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DURATION OF EXTENDED PARENTAL CARE IN MARINE AMPHIPODS

Martin Thiel

ABSTRACT

Several peracarid species provide parental care for their growing offspring after these have left the brood pouch of the female. In this study, I examined the duration of extended parental care in 3 soft-bottom dwelling amphipod species: the epibenthic suspension feeder *Dyopodos monacanthus* (Podoceridae), the burrow-dwelling filter-feeder *Leptocheirus pinguis* (Aoridae), and the burrow-dwelling deposit-feeder *Casco bigelowi* (Melitidae). Juvenile *D. monacanthus* remained on the mud whip of their mother for time periods of 10–20 days, maximally 27 days. Many juveniles left their mother before a second clutch was released onto her mud whip, indicating that factors other than the appearance of a second clutch limit the duration of care for the first clutch of juveniles. Juvenile *L. pinguis* left the burrow of their mother in distinct batches, usually after a molting event. Some juveniles remained in the burrow of their mother for 40–60 days. Juvenile *C. bigelowi* commonly remained in the burrow of their mother for >80 days, and departed over a period that lasted 20–40 days until all juveniles had left. A literature review revealed that in many epibenthic peracarids with extended parental care, juveniles usually remain with their mothers for about 3 weeks. Females of species that carry their offspring during parental care usually do not produce a second brood while carrying one brood, whereas females that do not carry but guard their offspring often produce a second brood while caring for the first brood. Duration of extended parental care is much more variable in tube-/burrow-dwelling species, lasting from minutes in some species up to 3 months in others. It is concluded that tube-/burrow-dwelling species have a higher potential for long-lasting (>>20 days) extended parental care than epibenthic species. Ecological constraints, such as availability of space and food, predation, disturbance, and competition, are discussed as factors limiting the duration of extended parental care. It is hypothesized that the potential for extended parental care is high in marine peracarids, but advanced social behavior is restricted to species that are living in dwellings of biotic origin.

Parental care for growing offspring is a relatively uncommon reproductive strategy among marine invertebrates. One of the most progressive forms of parental care in the marine environment can be found in peracarid crustaceans. In most peracarids, embryos and larvae develop in the female brood pouch, from which fully developed juveniles or advanced larvae emerge. While in most peracarid species, parental care ends after juveniles or larvae have emerged from the female brood pouch (see, e.g., Borowsky, 1980), in some species parental care extends beyond this stage. In species with extended parental care, one or both parents live together with their offspring for long time-periods. During this time, parents may actively feed, defend, or groom their offspring, or they may simply tolerate them on their body or in their dwellings (for examples, see Wilson, 1975; Clutton-Brock, 1991). Present knowledge about extended parental care in marine invertebrates is still very limited, and it is not always evident what kind of care parents provide for their offspring. Instead of focusing

on the quality of the parent-offspring association and the behavioral interaction of parents and offspring, I herein closely examine the duration of extended parental care in peracarid crustaceans.

Diverse forms of extended parental care have been reported for peracarids. Juveniles of epibenthic amphipods and isopods stay on the body of their mother or on structures built by her after emerging from her brood pouch (Sars, 1899; Harrison, 1940; Lim and Alexander, 1986; Mattson and Cedhagen, 1989; Aoki and Kikuchi, 1991; Svavarsson and Davidsdottir, 1995; Aoki, 1997; Thiel, 1997a). Juveniles of endobenthic, tube- or burrow-dwelling amphipods, isopods, and tanaids remain in tubes or burrows of their mothers after emerging from the brood pouch (Thamdrup, 1935; Goodhart, 1939; Watkin, 1947; Richter, 1978a, b; Johnson and Attramadal, 1982; Bird and Holdich, 1985; Hassack and Holdich, 1987; Shillaker and Moore, 1987; Messana *et al.*, 1994; Thiel *et al.*, 1997). Juveniles can reach considerable sizes while being cared for by their parents (see, e.g., Con-

lan and Chess, 1992; Svavarsson and Davidsdottir, 1995; Thiel *et al.*, 1997), and thus leave their parents at much larger sizes than most other peracarids where juveniles leave shortly after emerging from the brood pouch of the female. The major advantage gained from extended parental care is that juveniles at the time of recruitment are relatively large, thereby increasing their individual fitness (Thiel, 1997b). It is not known, however, what the costs of this sophisticated reproductive strategy are for the parents, which in most cases are the females. In several amphipod species, females produce subsequent broods while still caring for their growing offspring (Conlan and Chess, 1992; Thiel, 1997c, d; Thiel *et al.*, 1997). In these species, females can often be found caring for two or even three clutches of juveniles simultaneously. Since in these species, parental care allows for the simultaneous production of a new brood, it appears that the costs of caring for offspring are relatively low. Not all peracarid species exhibiting parental care produce consecutive broods, but rather invest all their resources into one brood per reproductive season. Juveniles that need not share parental attention with subsequent clutches may be able to remain longer with their parents and grow to larger sizes than juveniles competing with newborn siblings.

Although raising offspring to large sizes during parental care can have important consequences for recruitment success, knowledge about this reproductive behavior is very limited, particularly in tube-/burrow-dwelling species. Early observations on parental care in species of *Corophium* (see Thamdrup, 1935; Watkin, 1947) have been all but ignored, until Flach (1992, 1996) pointed out that the close spatial association of female and juvenile burrows is likely a result of parental care. Only one study (Shillaker and Moore, 1987) has thoroughly examined whether and how long juveniles remain in the burrows of their mother, while most other studies on endobenthic peracarids ignore the fact that juveniles may remain with their parents after leaving the marsupium. Some epibenthic peracarids are relatively well studied with respect to the existence and ecology of extended parental care (Stephan, 1980; Mattson and Cedhagen, 1989; Aoki and Kikuchi, 1991; Svavarsson and Davidsdottir, 1995; Aoki, 1997), but detailed knowledge on the

duration of extended parental care in these species is available only for a few caprellid species (Aoki, 1997).

