Journal of Natural History
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713192031

Extended parental care in two endobenthic amphipods

M. Thiel [a]; S. Sampson [a]; L. Watling [a]
[a] Darling Marine Center, University of Maine. Walpole, ME. USA

To cite this Article: Thiel, M., Sampson, S. and Watling, L. , 'Extended parental care in two endobenthic amphipods', Journal of Natural History, 31:5, 713 - 725
To link to this article: DOI: 10.1080/00222939700770351
URL: http://dx.doi.org/10.1080/00222939700770351

Journal of Natural History, 1997, **31**, 713–725

Extended parental care in two endobenthic amphipods

M. THIEL, S. SAMPSON and L. WATLING

Darling Marine Center, University of Maine, Walpole, ME 04573, USA

(Accepted 5 September 1996)

Extended parental care is described for two endobenthic amphipods which inhabit the estuarine soft-bottoms along the Gulf of Maine. The juveniles of both amphipod species, *Leptocheirus pinguis* and *Casco bigelowi*, remain in the burrow of their mother after they hatch from the brood pouch. Several consecutive clutches of *L. pinguis* can inhabit the female's burrow simultaneously, but in *C. bigelowi* there is always only one clutch of juveniles in the burrow of the female. Larger juveniles of *L. pinguis* start building their own small tubes at the bottom of the female's burrow. *Casco bigelowi* females increase the size of their burrows during the time when the juveniles grow. The juveniles of both species leave the female's burrow at about half adult size. The major tasks of female *L. pinguis* and *C. bigelowi* during the time of extended parental care is to irrigate and maintain the deep burrow. It is hypothesized that extended parental care in *L. pinguis, C. bigelowi* and other tube/burrow-living peracarids is a mechanism to protect small offspring from epibenthic predation.

Keywords: Reproduction, extended parental care, Amphipoda, Peracarida, endobenthic, soft-bottom, intertidal.

Introduction

The majority of marine macrobenthic organisms have planktonic larvae which spend some time in the water column before settling to the bottom. However, some species invest more energy into their offspring by releasing advanced larvae or even fully developed juveniles. Brooding of small juveniles is known for small bivalves (Gallardo 1993), some polychaetes (Dales, 1950; Bartels-Hardege and Zeek, 1990) and echinoderms (Sewell, 1994). The most sophisticated brooding behaviour has evolved in some peracarid crustaceans, where fully developed small juveniles hatch from the female's brood pouch.

While parental care until a juvenile stage is not uncommon in the marine environment, care beyond the juvenile stage is rare. Most cases of extended parental care in the marine environment occur in the peracarids. The marine isopods *Astacilla longicornis* and *Astacilla arietina* (Sars, 1899), *Arcturus baffini* (Svavarsson and Davidsdottir, 1994, 1995), the marine amphipods *Phronima sedentaria* (Richter, 1978a; Laval, 1980), *Caprella scaura typica* (Lim and Alexander, 1986), *C. monoceros* and *C. decipiens* (Aoki and Kikuchi, 1991), *Dyopedos monacanthus* and *D. porrectus* (Mattson and Cedhagen, 1989), *Dulichia falcata* (Kanneworff and Nicolaisen, 1973), *Siphonoecetes dellavallei* (Richter, 1978b) *Peramphithoe stypotrupetes* (Conlan and Chess, 1992), and the tanaids *Tanais dulongii* (Johnson and Attramadal, 1982; Borowsky, 1983) and *Heterotanais oerstedi* (Bückle-Ramirez, 1965) are among those peracarids for which extended parental care is documented. The occurrence of extended parental care among

0022-2933/97 $12·00 © 1997 Taylor & Francis Ltd.

very different peracarid orders suggests that this reproductive behaviour has evolved several times independently. In order to identify the factors leading to the evolution of extended parental care, a detailed knowledge of this form of reproductive behaviour is essential. In most of the above studies the finding of juveniles together with females or males is the only hint indicating the occurrence of extended parental care. No detailed examinations of the parent-juvenile relationship or the numbers and sizes of juveniles produced by each female are available. We describe the first observations of extended parental care in two endobenthic amphipods, *Leptocheirus pinguis* and *Casco bigelowi*, which inhabit burrows in estuarine soft-bottoms. In addition, we examined how many juveniles are cared for by each female and at what size these juveniles are released into the environment. We will restrict our discussion to peracarid crustaceans, despite the fact that there is a whole variety of other marine invertebrates with some form of extended parental care.

Methods

Study area

The study was conducted in Lowes Cove, which is a sheltered cove in the Damariscotta River Estuary, Maine. Salinities are about 30, and water temperatures vary between −1 and 19°C over the course of the year. The sediment in the cove is muddy to muddy clay. The organic matter content of the sediments varies between 2·5 in the intertidal and 3·5% in the shallow subtidal (unpublished data). Both amphipod species can be found in soft sediments (water content: 70–80%) at the low tide mark. Sampling was done at a station just at Mean Low Water (MLW) during spring low tides, when the tidal flats at the sampling station were emersed for about one hour.

Sampling of amphipods

In order to collect individual burrows and their inhabitants, we located the burrow openings at the sediment surface. One of us then used his fingers in a grab-like manner to take the whole sediment with the burrow. After retrieving the sediment we opened the burrow carefully but quickly and collected its inhabitants with a spoon. In this way we ensured that only the inhabitants of one individual burrow were sampled. Burrow inhabitants of *Leptocheirus pinguis* were collected every two weeks over the period June through beginning of September 1993. *Casco bigelowi* were only collected on one date (12 December 1993). Our main objective was to document the numbers and sizes of juveniles reared in the burrows of individual parents, and at each sampling date we tried to find six burrows containing adults and juveniles. We measured the size of all individuals which had been collected in order to find out up to what size the juveniles stay with their parents. For the size measurements we used a computer-based video-image analysis system. The amphipods were measured along their dorsal surface from the rostrum to the telson. All adult amphipods were sexed and for the females it was determined whether they were ovigerous or not. In the following we use the term 'rearing female' exclusively for those females which were rearing juveniles in their burrows, and 'non-rearing female' for those which did not host juveniles in their burrow.

