting amphipods during the second half of the year are also unlikely to represent a seasonal migration, such as is known for other amphipod species, because some individuals remain and survive the winter in the shallow waters of the estuaries.

Advantages and costs of extended parental care in *Leptocheirus pinguis*

The major advantage gained by *Leptocheirus pinguis* from this reproductive strategy is the remarkably large size of juveniles at time of recruitment, i.e. at a length of 5 to 7 mm. Young and small infauna in soft sediments are very susceptible to predation, particularly to epibenthic predation (Reise 1985). With increasing size, young macrofauna can burrow deeper in the sediment and reach a refuge from the abundant predators in coastal waters. Thus, organisms reaching larger sizes at time of recruitment (i.e. by means of extended parental care) are less susceptible to predation. Although juvenile amphipods (and other marine macrofauna) appear to gain considerable advantages from extended parental care in environments with high predation pressure, this reproductive strategy is not very common in marine macrofauna. This suggests that considerable costs may be involved with extended parental care resulting in a tradeoff between advantages and costs.

The availability of resources such as food and space probably limit the extent of parental care or its occurrence altogether. Food might become limiting depending on its temporal availability (many species in shallow coastal waters have reproductive cycles closely coupled to the occurrence of seasonal phytoplankton blooms – see Giese and Pearse 1974). In Lowes Cove, water collected near the sediment surface at and just below MLW contains relatively high concentrations of chl $a$ year-round with little seasonal variation (Thiel 1997b), indicating the continual presence of relatively fresh plant material. A large proportion of this material consisted of benthic diatoms, which are abundant food items in the foregut of *Leptocheirus pinguis* (personal observations). Continuously high levels of sedimentary and resuspended microphytobenthos in this habitat suggest that the occurrence of extended parental care is closely linked to the constant availability of food (Thiel 1997b). Two other amphipods, *Casco bigelowi* (Blake, 1929) and *Dyapodos monacanthus* (Metzger, 1875), occurring in the same habitat as *L. pinguis*, also engage in extended parental care (Thiel 1997b). In a burrow-dwelling species such as *L. pinguis*, spatial restrictions can also impose limits on the number of individuals inhabiting a burrow (Thiel 1997a). Resources such as food and space thus appear to be important factors determining the occurrence and extent of parental care in *L. pinguis*.

Surprisingly, the extent of parental care in *Leptocheirus pinguis* seems to vary over the course of the year. There were always some ovigerous females (also found by Wildish 1980), yet no small juveniles were found in female burrows in July to September 1994 and 31 December 1994 to 28 January 1995 (Fig. 5). Another indication for a varying extent of parental care is the fact that females in June 1994 and November 1994 had an average size of about 16.5 mm and thus probably similar burrow sizes, yet females in June 1994 hosted an average of > 80 juveniles whereas those in November 1994 (and later in the winter) only hosted about 40 juveniles or fewer. Thus, relatively few juveniles were found in burrows of females during the winter months despite relatively high egg numbers per female, indicating that juveniles leave their mothers earlier and at a smaller size during the winter months than during the summer months. Predation pressure on soft-sediment infauna in temperate estuaries is lower during the winter months than during the rest of the year because important predators leave the estuaries or show little feeding activity (Hacunda 1981). If protection from predation is the major advantage gained by juvenile *L. pinguis* from extended parental care, then there is less reason for them to stay in the mother’s burrow during the winter than during the rest of the year. During the winter months, juveniles may actually be better off leaving their mothers early, thus avoiding inefamilial resource competition within the confined space of the mother’s burrow. Thus, the
tradeoff between improved protection from predation on the one hand, and intrafamilial resource competition on the other, probably changes depending on the season. It is not known whether juvenile *Leptocheirus pinguis* leave the mother’s burrow voluntarily or whether they are actively expelled as has been observed for other peracarids (Borowsky 1983; Shillaker and Moore 1987). Some juveniles remain in the mother’s burrow for periods of 40 to 60 d after hatching (Thiel 1997a), and females could face a tradeoff between providing extended parental care for one brood and producing and sheltering a consecutive brood. During spring/early summer and fall many female *L. pinguis* hosted two consecutive broods in their burrows while incubating another clutch of embryos in their brood pouch. This indicates that at least during the major reproductive periods, costs of sheltering offspring do not prevent the production of consecutive broods.

Soft-sediments such as those inhabited by *Leptocheirus pinguis* provide a good food supply, but the low stability of these sediments (70 to 80% porosity) limits the size and persistence of a burrow system. Habitats that are relatively stable and expandable might allow for prolonged cohabitation of parents and offspring. The most stable habitat, however, is of little value, if resource supply to its inhabitants is not ensured. In the marine environment, these conditions (stable habitat and resource supply) are best met within biotic habitats such as kelp stipes, mangrove roots and sponges, bivalves, brachiopods or ascidians (i.e. filter-feeding metazoans). Several peracarid species spend their entire lives in biotic microhabitats (Costello and Myers 1987) where they may engage in extended parental care for one brood and producing and sheltering a consecutive brood. During spring/early summer and fall many female *L. pinguis* hosted two consecutive broods in their burrows while incubating another clutch of embryos in their brood pouch. This indicates that at least during the major reproductive periods, costs of sheltering offspring do not prevent the production of consecutive broods.

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In the present study it was shown that a soft-sediment dwelling amphipod engages in extended parental care, an apparently successful reproductive strategy in an environment with abundant food supply. The potential for evolution of advanced social behavior is low in this species, since parental burrows in soft muds have limited stability and expandability.

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