The three amphipod species under investigation, *Leptocheirus pinguis* (Stimpson, 1853), *Casco bigelowi* (Blake, 1929), and *Dyopodos monacanthus* (Metzger, 1875), reach high densities on soft bottoms at and just below mean low water (MLW). *Leptocheirus pinguis*, a filter-feeder, and *C. bigelowi*, a deposit-feeder, both inhabit burrows in soft-sediments (Thiel *et al.*, 1997; Thiel, 1997b). Juveniles of both species are hosted by their mothers in the maternal burrow until they have reached considerable sizes (length about 5 mm in *L. pinguis* and about 12 mm in *C. bigelowi*). *Dyopodos monacanthus* is an epibenthic species that uses self-constructed mud whips as vantage points for suspension-feeding (Mattson and Cedhagen, 1989; Thiel, 1997c). A female *D. monacanthus* hosts its juveniles on her mud whip after these emerge from her brood pouch. In all three species, one important benefit that juveniles gain from extended parental care is increased survival in environments with high predation pressure (Thiel, 1997b). Although all three amphipod species cooccur in a narrow zone at and just below mean low water (MLW), the sizes that juveniles reach during extended parental care differ substantially, suggesting that the duration of extended parental care shows similar differences. The major goal of this study is to examine the duration of extended parental care in the three amphipod species and to compare it to that reported for other marine peracarids.

MATERIALS AND METHODS

All observations and experiments were conducted in the sea-water laboratory of the Darling Marine Center, located at the Damariscotta River estuary, Maine (43°56'N, 69°35'W). Observations on the females of *Dyopodos monacanthus* and their offspring were conducted in a large glass aquarium (160 l) with flowing sea water. The aquarium contained a thin layer of mud (3 cm deep) that was collected from the field habitat of the amphipods. In March 1995, several adult *D. monacanthus* were collected in the field and introduced to the glass aquarium where they readily built mud whips. Between March and May, the number of juveniles cared for by females on their mud whips was counted every morning. Since very small (0.8–1.4 mm; see Thiel, 1997c) juveniles were clinging to the mud whips in a dense group, it was impossible to distinguish and count individual juveniles. Therefore, numbers of small juveniles were estimated, but larger juveniles were counted individually. Data of these observations have been presented elsewhere (Thiel, 1997c), but

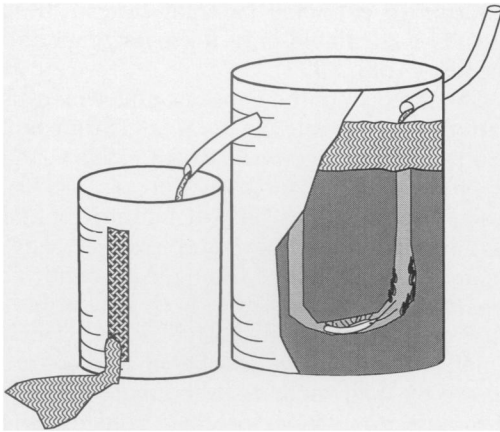


Fig. 1. Drawing of containers in which ovigerous female *Leptocheirus pinguis* and *Casco bigelowi* were maintained during parental care. Continuous flow of sea water (approximately 1 l min⁻¹) was maintained, entering the container at the inflow pipe and leaving through outflow into a trap (500- μ m screen) where all emigrants were retained. Containers were filled with a 12–15 cm deep layer of mud from the amphipod habitat; only one ovigerous female per container. For further details, see text.

are reexamined here with respect to the appearance of a subsequent clutch of juveniles. In the glass aquarium, several males readily attended and refertilized reproductive females (for details, see Thiel, 1997c). Both females and their offspring fed on phytoplankton and resuspended microphytobenthos contained in the sea water flowing through the glass tank at a rate of approximately 20 l min⁻¹.

Leptocheirus pinguis and *Casco bigelowi* were collected at a field site in Lowes Cove near the Darling Marine Center, and immediately transferred to the laboratory. Large females (*L. pinguis* > 15 mm; *C. bigelowi* > 20 mm) were quickly examined for the contents of their brood pouch and, if ovigerous, one individual was introduced to small containers that were filled with mud (12–15 cm deep). The ovigerous females readily buried in the mud-filled containers after their introduction. Sea water (salinities 29–31 psu; see McAlice, 1993) was continuously flowing (about 1 l min⁻¹) through the containers from which it exited through a pipe (Fig. 1). Containers for *L. pinguis* had a diameter of 9 cm and a depth of 16 cm, containers for *C. bigelowi* had a diameter of 16 cm and a depth of 16 cm. *Leptocheirus pinguis* fed on phytoplankton and resuspended microphytobenthos in the sea water flowing through their containers (5–10 μ g chlorophyll *a* l⁻¹; unpublished data), while *C. bigelowi* probably fed on rich microphytobenthos resources contained in the mud (Thiel, 1997b). Juveniles that left the containers were trapped in the outflow trap (mesh size 0.5 mm), from where they were collected every second day until numbers of emigrating juveniles substantially decreased (i.e., when it was assumed that most juveniles had