Results

Burrow structure and organization

Leptocheirus pinguis. The burrow of *L. pinguis* has a U-shaped form and the inhabitants can usually be found at the bottom shaft of their burrow (Fig. 1). The burrow extends 3–6 cm below the sediment surface and those of rearing females may

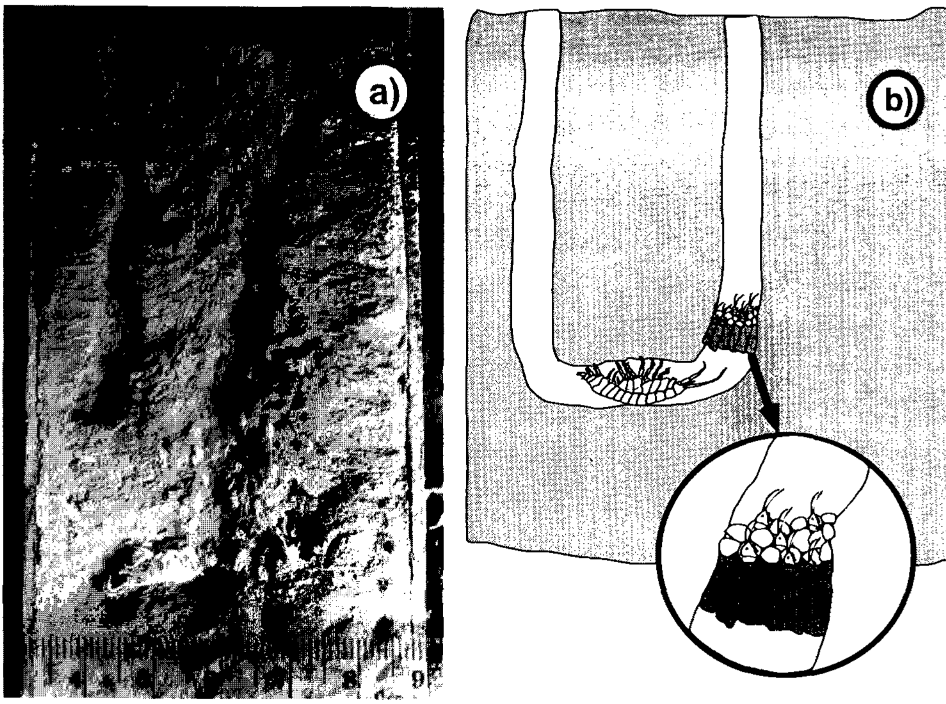

FIG. 1 (a) Burrow with a rearing female *Leptocheirus pinguis* and its juveniles; female at the bottom and juveniles in the right branch of the U-shaped burrow; sediment core was frozen in liquid N immediately after retrieval and later freeze-dried in the lab; (b) simplified drawing of typical burrow with female at the bottom and juveniles in tubes in bottom of right branch of the burrow.

be up to 10 cm deep (Fig. 1). At the surface the two burrow openings have a sharp edge, and they are flush with the surrounding sediment surface. The burrow shape is relatively stable, the burrow wall is firm and oxygenated, but no tube with mucus-lined walls is built. Not much sediment reworking seems to occur after the establishment of the burrow. The juveniles usually live at the bottom of the burrow, with larger juveniles inhabiting their own tubes at the bottom of the female burrow (Fig. 1). These juvenile tubes are built from mucus-lined walls and usually organized in a manner resembling a honeycomb. The female stays at the bottom of the burrow immediately behind the tubes of the juveniles (Fig. 1). It appears that the juvenile tubes fill the entire diameter of the U-shaped burrow. No information is available on how the female maintains the burrow while rearing these large juveniles. Water is drawn into the burrow and first passes through the juvenile tubes before it reaches the female. While sampling the burrows in the field, we sometimes found juveniles established their own burrow as side-branches from their mother's burrow.

Casco bigelowi. The structure of the burrows of *C. bigelowi* is much less regular and they are frequently modified by their inhabitants (Fig. 2). Single inhabitants usually live in U-shaped burrows which can extend down to more than 10 cm below the sediment surface. In some cases the amphipods were also found in simple tubes with a cave at the bottom. The burrow wall is very soft and bordering sediments are rarely oxygenated. Females with juveniles inhabit variously branched burrows which may have multiple openings to the surface (Fig. 2). The continuous modification of the burrow can be inferred from mounds of freshly excavated sediments at the surface. Laboratory observations have shown that

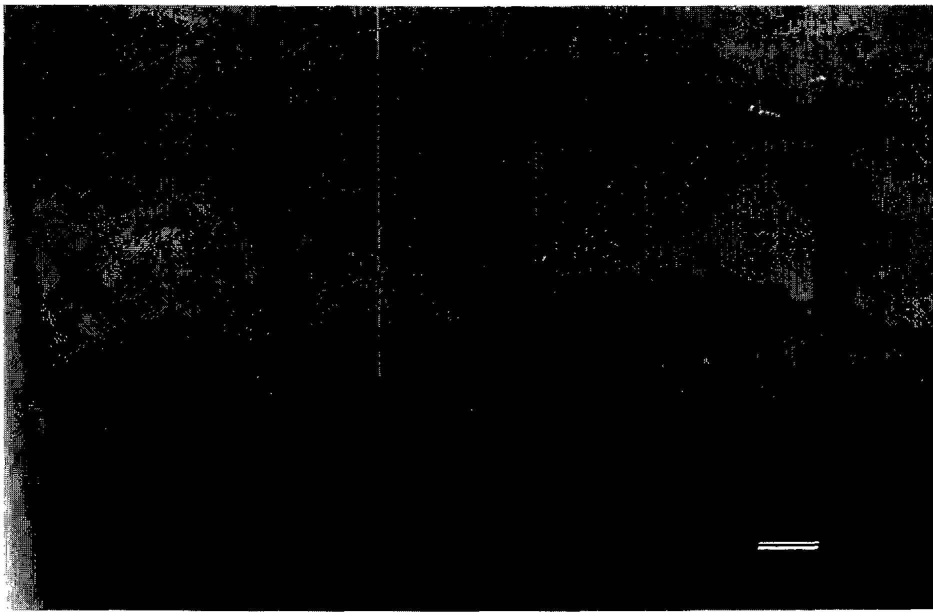

FIG. 2. Burrow of rearing female *Casco bigelowi*; scale bar = 1cm.

