Extended parental care in a high food environment - 'Babies don't go in the mud'

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Abstract
Extended parental care is described for three benthic amphipods, the burrowing species *Leptocheirus pinguis* and *Casco bigelowi*, and the stalk-building *Dyopedos monacanthus*. Juveniles of *L. pinguis* reach a size of more than 5 mm in their mothers' burrows, and up to 98 juveniles were found in the burrow of one female (average: 79). On average 45 juvenile *C. bigelowi* were staying in the burrow of one female, and they can reach sizes of more than 12 mm in their mother's burrow. On average 62.5 juvenile *D. monacanthus* were found on the mud-stalks of one female. The number of juveniles substantially decreased above a size of about 1.5 mm, and only very few reached a size of 3 mm on their mother's stalk.

High concentrations of total organic matter and chlorophyll a were found in sediments at and below mean low water (MLW). This is reflected by high values of Chl a in bottom waters at these stations. High concentrations of Chl a are assumed to indicate the presence of important food resources for these suspension- and deposit-feeding amphipods. These fresh food resources permit the long persistence of parent-offspring groups. The relatively large size of juveniles at the time of recruitment enables the three amphipod species to inhabit the sediments at and below MLW, a region in which high predation pressure is reported from other studies. The occurrence of species with extended parental care is thus closely linked to the combination of a high-food environment and high predation pressure at and below MLW.

Keywords: extended parental care, reproduction, Amphipoda, soft sediment.

Introduction
The juveniles of species with parental care stay with their parents for extended time periods after the egg or larval stage. Although extended parental care is not very common among marine invertebrates, almost every phylum contains a few species for which this reproductive behaviour has been reported. Brooding of larvae to the juvenile stage is common among small bivalves (Gallardo, 1993). In some polychaetes the larvae grow to the juvenile stage within the burrows or tubes of the female (Dales 1950; Knight-Jones & Thorp, 1984; Bartels-Hardege & Zeek, 1990), or they develop into small juveniles in close body contact to the female (Pocklington & Hutcheson, 1983; Giangrande, 1990). The larvae of some echinoderms develop into small juveniles on or within the body of the females (Hess et al., 1988; McClary & Mladenov, 1988, 1989, 1990; Mooi & David, 1993a,b; Sewell, 1994). Small juvenile worms have been found in the tubes of sipunculids and pogonophorans (Åkesson, 1958; Bakke, 1990). Some spider crab species carry their juveniles under the abdomen for considerable time periods (Morgan, 1987). Reports of extended parental care are particularly common among peracarid crustaceans (Thiel et al., 1997). Most of the above mentioned reports, however, are only observational. Knowledge of the numbers of juveniles produced and their size at the time of leaving their parents is only scanty.

The limited knowledge of the details of extended parental care among marine invertebrates is surprising, as the size of juveniles is extremely important for their recruitment success. Larger individuals usually recruit more successfully than small ones. An important consequence of extended parental care is that juveniles attain a relatively large size before leaving their parents, which consequently may enhance their recruitment success.

Theoretical considerations suggest that the food requirements of a large parent-offspring group will increase during the growth of the juveniles. The amount of food available to a group of many individuals limits the persistence of the group, particularly in sedentary species. Food-availability may determine the duration of extended parental care and the size at which juveniles leave their parents. Determining the food supply and the size of juveniles is therefore of primary importance for an initial investigation of extended parental care among marine invertebrates.

In this study extended parental care is reported in three benthic amphipods, *Leptocheirus pinguis*, *Casco bigelowi* and *Dyopedos monacanthus*. The two main objectives of this initial
study are: 1. to document the size and number of juvenile amphipods during the period of parental care; 2. to document the food situation in the amphipod habitat.

Materials and Methods

The amphipod species

*Leptocheirus pinguis* (Stimpson 1853) and *Casco bigelowi* (Blake 1929) are common infaunal inhabitants in estuarine soft-bottoms (Wildish, 1980). *Dyopedos monacanthus* (Metzger 1875) is an epifaunal species living on soft-bottoms. It clings to mud-stalks which it builds from filamentous algae and mud (Mattson & Cedhagen, 1989). The burrow of *L. pinguis* is U-shaped, and the inhabitants are usually found at the bottom of the burrow. The burrow extends 3-6 cm below the sediment surface and those of breeding females may be up to 10 cm deep. The two burrow openings are easily recognised at the sediment surface by their sharp edges. The inner lining of the burrow is relatively stable, as the burrow wall is partly mucus-lined and well oxygenated. The amphipod frequently irrigates the burrow and feeds on suspended particles. Little sediment reworking seems to occur after the establishment of the burrow.