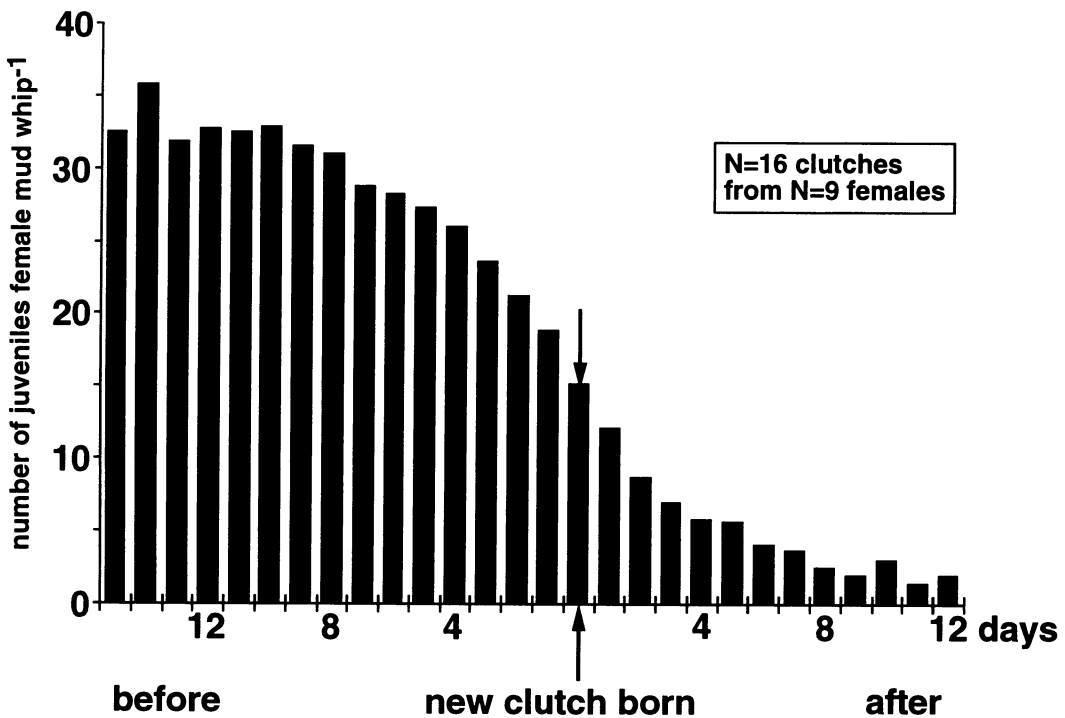


Fig. 2. Average numbers of juvenile *Dyopodos monacanthus* on the mud whips of their mothers before and after a subsequent clutch was born and began to occupy space on the mud whip. Juveniles were counted each day.