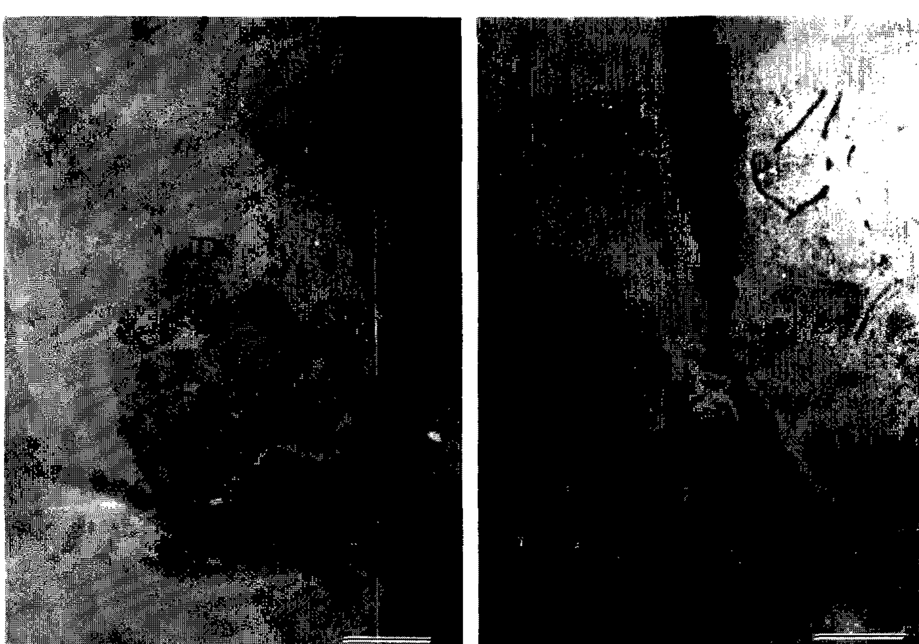

FIG. 3. Photograph of the interior of a burrow of *Casco bigelowi*, showing the female and some of its juveniles: female transporting mud bolus (left) and female irrigating the burrow (right); juveniles visible in horizontal burrow gallery; scale bar = 1cm.

sediment is also deposited within the burrow. Rearing females have been observed to modify the burrow shape continuously (Fig. 3). They also ventilate the burrow frequently at different positions in the burrow. The juveniles of *C. bigelowi* move about freely in the burrow of their mother (Fig. 3).

Reproductive stage and size of females

Leptocheirus pinguis. Juveniles of *L. pinguis* were always accompanied in the burrow by an adult female. In one case a male was found in the burrow of an ovigerous, rearing female. In June and early July most rearing females were either ovigerous or had developing juveniles in the brood pouch (Fig. 4a). At the end of July no rearing females were ovigerous but after this date the proportion of ovigerous females increased again (Fig. 4a). The same trend can be observed for non-rearing females with no ovigerous females at 21 July (Fig. 4b). In July no males were found attending females, but during other times (June and August) there was always at least one male found attending a female (Fig. 4).

From the limited information on the size of the rearing and non-rearing females of *L. pinguis* no clear temporal trend is recognizable. The size of the rearing females varied between 13·5 and 21·8 mm. On average, the rearing females were always > 15 mm (Fig. 5). The size of the non-rearing females varied between 8·1 and 19·8 mm. The average size of non-rearing females was always below 15 mm (Fig. 5).

Casco bigelowi. Also in *C. bigelowi* the care of the juveniles was exclusively done by the female. The size of the rearing females varied between 19·6 and 25·8 mm at 12 December 1993 (mean 23·02 mm ± 0·85 s.e.; $n = 7$). At this time all seven rearing females were non-ovigerous.

Numbers and sizes of juveniles in females' burrows

Leptocheirus pinguis. Up to 144 juveniles have been found in the burrow of one female *L. pinguis*, but there were also females which hosted only five juveniles at the time of sampling. The average number of juveniles in their mother's burrows decreased towards the beginning of August (Fig. 6). At the end of August no rearing females were found, and at 1 September we found only one rearing female with 17 juveniles. The smallest juveniles which we found in the burrows of their mother were about 2 mm in length and the largest were about 10 mm (Fig. 7). When juveniles were larger than about 5 mm, their numbers in the female's burrows clearly decreased (Fig. 7). In some burrows, two clutches of juveniles can easily be distinguished (see e.g. Fig. 7, 8 June 1993, female #1). Between June and the beginning of July, there were always some females with small juveniles, but later we did not find large numbers of small juveniles in the burrows of the females (Fig. 7). At the end of July/beginning of August the majority of the juveniles found in their mothers' burrows were > 5 mm (Fig. 7).

Casco bigelowi. Between 35 and 58 juveniles (mean 45·0 ± 3·31 s.e.; $n = 7$ burrows) have been found in the burrow of one female *C. bigelowi* at the 12th December. The smallest juvenile found at that date was 3·6 mm long and the largest was 12·6 mm in size. In no burrow were two clutches of juveniles recognizable (Fig. 8).