The structure of the burrows of *C. bigelowi* is much less regular, and burrows are frequently modified by their inhabitants. Single inhabitants usually live in U-shaped burrows which can extend down to more than 10 cm below the sediment surface. Amphipods were also occasionally found in simple tube-like burrows with an expanded chamber at the bottom. The burrow wall is very soft and the sediments are rarely oxygenated. The continuous modification of the burrow can be recognised by mounds of freshly excavated sediments at the surface. Laboratory observations have shown that sediment is also deposited in the inner parts of the burrow. The continuous handling of sediment within the burrow suggests that *C. bigelowi* is a deposit-feeding amphipod. *D. monacanthus* clings to its mud-stalks and extends its antennae into the water current during feeding-periods. Suspended particles transported by the water currents accumulate in the fine setae of the antennae, which are frequently cleaned by the amphipods.

The Study Area

Figure 1  Sampling stations in Lowes Cove in the Damariscotta River. The stations in the high and low infratidal are exposed only during spring low tides; infratidal mudflats are shown in grey shading, filled dots represent stations where infaunal samples and sediment samples for analysis of TOM and Chl a have been taken, open circles represent stations where bottom waters have been collected.

MLW. The sediments at the latter station are exposed only during spring low tides. The shallow subtidal station is 2 m below MLW. Bottom water samples were taken along the same tidal transect, with the modification that only one combined infratidal station and an additional deep subtidal station (5 m below MLW) were sampled. Faunal samples (n = 6 x 176 cm² surface area) were taken to a depth of 15 cm. The samples were sieved over a 500 μm-mesh, fixed with
4% formaldehyde, transferred to 70% ethanol, and later sorted for amphipods under a dissecting microscope.

**Sampling**

At spring low tide individual females of *L. pinguis* with their juveniles were collected in the high infratidal, and females of *C. bigelowi* in the low infratidal. The collection of these two amphipod species required two people. We located the burrow openings at the sediment surface. One person then used his fingers as a grab to remove the mass of sediment containing the burrow. Immediately after retrieving the sediment, we carefully opened the burrow and collected its inhabitants with a spoon. This ensured that we sampled all inhabitants of one individual burrow. Females of *D. monacanthus* with their juveniles were collected in the shallow subtidal. A diver located a stalk containing a female and its offspring, carefully lowered a jar over the stalk and then closed the jar under the sediment surface with a tight lid. For each species at least 6 adult females with their juveniles were collected during their respective main reproductive periods. The sizes of all collected individuals were measured with a computer-based image analysis system connected to a dissecting microscope.

Total organic matter and Chl *a* were measured to represent food-equivalents for these suspension- and deposit-feeding amphipods. Chl *a* can be used as a relatively good food-equivalent for suspension- and deposit-feeding species, as it represents primarily fresh, undigested plant materials. At each of the five stations (high intertidal - shallow subtidal) two sediment cores (44.2 cm² surface-area) were taken and separated into six different layers (0-1, 1-2, 2-4, 4-6, 6-10 and 10-15 cm). Each sediment layer was carefully mixed and 2 cm³ of this sediment were taken for analysis of total organic matter and Chl *a*. Total organic matter was analysed by drying sediment for 24 h at 70°C, and then burning it for 4 h at 510°C. Sediment Chl *a* was analysed by the method of Whitney & Darley (1979).

Water samples from immediately above the sediment surface were taken one hour before high tide with a custom-designed bottom-water sampler. The water sampler consists of two metal plates (25 x 25 cm), arranged like a sandwich with an open space of 1 cm between them. During sampling the lower plate rested on the sediment surface. The upper plate has a pipe connection in the centre, and water was pumped with a hand pump directly into a sampling jar on board the research vessel. This design ensured that currents induced by pumping water from the sediment surface did not artificially resuspend sediment material from the bottom, as was confirmed on several occasions by diver observations. Samples were taken every two weeks along the same intertidal transect as the sediment samples: in the high intertidal, the low intertidal, the infratidal, the shallow subtidal and additionally in the deeper subtidal (= 5 m below the low tide line). At each station and sampling date two water samples were taken. One hundred ml of each sample were filtered onto a 0.45 μm filter and transferred into 90% acetone. After storing the samples in the freezer for several days, absorbance was measured at 664 nm wavelength with a fluorometer.