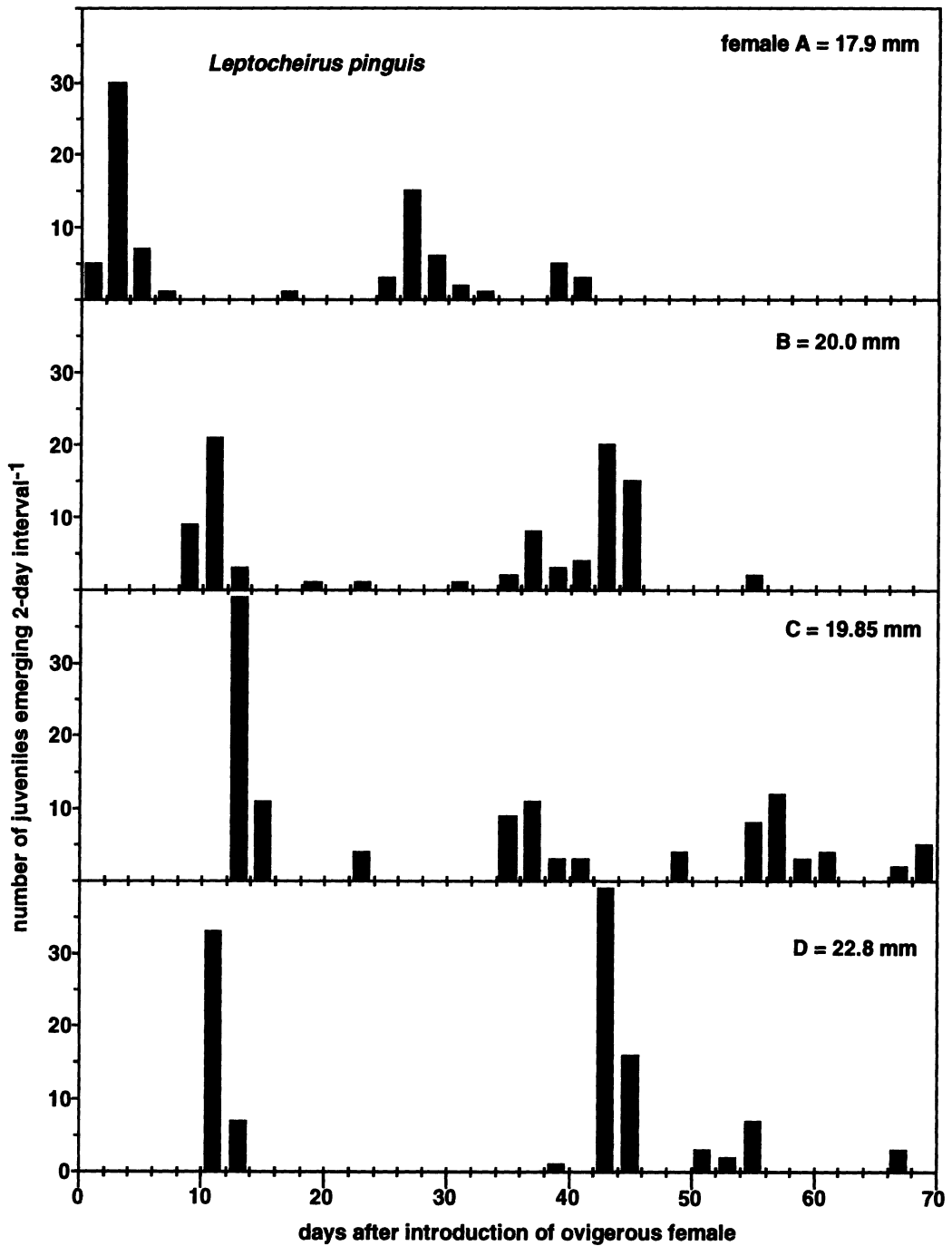


Fig. 3. Numbers of juvenile *Leptocheirus pinguis* leaving the burrow of their mothers over a time interval of 2 days. Only females with typical offspring numbers ($N > 80$ juveniles) are shown; sizes of the individual females are provided.

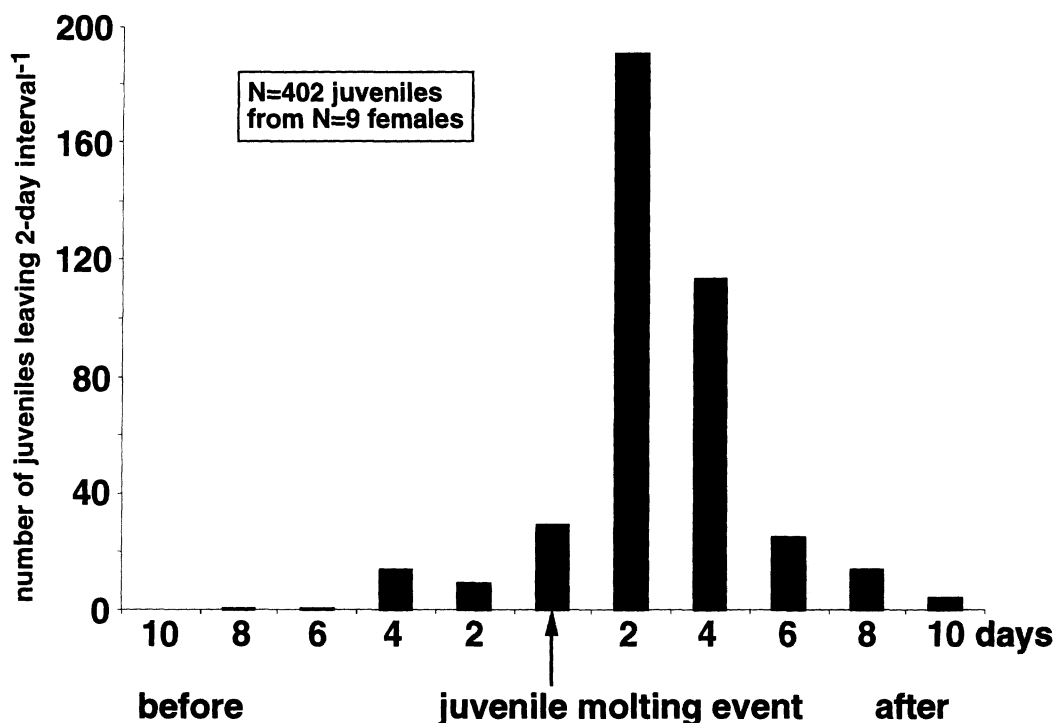


Fig. 4. Total number of juvenile *Leptocheirus pinguis* leaving the burrows of their mothers before and after molting events. All juveniles from ovigerous females ($N = 9$) leaving within 10 days before or 10 days after a molting event were included in the analysis.

left). Juveniles that established their own burrows in the containers were carefully removed as soon as their burrows were noticed.

In the experiment with *L. pinguis*, 10 ovigerous females were monitored between 23 April and 1 July 1995. Since typical numbers of offspring for females of *L. pinguis* >15 mm are about 80 (Wildish, 1980; Thiel *et al.*, 1997), the detailed results are presented only for those females having at least 80 juveniles (4 females). During the experiment with *L. pinguis*, it was noted that on some days large numbers of juvenile exuviae appeared in the traps. Beginning with day 16 of the experiment with *L. pinguis*, days with large numbers of juvenile exuviae were recorded and classified as molting events. The appearance of juveniles in the traps in relation to the next or the last occurrence of exuviae (=molting event) was evaluated. All juveniles (from 9 females, 1 female with only 5 juveniles was excluded) leaving the females within 10 days before or after a molting event were included in this analysis. If fewer than 20 days passed between 2 molting events, the day nearest to a molting event was recorded (e.g., if juveniles emerged 6 days after a molting event but 4 days before the next molting event, they were categorized as "4 days before a molting event"). In contrast to *L. pinguis*, very few exuviae of *C. bigelowi* were found in the traps. In the experiment with *C. bigelowi*, 7 females were monitored between 31 October 1995 and 30 April 1996. Since typical numbers of offspring of *C. bigelowi* are about 30–50 (Wildish, 1980; Thiel *et al.*, 1997), the detailed results are presented only for those females that had at least 30 juveniles (4 females).

Since in the experiments with *L. pinguis* and *C. bigelowi*, juveniles could not be directly observed in the burrows of their mothers, measurement of the duration of extended parental care was achieved indirectly by counting the juveniles that left the burrows of their mothers and were caught in the traps (see Fig. 1). In order to prevent confusion by juveniles originating from subsequent clutches, females were prevented from producing a second brood by excluding males from the containers. All females of *L. pinguis* and *C. bigelowi* were collected at the end of the experiment, and, after preservation in 4% Formalin, were measured with a computer-based video-image analysis system along their dorsal surface from the rostrum to the base of the telson.