Discussion

Extended parental care was found in two endobenthic amphipods which both inhabit estuarine soft-bottoms. The structure and maintenance of the burrow differs substantially between the two species, but in both cases only females engaged in the care of the juveniles. Juveniles grew to > 0·5 the adult size during the period of extended parental care.

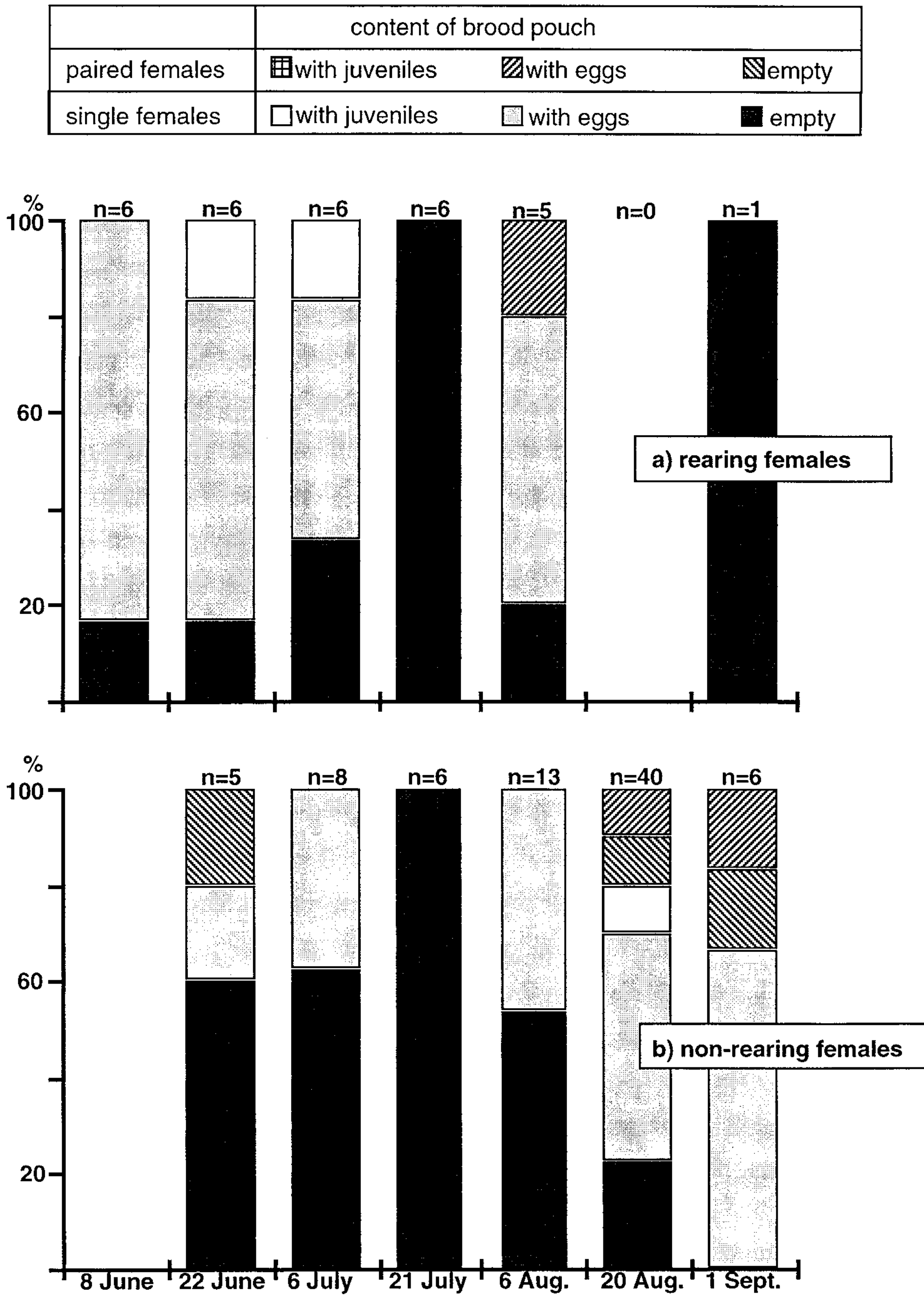

FIG. 4. (a) Reproductive stage of rearing females; and (b) non-rearing females of *Leptocheirus pinguis* between 8 June and 1 September 1993. One rearing female was lost during sampling at 8 August, none was found at 20 August and only one rearing female was found at 1 September. No effort was made to collect similar numbers of non-rearing females at each sampling date; therefore numbers vary greatly between the various dates.

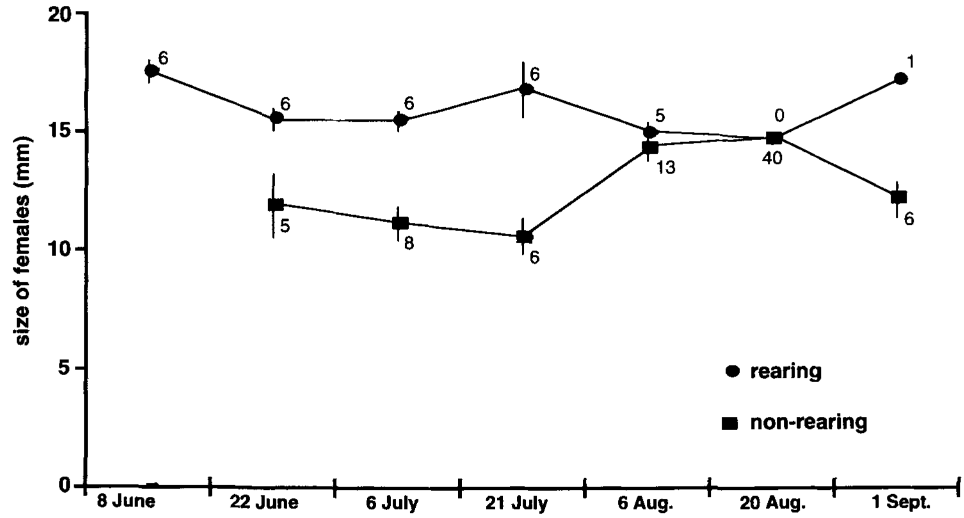

FIG. 5. Mean size (±standard error) of rearing females and non-rearing females of *Leptocheirus pinguis*; n = numbers of females measure; see also Fig. 4.