**Results**

*Numbers and sizes of brooded juveniles*

Between 49 and 98 juveniles (average: 79 ± 16.47 SD; n = 6 burrows) were found in each burrow of female *L. pinguis* on 8 June 1993. The smallest juveniles found in the burrows of their mother were about 1 mm long and the largest were about 10 mm long. Above a size of about 5 mm the number of juveniles in the mother's burrows clearly decreases. In some burrows two clutches of juveniles can easily be distinguished (see Figure 2a - female #1). Small juveniles usually live free at the bottom of their mother's burrow, but later start to build mud tubes resembling a honeycomb at one corner of the U-shaped burrow.

Between 35 and 58 juveniles (average: 45 ± 8.58 SD; n = 7 burrows) were found in each burrow of female *C. bigelowi* on 12 December. The length of the smallest juvenile found on that date was 3.6 mm, and that of the largest was 12.6 mm. In no burrow were two clutches of juveniles recognisable. The juveniles of *C. bigelowi* move freely in their mother's burrow.
Numbers of juvenile *L. pinguis* (a - n = 6 individual females collected at 8th June 1993), *C. bigelovi* (b - n = 7 individual females collected at 12th December 1993) and *D. monacanthus* (c - n = 6 individual females collected at 10 May 1995) found with each individual female; each column represents the number of juveniles in the respective size classes.

Abundance (individuals m$^{-2}$) of *L. pinguis* (a), *C. bigelovi* (b) and *D. monacanthus* (c) at the five stations along the tidal transect through Lowes Cove; n = 6 replicate samples of 176 cm$^2$ surface area collected in May 1994 at each station.
Figure 4  Total organic matter (%) and Chl a (mg g\(^{-1}\) sediment) at each of the five stations along the tidal transect through Lowes Cove; n = 2 replicate samples of 44.2 cm\(^2\) surface area were taken at each station in June 1994, August 1994, November 1994 and March 1995.

Females of *D. monacanthus* had between 34 and 92 juveniles (average: 62.5 ± 23.05 SD; n = 6 stalks) on their stalks on 10 May 1995. Most juveniles were smaller than 1 mm, and the largest juvenile found among six females was about 3.5 mm long. The majority of juveniles seem to leave the females at a size of about 1.5 mm. On some stalks two clutches of juveniles were found together with their mother (see Figure 2c - female #1). The juveniles usually cling to the upper part of the mud-stalk, and the female defends its brood against intruders which invade from the base of the stalk.

**Abundance and distribution of amphipods**

*L. pinguis* is most abundant in the high infratidal (MLW) (Figure 3a). Brooding females were commonly found in this zone. Abundances of more than 500 individuals m\(^{-2}\) can be reached during the breeding period. *C. bigelowi* is most abundant in the low infratidal (0.2 m below MLW), but densities are lower than those of *L. pinguis* (Figure 3b). *D. monacanthus* occurred only in the shallow subtidal, and densities during the time of sampling were relatively low (Figure 3c)
Spatial and seasonal distribution of total organic matter and Chl a

The total organic matter (TOM) in the sediments from the high intertidal toward the shallow subtidal did not show a clear seasonal trend (Figure 4a). TOM did not decrease substantially in deeper sediment layers. The lowest values of TOM were usually found in the high intertidal sediments and the highest values were found in the sediments of the infratidal and the shallow subtidal (Figure 4a).

There was no seasonal change in the amounts of Chl a in the sediments at each of the five stations but there were spatial differences. The highest values of Chl a were found in the surface sediments at and below MLW (Figure 4b). Values of Chl a were highest at the shallow subtidal station (Figure 4b). The distribution of Chl a in the surface sediments corresponds relatively well to the distribution of Chl a in the bottom waters along the tidal transect from the high intertidal toward the subtidal (Figure 5). The values of Chl a in bottom waters are usually higher at the stations near MLW (Figure 5).

Discussion

Extended parental care is described for three benthic amphipod species which inhabit estuarine soft-bottoms. Female-juvenile groups usually consist of 50-70 individuals. The juveniles pass through several mouls during the period of extended parental care, and at least two clutches of juveniles are occasionally raised simultaneously by one female. The habitat in which this extended parental care has been observed is characterised by high concentrations of Chl a.