RESULTS

Dyopedos monacanthus

Immediately after emerging from the brood pouches of the females, small juvenile *D. monacanthus* accumulated in dense groups on the mud whips of their mothers. During the following days, juveniles spread over the whole length of the whip, and their numbers began to decrease (Fig. 2). Many juveniles disappeared from the mud whips of their mothers (possibly drifting away via the water column; for details see Thiel, 1997c) be-

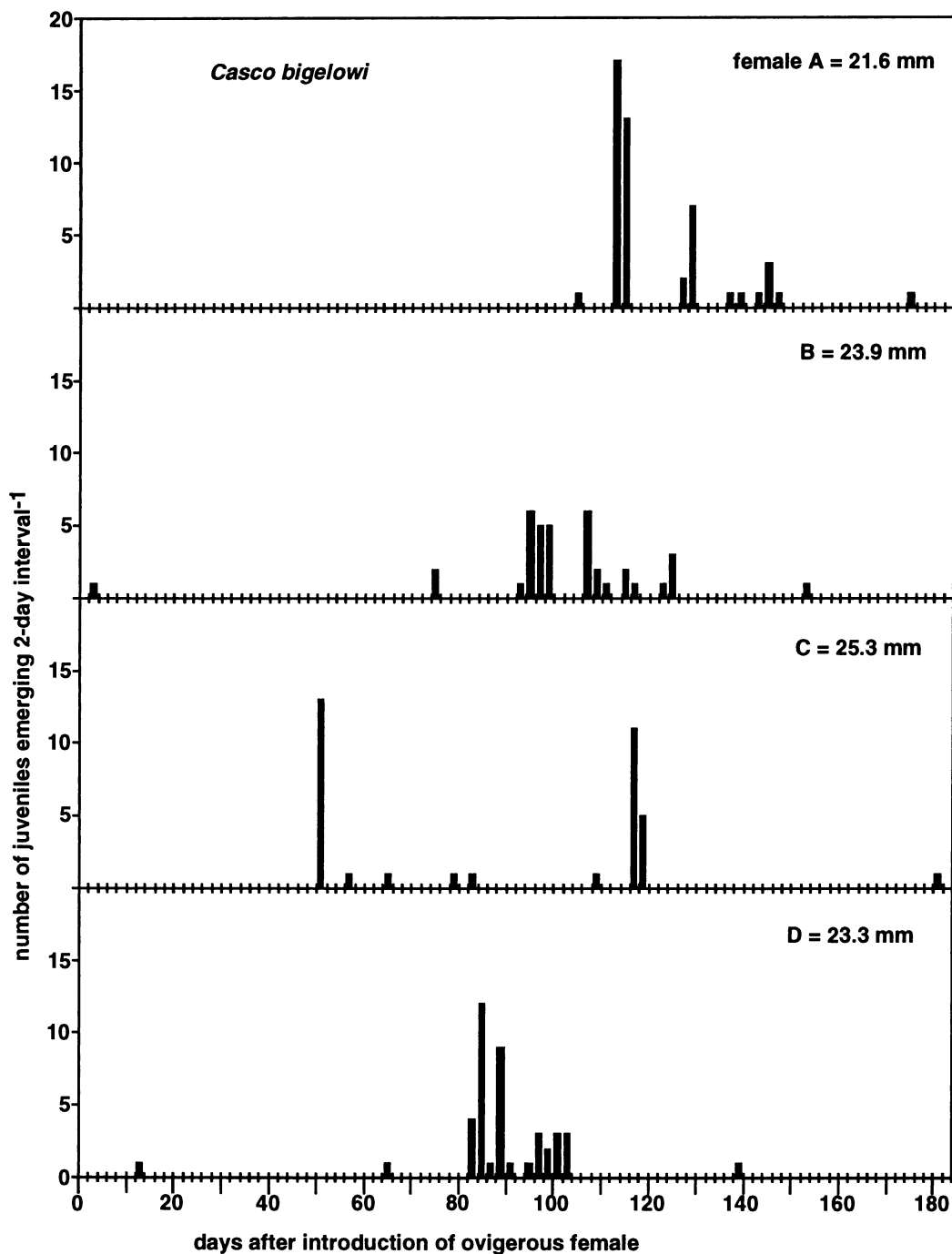


Fig. 5. Numbers of juvenile *Casco bigelowi* leaving the burrow of their mothers over a time interval of 2 days. Only females with typical offspring numbers ($N > 30$ juveniles) are shown; sizes of the individual females are provided.

fore a new clutch of juveniles was born. No distinct drop in numbers of older juveniles was discernible after the birth of a new clutch, and a few juveniles remained on the mud whip of their mothers for more than 10 days after a new clutch was born (Fig. 2). Two juveniles remained on the mud whip of their mother for 27 days, which was the maximum time observed during this experiment.

Leptocheirus pinguis

Some juveniles emerged from the burrows of their mothers shortly after leaving the marsupium, usually within 15 days after the ovigerous females had established their burrows in the experimental containers (Fig. 3). A large proportion of the juveniles, however, remained in the burrows of their mothers for time periods of 40–60 days. Juveniles did not leave the burrows of their mothers continuously, but in distinct batches (Fig. 3). Time periods of 20–30 days passed between the emergence of subsequent batches of juveniles (Fig. 3).

Large numbers of juvenile exuviae were found for time periods of 2–4 days, and usually no or only few exuviae were found during the other days. The short time periods of 2–4 days during which exuviae were found in the traps indicate that most juveniles within one burrow molt simultaneously. Many juveniles left the burrows of their mothers within a few days after a molting event (Fig. 4).