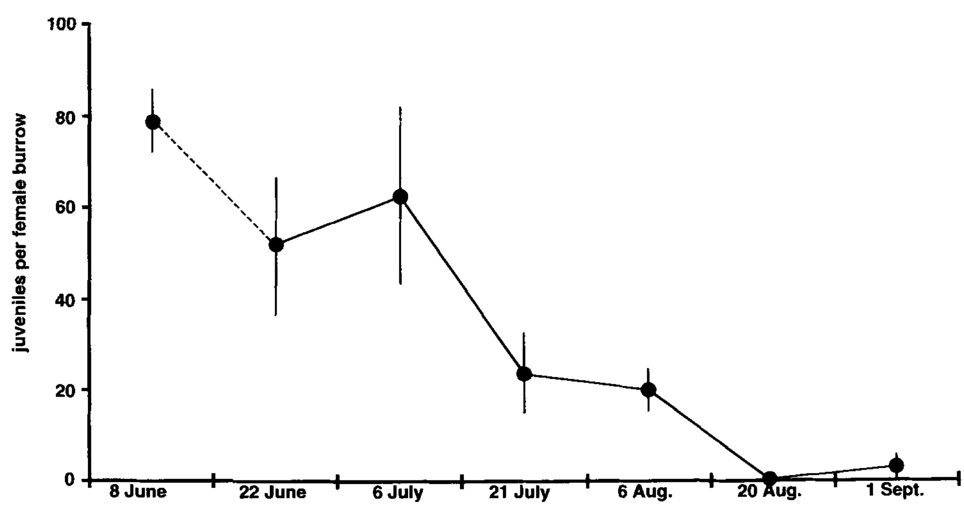

FIG. 6. Mean numbers (±standard error) of juvenile *Leptocheirus pinguis* in each female's burrows between 8 June and 1 September 1993; each sampling date the juveniles of six rearing females were counted; no rearing females were found at 20 August and only one was found at 1 September.

Biology of Leptocheirus pinguis and Casco bigelowi

The data suggest that *L. pinguis* produces several consecutive broods in the spring/early summer. Several clutches of different sizes (and ages) were found in one female's burrow on several occasions. *Casco bigelowi* females, in contrast, produce only one brood (Wildish, 1980), so each female only hosted one clutch of juveniles in its burrow.

To our present knowledge, *L. pinguis* filters suspended particles out of the water which it pumps through its burrow. *Casco bigelowi* is a deposit-feeder excavating subsurface