Evolution of extended parental care

Different factors such as improved protection from interspecific predation or reduction of intraspecific competition may favour the evolution of extended parental care. Reduction of larval mortality and unpredictable recruitment success have been brought forward as hypotheses for the evolution of brooding in small bivalve species (Strathmann & Strathmann, 1982; Kabat, 1985). Hassack & Holdich (1987) report extended parental care from some tubicolous tanaids and discuss the tubes as a shelter from predation. The juveniles of epifaunal caprellids with maternal care have a much higher survival rate than those of species lacking extended parental care (Aoki & Kikuchi, 1991). Mattson & Cedhagen (1989) reported that female podocerid amphipods defend their juveniles against other conspecific individuals, which has also been mentioned for caprellid amphipods by Lim & Alexander (1986) and Aoki & Kikuchi (1991). The feeding conditions of small suspension-feeding juveniles may be improved when they are lifted above the bottom boundary layer on the body appendages of their mother or on structures such as mud-stalks built by their mother. Filter-feeding juveniles such as L. pinguis may profit from the water current produced by their mother in her burrow. In another infaunal amphipod species, Lembos websteri, Shillaker & Moore (1987) observed the juveniles feeding on detritus particles drawn into the tube by the female. Residence time of the juveniles are, however, much shorter (maximal 4 days after hatching from the brood pouch in L. websteri - see Shillaker & Moore, 1987) than in any of the three species described in this study.

Duration of extended parental care

Only one description can be found of extended parental care in which more than one cohort of juveniles enjoy the protection of their parent's home simultaneously (Conlan & Chess, 1992). In most other species with extended parental care the juveniles remain with the female until it is revisited by a male. Because the female amphipods usually become receptive shortly after releasing juveniles from their brood pouches, the periods of extended parental care are of only short duration in these species. Juveniles of L. pinguis and D. monacanthus do not leave when males attend the females and therefore enjoy long periods of extended parental care, growing to remarkable sizes. Because female C. bigelowi produce only one brood per year and the males disappear soon after fertilising the females, there is no active expulsion from the female's burrow by the attending males in this species.
Extended parental care and food supply to parent-offspring groups

Increased protection from predation is probably an important factor enabling the three amphipod species *L. pinguis*, *C. bigelowi* and *D. monacanthus* to live and reproduce in the shallow water environment around MLW. Predation pressure from epibenthic predators is very high in this environment. In the zone around MLW, bivalves and polychaetes are substantially reduced in numbers during the period of highest predator activity (summer), despite the fact that growth conditions are most favourable in this area (see e.g. Reise, 1985; Günther, 1990). The large juveniles leaving the females of *L. pinguis* and *C. bigelowi* are able to establish their own burrow at a depth where they are out of the reach of most epibenthic predators such as shrimp, hermit crabs, brachyuran crabs and fishes. Larger juveniles of *D. monacanthus* can build mud-stalks which are relatively large and not in the immediate foraging range of abundant epibenthic predators such as shrimp. Extended parental care might therefore enable these (and other species) to inhabit areas with high predation pressure. However, the food-requirements of large parent-offspring groups will increase during the growth of the juveniles. A spatially limited home such as a burrow or a mud-stalk can support only a limited number of individuals, and competition for food among group members may become the most important factor limiting the persistence of the group. High concentrations of Chl *a* in the shallow waters near MLW indicate a very profitable food-resource for suspension- and deposit-feeding organisms. Large amounts of Chl *a* in the sediments at and below MLW indicate high standing stocks of benthic diatoms which are the main food resource for the three amphipods *L. pinguis*, *C. bigelowi* and *D. monacanthus*. This leads to the assumption that the observed extended parental care in these amphipods is made possible by a plentiful food supply. The time periods which the juveniles spend with their mothers extend over several weeks (*L. pinguis* and *D. monacanthus*) or up to 2 months (*C. bigelowi*) (pers. obs.). The juveniles can reach more than half the adult size within this time period. These time periods and juvenile sizes attained during extended parental care exceed those reported for any other marine invertebrates.

With the present stage of knowledge I speculate that the occurrence of the three amphipod species performing extended parental care at and below MLW is closely linked to the high concentrations of food and the high predation pressure in this zone. The high predation pressure suppresses other suspension- and deposit-feeding organisms, and consequently the amphipods enjoy reduced interspecific competition for food in this environment. The production of relatively large juveniles made possible by this high food-supply in turn enables these amphipods to inhabit the zone at and just below MLW.

Acknowledgements

I would like to thank my principal thesis advisors Les Watling and Larry Mayer for their support during this study. My special thanks go to Steve Sampson for taking me to the mudflats. Steve was the first to direct my attention toward parental care in amphipods and he helped me collect many of the samples. G. Francés-Zubillaga and T. Dernede helped collect and process some of the samples. T. Miller shared my excitement in discovering *D. monacanthus* in the shallow subtidal and accompanied me to take samples when water temperatures were still far from pleasant. D. Bethune, M. Hostetter, K. Lapham, S. Sampson and L. Stearns helped to collect the bottom water samples. Their help is greatly appreciated. During this study I was supported by a graduate fellowship from the Center for Marine Studies at the University of Maine.

References