Casco bigelowi

Very few juvenile *Casco bigelowi* emerged from the burrows of their mothers within the first 50 days after the introduction of the ovigerous females (Fig. 5). Many juveniles remained for time periods of 80–120 days in the burrows of their mothers. In only one female (C), considerable time periods (about 60 days) passed between the emergence of one batch of juveniles and a subsequent batch of juveniles (Fig. 5). In the other three females, most juveniles continuously left their mothers over time periods of 20–40 days. Very few exuviae of *C. bigelowi* were found in the traps, and no exuviae were found in the containers housing the parental females and their offspring.

DISCUSSION

The duration of parental care differs substantially in the three amphipod species examined. The majority of juvenile *Dyopodos*

monacanthus left the mud whips of their mothers within 10–20 days after they were born. Many juveniles of *Leptocheirus pinguis* remained in burrows of their mothers for periods of 40–60 days, whereas in *Casco bigelowi* almost all juveniles remained for periods of 80–120 days. A comparison of the duration of parental care in the three amphipod species examined with that of other “parental” peracarids follows. The possible reasons for the considerable variation in the extent of parental care among peracarid crustaceans are discussed.

Duration of Extended Parental Care

Extended parental care in epibenthic peracarids from temperate waters generally lasts for time periods of 2–3 weeks (Table 1). For the epibenthic caprellid amphipod *Pseudoprotella phasma* Montagu, Harrison (1940) reported that juveniles remain on the bodies of their mothers for about three weeks. For *Caprella scaura typica* Mayer, up to one week has been reported (Lim and Alexander, 1986). For *C. monoceros* Mayer a duration of parental care of 12–18 days has been reported (Aoki and Kikuchi, 1991). For *C. subinermis* Mayer a period up to 4 days has been reported (Aoki, 1997) (Table 1). In *C. decipiens* Mayer, the juveniles do not usually stay on the body of their mothers, but remain with her for up to 32 days, during which time they are guarded by her (Aoki and Kikuchi, 1991; Aoki, 1997). Stephan (1980) mentioned that juveniles of *Dyopodos monacanthus* and *Dulichia* sp. remain on the mud whips of their mothers until they have attained sexual maturity (about 35 days after emerging from the marsupium). Most juvenile *D. monacanthus* observed in the present study left the maternal mud whip within the first 10–20 days after emerging from the marsupium (Fig. 2). This early departure of juveniles in my study may have been due to better feeding conditions in the continuously renewed flowing sea water compared to Stephan (1980) who, in his study, used standing sea water with added food. Field observations indicate that under natural conditions the juveniles of *D. monacanthus* remain on the mud whip of their mother for 2–3 weeks (Thiel, 1997c). In cold-water arcturid isopods, juveniles cling to the female body in a similar fashion as in caprellid amphipods (Sars, 1899; Kussakin, 1982; Svavarsson and Davidsdottir, 1995). Juveniles

appear to reach remarkable sizes while clinging to their mothers (see figs. in Kussakin, 1982; Svavarsson and Davidsdottir, 1995). Some of them reach the manca 3 stage, but nothing is known about the duration of extended parental care. These arcturid isopods are slow-growing cold-water species, and therefore it is not unlikely that parental care lasts ≥ 4 weeks (Svavarsson, personal communication).

The duration of parental care in tube-/burrow-dwelling peracarids appears to be much more variable than in epibenthic peracarids, as indicated by the data in Table 1. For most species, the duration of parental care ranges from days to weeks (Table 1). Unfortunately, no data are available for *Peramphithoe stypotruripes* Conlan and Chess, but, since up to 3 cohorts can be found in one parental dwelling (Conlan and Chess, 1992; Chess, 1993), it appears safe to assume that parental care can last >1 month in this species. In *Leptocheirus pinguis* no more than two cohorts have been found simultaneously in the burrow of one female. The duration of extended parental care in *L. pinguis* is relatively long, when compared to other infaunal species such as *Lembos websteri* Bate and *Corophium volutator* Pallas, but it is still far shorter than that measured for *Casco bigelowi*. In both *L. pinguis* and *C. bigelowi*, there is some uncertainty about the actual time of when juveniles were released from the marsupium, since ovigerous females could not be observed in their burrows. A visual examination of ovigerous females at the beginning of the experiment revealed that the embryos were in a relatively advanced stage. Therefore, it is safe to assume that most juveniles emerged from the marsupium within 10 days after the start of the experiment.

Factors Affecting the Duration of Extended Parental Care

Raising offspring to large sizes would probably be advantageous to most peracarid species, but extended parental care might often be limited by ecological constraints, such as resource availability, predation, disturbance, and other factors.

In tube-/burrow-dwelling peracarids, there is a higher potential for long-lasting extended parental care (e.g., *Peramphithoe stypotruripes*, *Leptocheirus pinguis*, and *Casco bigelowi*) than in other peracarids. At least in two

of these species (*P. stypotruripes*, *L. pinguis*), subsequent clutches of juveniles occasionally cohabit in maternal burrows. In some burrow-dwelling species, juveniles are known to leave the burrow of the female within a day after emerging from the brood pouch (Borowsky, 1983), possibly as a consequence of male attendance (see Shillaker and Moore, 1987). Apparently, male attendance does not interfere with the presence of juveniles in the female burrow in *P. stypotruripes* and *L. pinguis*. The tolerance of reproductive adults toward offspring of the female allows for production of a subsequent clutch during parental care. In some epibenthic amphipods, where juveniles are not always on the female body (e.g., *Caprella decipiens*, *Dyopedos* sp., and *Dulichia* sp.), females successfully produce subsequent broods during extended parental care (Aoki and Kikuchi, 1991; Thiel, 1997c). For the epibenthic amphipod *C. monoceros*, which continually carries its offspring during parental care, Aoki and Kikuchi (1991) mentioned that parental females of *C. monoceros* do not molt and reproduce while carrying offspring. However, if juveniles were experimentally removed from the body of the parental female *C. monoceros*, these females molted and deposited new eggs in the brood pouch within three days (Aoki and Kikuchi, 1991). Thus, carrying offspring, as in many caprellid amphipods and arcturid isopods, may prevent the production of a subsequent brood, thereby lowering the total reproductive output in these species. However, this apparent cost of extended parental care in these juvenile-carrying peracarids may be compensated for by the high survival rates of their offspring.