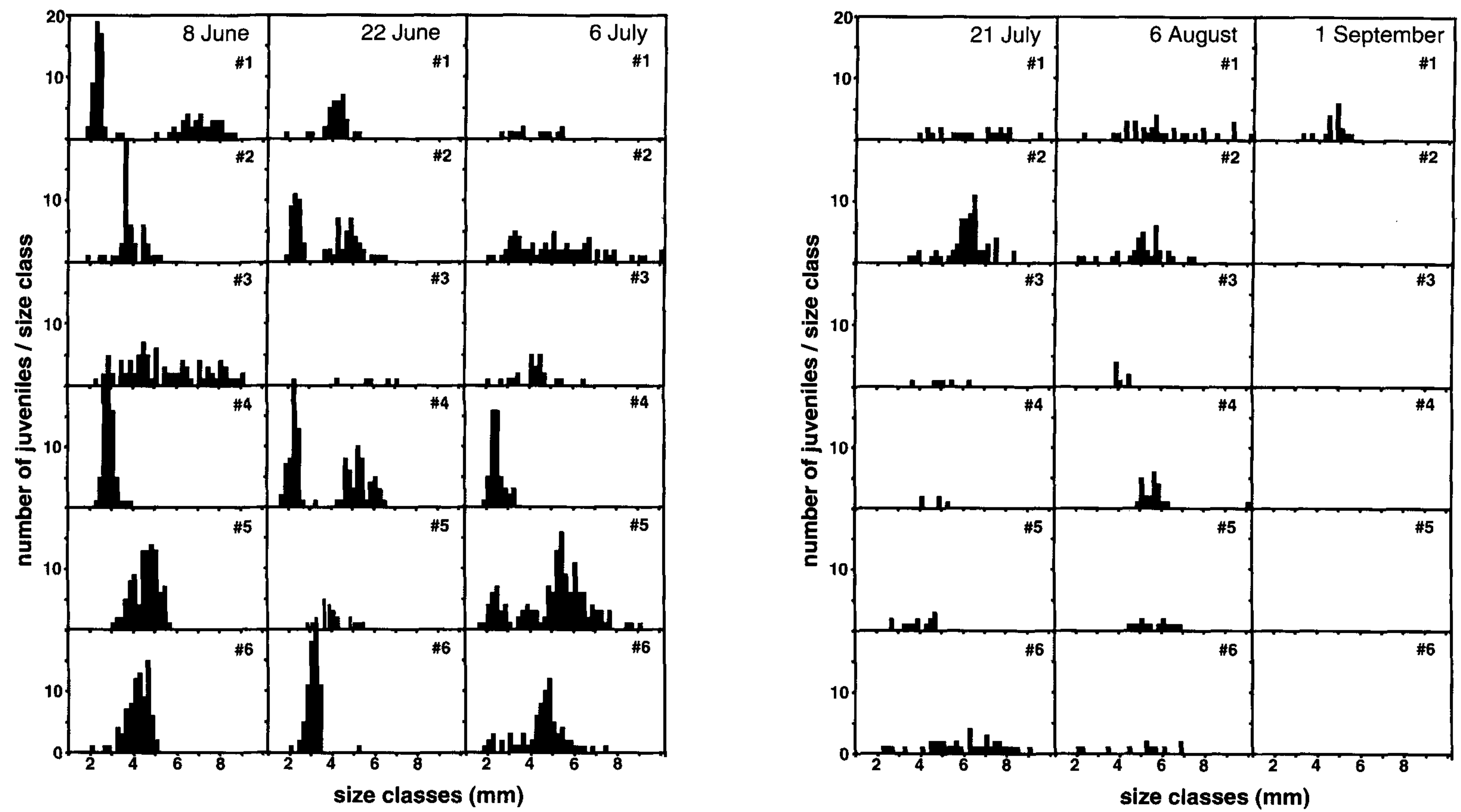

FIG. 7. Numbers of juvenile *Leptocheirus pinguis* in the size classes found in burrows of each individual female (#1–6) at the respective sampling dates (8 June–1 September 1993); no rearing females were found at 20 August, and only one was found on 1 September 1993.

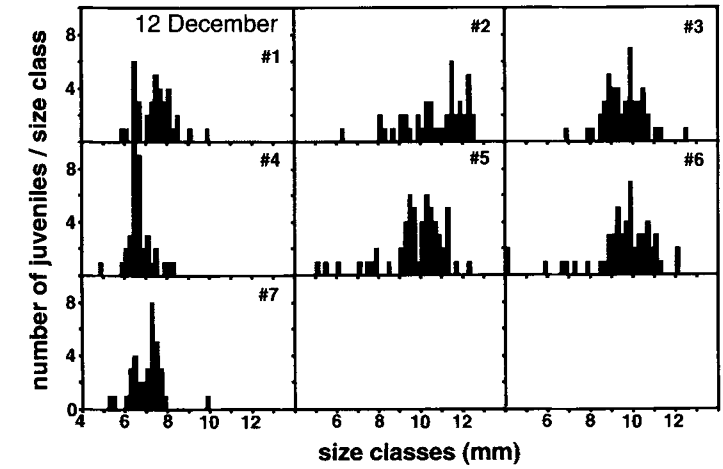

FIG. 8. Number of juvenile *Casco bigelowi* in the size classes found in the burrows of each individual female (#1–7) at the 12 December 1993.

deposits within its burrow. During the time periods of extended parental care, the females *L. pinguis* and *C. bigelowi* probably have two major tasks: maintaining a deep burrow and irrigating it. The diameter of the burrows is too big for smaller juveniles to engage in irrigation activities. We noticed that medium-sized juveniles *L. pinguis* started building their own tubes at the bottom of the female's burrow, which probably is necessary when these juveniles start to become true filter-feeders. We speculate that there might be a shift in feeding mode of the juveniles *L. pinguis* from deposit-feeding or grazing to filter-feeding at the time when they start building their own tubes in the burrow of their mother. Juvenile *C. bigelowi* were observed to stay close to their mother while she was manipulating sediment within the burrow (own observations). They probably feed on sediments loosened by her burrowing activities. After the juveniles are born, burrows of rearing female *C. bigelowi* with multiple openings indicated increased burrowing activity of the female. Juvenile *C. bigelowi* have never been observed to engage in active burrow irrigation. The burrows of rearing females *L. pinguis* and *C. bigelowi* are 6–10 cm below the sediment surface, a depth not achievable by an individual juvenile. The depth of the female burrow might also be the reason why Wildish (1980) never encountered any juvenile *C. bigelowi* during his study. His intensive study provided important data on the population dynamics of the two amphipods *L. pinguis* and *C. bigelowi*, but the methods employed failed to reveal their extended parental care. This fact leads us to suspect that there may be more, as yet unrecognized, amphipod (peracarid, marine invertebrate) species which engage in extended parental care.

Extended parental care in marine peracarids

Most references on parental care of juvenile offspring are from peracarid crustaceans. In at least a few peracarid species the time period of parental care is extended, so that parents actively care for growing juveniles after they hatch from the female's brood pouch. In the following, we will refer to these species as those with extended parental care. We distinguish these peracarid species with extended parental care from the rest of peracarids which display the common reproductive strategy where the juveniles are released into the environment as soon as they hatch from the female's brood pouch. Not surprisingly, in