Space appears to become a limiting resource in many peracarids during extended parental care. In epibenthic species, numbers of juveniles steadily decrease (see fig. 4 in Aoki and Kikuchi, 1991; Thiel, 1997c; this study), possibly reflecting the continuous decrease of available substratum during juvenile growth. Juveniles spread over the entire available substratum (female body or mud whip) during growth (Aoki and Kikuchi, 1991; Thiel, 1997c), indicating that in epibenthic peracarids the availability of space might be a major factor limiting the duration of extended parental care. The continuous decline in juvenile numbers suggests that some juveniles leave at small sizes (about one-tenth

Table 1. Duration and type of extended parental care in epibenthic and tube-/burrow-dwelling peracarids; A = Amphipods, I = Isopods, T = Tanaids.

Order	Duration	Type	Reference	
EPIBENTHIC FORMS				
<i>Pseudoprotella phasma</i> Montagu, 1804	A	3 weeks	maternal body	Harrison, 1940
<i>Caprella scaura typica</i> Mayer, 1890	A	1 week	maternal body	Lim and Alexander, 1986
<i>Caprella monoceros</i> Mayer, 1890	A	12–18 days	maternal body	Aoki and Kikuchi, 1991
<i>Caprella decipiens</i> Mayer, 1890	A	up to 32 days	female vicinity	Aoki and Kikuchi, 1991
<i>Caprella subinermis</i> Mayer, 1890	A	up to 4 days	maternal body	Aoki, 1997
<i>Aeginina longicornis</i> Krøyer, 1842	A	about 2 weeks	maternal body	Thiel, 1997a
<i>Dulichia rhabdoplastis</i> McCloskey, 1970	A	not known	maternal strand	McCloskey, 1970
<i>Dulichia falcata</i> (Bate, 1857)	A	(35 days)	maternal mud whip	Stephan, 1980
<i>Dyopedos porrectus</i> (Bate, 1857)	A	(35 days)	maternal mud whip	Stephan, 1980
<i>Dyopedos monacanthus</i> Metzger, 1875	A	(35 days)	maternal mud whip	Stephan, 1980
<i>Dyopedos monacanthus</i>	A	10–20 days	maternal mud whip	this study
<i>Arcturus baffini</i> (Sabine, 1824)	I	(>4 weeks)	maternal body	Svavarsson and Davidsdottir, 1995
<i>Arcturus ulbani</i> Gurjanova, 1933	I	not known	maternal body	Kussakin, 1982
<i>Arcturus hastiger</i> Richardson, 1909	I	not known	maternal body	Zoological Museum, St. Petersburg
<i>Arcturus setosus</i> Gurjanova, 1933	I	not known	maternal body	Kussakin, 1982
<i>Arcturus crassispinis</i> Richardson, 1909	I	not known	maternal body	Kussakin, 1982
<i>Arcturus granulatus</i> Richardson, 1909	I	not known	maternal body	Kussakin, 1982
<i>Astacilla longicornis</i> (Sowerby, 1806)	I	not known	maternal body	Sars, 1899; Kussakin, 1982
TUBE-/BURROW-DWELLING FORMS				
<i>Phronima sedentaria</i> (Forskål, 1775)	A	≥10 days	maternal salp	Richter, 1978a
<i>Parajassa pelagica</i> (Leach, 1814)	A	not known	parental nest	Bate, 1862
<i>Jassa stauderi</i> Conlan, 1990	A	not known	maternal tube	Conlan, 1990; C. Staude, personal communication
<i>Peramphithoe stypotrupetes</i> Conlan and Chess, 1992	A	(weeks)	parental burrow	Conlan and Chess, 1992
<i>Siphonoecetes dellavallei</i> Stebbing, 1899	A	(weeks)	paternal dwelling	Richter, 1978b
<i>Lembo websteri</i> Bate, 1856	A	1–7 days	maternal burrow	Shillaker and Moore, 1987
<i>Corophium bonnellii</i> (Milne Edwards, 1830)	A	minutes	maternal burrow	Shillaker and Moore, 1987
<i>Corophium volutator</i> (Pallas, 1766)	A	(days)	maternal burrow	Thamdrup, 1935; Watkin, 1947
<i>Corophium arenarium</i> Crawford, 1937	A	(days)	maternal burrow	Crawford, 1937
<i>Leptocheirus pilosus</i> Zaddach, 1844	A	(days–weeks)	maternal tube	Goodhart, 1939
<i>Leptocheirus pinguis</i> (Stimpson, 1853)	A	40–60 days	maternal burrow	this study
<i>Casco bigelowi</i> (Blake, 1929)	A	80–120 days	maternal burrow	this study
<i>Leucothoe spinicarpa</i> (Abildgaard, 1789)	A	not known	parental tunicate	own observations
<i>Metopa glacialis</i> Krøyer, 1842	A	not known	parental bivalve	Vader and Beehler, 1983
<i>Tanais cavolinii</i> Milne Edwards, 1829	T	not known	maternal tube	Johnson and Attramadal, 1982
<i>Heterotanais oerstedii</i> Krøyer, 1842	T	not known	maternal tube	Bückle-Ramirez, 1965
<i>Nematotanais mirabilis</i> Bird and Holdich, 1985	T	not known	maternal tube	Bird and Holdich, 1985
<i>Mirandotanais vorax</i> Sieg, 1984	T	not known	maternal tube	Sieg, 1986
<i>Langitanais willemoessi</i> (Studer, 1883)	T	not known	maternal “nest”	Shino, 1978
<i>Leptochelia dubia</i> (Krøyer, 1842)	T	not known	maternal tube	Mendoza, 1982
<i>Edotea magellanica</i> Cunningham, 1871	I	not known	maternal bivalve	Gonzalez and Jaramillo, 1991
<i>Echinothambema</i> , undescribed new species	I	not known	maternal tube	Wolff, 1976
<i>Sphaeroma terebrans</i> Bate, 1866	I	(days–weeks)	maternal burrow	Messana <i>et al.</i> 1994; own observations