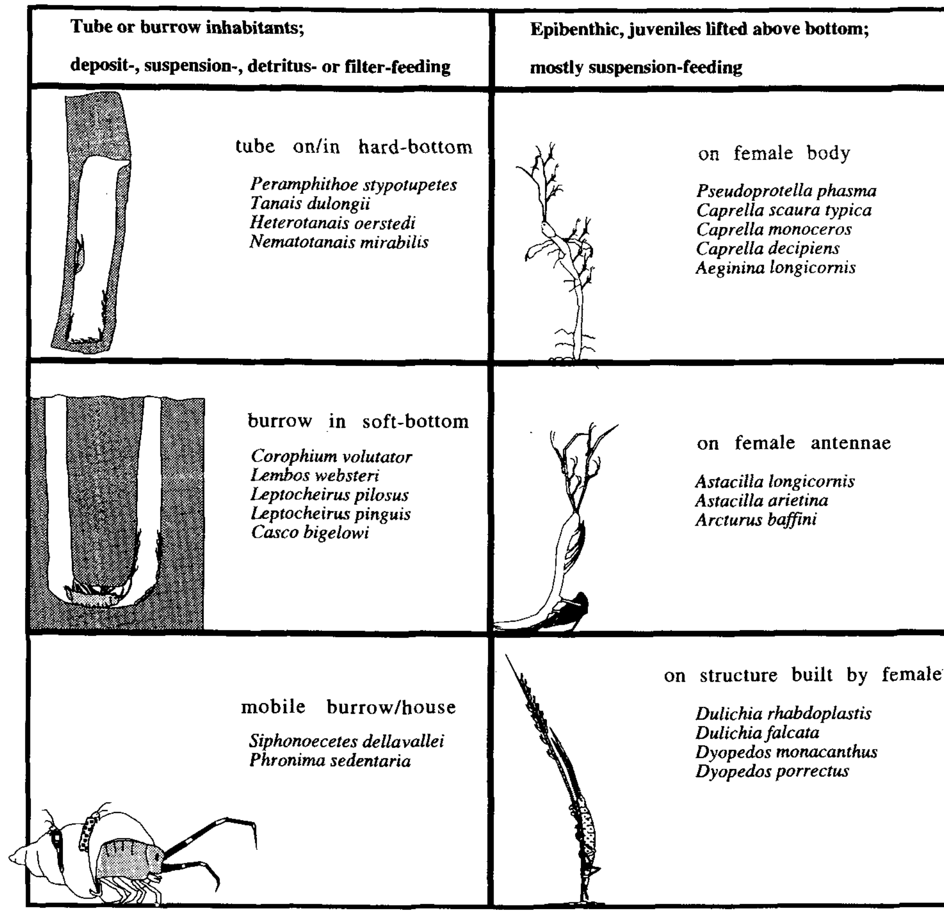

FIG. 9. Classification of peracarids with extended parental care. References are from (in alphabetical order): Aoki and Kikuchi (1991); Bird and Holdich (1985); Bückle-Ramirez (1965); Conlan and Chess (1992); Chess (1993); Goodhart (1939); Harrison (1940); Johnson and Attramadal (1982); Kanneworff and Nicolaisen (1973); Laval (1980); Lim and Alexander (1986); Mattson and Cedhagen (1989); McCloskey (1970); Richter (1978a, 1978b); Sars (1899); Shillaker and Moore (1987); Svavarsson and Davidsdottir (1994, 1995); Watkin (1947).

species with extended parental the juveniles are much larger before being released into the environment than in species without parental care.

Extended parental care is reported from a whole variety of phylogenetically distinct peracarids, which include pelagic amphipods (Richter, 1978a, Laval, 1980), and benthic isopods, amphipods and tanaids (Hassack and Holdich, 1987) with a wide range of life histories. Among the benthic peracarids with extended parental care, two major categories can be distinguished: one where the juveniles are sheltered in a tube, burrow or cave, and the other where the juveniles are living exposed on the body of the female or attached to an epibenthic structure built by the female (Fig. 9).

Peracarids from the first category are almost exclusively species from shallow-water coastal environments, where the disturbance potential and predation pressure is very high. The two endobenthic amphipods *Leptocheirus pinguis* and *Casco bigelowi* belong to this first category of burrow/tube inhabitants. Their juveniles grow to remarkably large sizes in their mother's burrows. In soft-bottom environments small recruits are very susceptible to epibenthic predators such as shrimp, hermit crabs, brachyuran crabs and fishes (e.g. Reise, 1985), whereas larger individuals are relatively safe from epibenthic predation as they can inhabit deeper tubes or burrows. This would also be true for juvenile *L. pinguis* and *C. bigelowi* which have reached sizes of about 6 to 12 mm at the time of leaving the female's burrow. Other tube-dwellers, e.g. *Peramphithoe stypotrupetes* or *Siphonoecetes dellavallei* (Richter, 1978b; Conlan and Chess, 1992; Chess, 1993), also live in environments with relatively high predation pressure, such as the East Pacific kelp forests or the shallow Mediterranean. Tube-dwelling tanaids with extended parental care live in depths along the continental shelf where abundant ground-fish stocks occur. Thus, in this category of peracarids with extended parental care, high disturbance potential (in shallow waters) or predation pressure seems to favour a sheltered life style of small juveniles in the safety of a big and deep parent's burrow/tube.

The other category of peracarids with extended parental care leads a very exposed life, as depicted by the caprellid amphipods and the arcturid isopods. Intuitively one would not expect extended parental care within this group of peracarids. A female-offspring group might be more obvious to an epibenthic predator than a single individual. Interestingly, in sheltered laboratory environments, Aoki and Kikuchi (1991) found much higher survival for a caprellid species with extended parental care than for one not engaging in this reproductive behaviour. Intraspecific competition and predation can be important within this group and particularly caprellid males have been found to attack and prey on their own species (Lim and Alexander, 1986). Extended parental care within this category of peracarids might be an important strategy to reduce intraspecific competition and predation on the offspring (see also reports in Mattson and Cedhagen, 1989; and Lim and Alexander, 1986). However, probably more important with respect to the evolution of extended parental care in this category of peracarids is the fact that all species within this category are suspension-feeders. Very small juveniles might not be able to reach above the benthic boundary layer into water layers with sufficient flow speeds and suspended particle delivery without parental assistance.

Extended parental care in the marine environment

Our classification of peracarid species with extended parental care most likely is incomplete. The major reason for this is that the life history of many marine invertebrates is unknown, and that assumptions about their reproductive biology are counterfeit by methodological limitations. We assume that our general conclusions with regard to the evolution of extended parental care (protection from predation, reaching above the benthic boundary layer) are valid, but other factors need to be considered in future studies. A thorough examination of this presocial extended parental care also might provide important clues for a better understanding of higher social behaviour among marine invertebrates (see, e.g. Duffy, 1996).

Acknowledgements

Our particular thanks go to Larry Mayer who gave M.T. the freedom to explore the mudflats of Maine, while he was supposed to study the feeding and digestive behaviour of deposit-feeders. M.T. was supported by a graduate fellowship from the Center for Marine Studies at the University of Maine.

References

Aoki, M. and Kikuchi, T., 1991, Two types of maternal care for juveniles observed in *Caprella monoceros* Mayer, 1890 and *Caprella decipiens* Mayer, 1890 (Amphipoda: Caprellidae), *Hydrobiolgia*, **223**, 229–237.

Bartels-Hardege, H. D. and Zeek, E., 1990, Reproductive behavior of *Nereis diversicolor* (Annelida: Polychaeta), *Marine Biology*, **106**, 409–412.

Bird, G. J. and Holdich, D. M., 1985, A remarkable tubicolous tanaid (Crustacea: Tanaidacea) from the Rockall Trough, *Journal of the Marine Biological Association of the United Kingdom*, **65**, 563–572.

Borowsky, B., 1983, Reproductive behavior of three-tube-building peracarid crustaceans: the amphipods *Jassa falcata* and *Amphithoe valida* and the tanaid *Tanais cavolinii, Marine Biology*, **77**, 257–263.

Bückle-Ramirez, L. F., 1965, Untersuchungen über die Biologie von *Heterotanais oerstedi* Kröyer (Crustacea, Tanaidacea), *Zeitschrift für Morphologie und Ökologie der Tiere*, **55**, 714–782.

Conlan, K. E. and Chess, J. R., 1992, Phylogeny and ecology of a kelp-boring amphipod, *Peramphithoe stypotrupetes*, new species (Corophioidea: Amphithoidae), *Journal of Crustacean Biology*, **12**, 410–422.

Chess, J. R., 1993, Effects of the stipe-boring amphipod *Peramphithoe stypotrupetes* (Corophioidea: Amphithoidae) and grazing gastropods on the kelp *Laminaria setchellii, Journal of Crustacean Biology*, **13**, 638–646.

Dales, R. P., 1950, The reproduction and larval development of *Nereis diversicolor* O. F. Müller, *Journal of the Marine Biological Association of the United Kingdom*, **29**, 321–360.

Duffy, J. E., 1996, Eusociality in a coral-reef shrimp, *Nature*, **381**, 512–514.

Gallardo, C. S., 1993, Reproductive habits and life cycle of the small clam *Kingiella chilenica* (Bivalvia: Cyamiidae) in an estuarine sand flat from the South of Chile, *Marine Biology*, **115** 595–603.

Goodhart, C. B., 1939, Notes on the bionomics of the tube-building amphipod, *Leptocheirus pilosus* Zaddach, *Journal of the Marine Biological Association of the United Kingdom*, **23**, 311–325.

Harrison, R. J., 1940, On the biology of the Caprellidae. Growth and moulting of *Pseudoprotella phasma* Montagu, *Journal of the Marine Biological Association of the United Kingdom*, **24**, 483–493.

Hassack, E. and Holdich, D. M., 1987, The tubicolous habit amongst the Tanaidacea (Crustacea, Peracarida) with particular reference to deep-sea species, *Zoologica Scripta*, **16**, 223–233.

Johnson, S. B. and Attramadal, Y. G., 1982, Reproductive behaviour and larval development of *Tanais cavolinii* (Crustacea: Tanaidacea), *Marine Biology*, **71**, 11–16.

Kanneworff, E. and Nicolaisen, W., 1973, The ''Haps'', a frame-supported bottom corer, *Ophelia*, **10**, 119–129.

Laval, P., 1980, Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton, *Oceanography and Marine Biology, an Annual Review*, **18**, 11-56.

Lim, S. T. A. and Alexander, C. G., 1986, Reproductive behaviour of the caprellid amphipod, *Caprella scaura typica*, Mayer 1890, *Marine Behaviour and Physiology*, **12**, 217–230.

Mattson, S. and Cedhagen, t., 1989, Aspects of the behaviour and ecology of *Dyopedos monacanthus* (Metzger) and *D. porrectus* Bate, with comparative notes on *Dulichia tuberculata* Boeck (Crustacea: Amphipoda: Podoceridae), *Journal of Experimental Marine Biology and Ecology*, **127**, 253–272.

McCloskey, L. R., 1970, A new species of *Dulichia* (Amphipoda, Podoceridae) commensal with a sea urchin, *Pacific Science*, **24**, 90–98.

Reise, K., 1985, Tidal flat ecology, *Ecological Studies*, **54**, 191 (Berlin: Springer-Verlag).

Richter, G., 1978a, Beobachtungen zu Entwicklung und Verhalten von *Phronima sedentaria* (Forskal), (Amphipoda), *Senckenbergiana maritima*, **10**, 229–242.

Richter, G., 1978b, Einige Beobachtungen zur Lebensweise des Flohkrebses *Siphonoecetes dellavallei, Natur und Museum*, **108**, 259–266.

Sars, G. O., 1899, *An account of the Crustacea of Norway*, Volume 2. Isopoda (Bergen: Bergen Museum) 270pp.

Sewell, M. A., 1994, Small size, brooding and protandry in the apodid sea cucumber *Leptosynapta clarki, Biological Bulletin*, **187**, 112–123.

SHILLAKER, R. O. and MOORE, P. G., 1987, The biology of brooding in the amphipods *Lembos websteri* Bate and *Corophium bonnellii* Milne Edwards, *Journal of Experimental Marine Biology and Ecology*, **110**, 113–132.

SVAVARSSON, J. and DAVIDSDOTTIR, B., 1994, Foraminiferan (Protozoa) epizoites on Arctic isopods (Crustacea) as indicators of isopod behavior? *Marine Biology*, **118**, 239–246.

SVAVARSSON, J. and DAVIDSDOTTIR, B. 1995, *Cibicides* spp. (Protozoa, Foraminifera) as epizoites on the Arctic antenna-brooding *Arcturus baffini* (Crustacea, Isopoda, Valvifera), *Polar Biology*, **15**, 569–574.

WATKIN, E. E., 1947, The yearly life cycle of the amphipod *Corophium volutator, Journal of Animal Ecology*, **10**, 77–93.

WILDISH, D. J., 1980, Reproductive bionomics of two sublittoral amphipods in a Bay of Fundy estuary, *International Journal of Invertebrate Reproduction*, **2**, 311–320.