adult size), while others may reach about one-third adult size during extended parental care. In tube-/burrow-dwelling species, the number of juveniles does not appear to decline steadily, but rather in discrete pulses. In *L. pinguis*, juveniles emerge in large numbers after molting events. Immediately after molting, juveniles grow substantially and occupy more space in the burrow of the parent. Subsequently, competition for space may force some juveniles to leave the parental burrow. This indicates that increasing space requirements can also affect the duration of extended parental care in tube-/burrow-dwelling species. Female *C. bigelowi* expand their burrows while they care for their offspring (Thiel *et al.*, 1997; Thiel, 1997b), thereby increasing the available space for the female-offspring group. It is not known whether space becomes limiting in these extensive burrow systems as the size of the juveniles increases, or whether other factors affect the duration of extended parental care in *C. bigelowi*.

The availability of a safe, stable, and possibly expandable dwelling for the offspring or the lack thereof thus affects the duration of parental care in tube-/burrow-dwelling peracarids. If burrows of parental peracarids are frequently destroyed by physical or biological processes, parents and their offspring may be easily separated, thus limiting the potential for and the duration of extended parental care. This may be a reason why so little attention has been given to extended parental care in species of *Corophium* (for the only exception, see Flach, 1992, 1996). In dense assemblages, burrowing activity of conspecifics may frequently destroy female burrows, thereby limiting the duration of extended parental care at an early stage. Extended parental care may last longer and be of more importance when abundances of *Corophium* spp. are low.

Other factors, such as availability of food, may affect the duration of extended parental care, but too little is known to speculate on its effects. It should be noted, however, that the three amphipod species examined in this study occur in an area with high standing stock of microphytobenthos, which represents a major food resource for these amphipods. Extended parental care may be more prevalent in environments with high and predictable food resources (Thiel, 1997d).

Predation is another important factor af-

fecting the success of extended parental care, but the effects of predation on this reproductive strategy probably differ substantially between epibenthic and tube-/burrow-dwelling species. In epibenthic peracarids, parent-offspring groups might be more susceptible to fish predators than single individuals. Caine (1991) found that large caprellids are more susceptible to fish predation than are small ones (see also Edgar and Aoki, 1993), and juveniles of epibenthic species may have a better chance of surviving away from their parents. Endobenthic macrofauna is very susceptible to predation, and small individuals that can build only shallow burrows are usually more susceptible than larger ones (Reise, 1985; Thiel, 1997e; Zaklan and Ydenberg, 1997). Therefore, it may be advantageous for juveniles to remain in the deep burrows of their parents for extended time periods.

Evolution of Extended Parental Care and Advanced Social Behavior in Marine Peracarids

Among peracarid crustaceans, there is a very high potential for the evolution of extended parental care, since parent individuals are present at the time when juveniles are released from the marsupium. Extended parental care for small juveniles can substantially improve the reproductive success of some species by positively affecting juvenile growth or survival (Aoki, 1997; Thiel, 1997b). The compilation of observations from the literature (e.g., Table 1; Thiel *et al.*, 1997) reveals that extended parental care is not uncommon in marine peracarids, and it is likely that additional species will be found to engage in this form of reproduction.

Persisting parent-offspring groups comprising parents, small juveniles, and mature siblings have not yet been reported for marine peracarids. While the evolution of extended parental care may be favored in stressful environments (Wilson, 1971, 1975; Clutton-Brock, 1991), such as intertidal or shallow subtidal soft-bottoms, it appears that these environments do not permit a long-lasting coexistence of siblings. Ecological constraints, such as habitat stability, predation, disturbance, and competition probably impede the existence of stable dwellings in coastal soft-bottoms, an important prerequisite for long-lasting group assemblages. I hypothesize that the evolution of advanced social behavior is

limited to dwellings that are stable enough to provide protection from predation and disturbance and simultaneously provide predictable food resources for inhabitants. Marine dwellings that fulfill these requirements are sponges, tunicates, bivalves, mangrove roots, wood, or other biotic microhabitats. If these biotic microhabitats exist for sufficiently long time-periods, they may provide a suitable environment for long-lasting parental care. When the lifetime of their biotic microhabitat substantially exceeds the lifetime of an inhabitant that engages in extended parental care, we may expect to find overlapping generations and advanced social behavior (see, e.g., Duffy, 1996). Thus, although the potential for extended parental care is high in marine peracarids, advanced social behavior will most likely be limited to species that are inhabitants of stable, long-lived, biotic microhabitats (e.g., leucothoid and anamixid amphipods).

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