



Extended parental care in marine amphipods II. Maternal protection of juveniles from predation

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Abstract

Many terrestrial invertebrate parents effectively protect their offspring from predation. In this study, I examined whether marine amphipods that engage in extended parental care are able to provide protection from predation for their offspring. Two species, *Leptocheirus pinguis* and *Casco bigelowi*, host their juveniles in burrows while the epibenthic *Dyopededos monacanthus* cares for its offspring on mud whips. The size of amphipod dwellings was positively correlated with their body size, with large individuals of the burrow-dwelling *L. pinguis* and *C. bigelowi* inhabiting deeper burrows. The survival rates of adult females of *L. pinguis* and *C. bigelowi* exposed to sand shrimp (*Crangon septemspinosa*) predators were very high, while those of *D. monacanthus* females were relatively low. Juveniles of *L. pinguis* (filter-feeder), *C. bigelowi* (deposit-feeder) and *D. monacanthus* (suspension-feeder) in presence and absence of their mothers were exposed to predators. In the filter-feeding species *L. pinguis*, the effects of predators on juvenile survival was significantly reduced by maternal protection. In the experiment with *C. bigelowi*, juvenile survival was significantly affected by predation but not by maternal protection. Many *C. bigelowi* juveniles that left the burrows of their mothers during the experiment were severely affected by predation, but smaller juveniles that remained in the maternal burrows survived in the predator treatments. Juvenile *D. monacanthus* were significantly affected by predation but not by maternal care. Juvenile *D. monacanthus* that remained on the maternal mud whip during the experiment survived exposure to predators, while those that had already built their own mud whips did not. Despite the experiments for *C. bigelowi* and *D. monacanthus* revealed parental protection only at a closer look, it is concluded that extended parental care in all three amphipod species is an effective mechanism to protect juveniles from predation. The results indicate that maternal dwellings are important structures where juveniles find protection. While protection from predation may be one of the most important benefits of extended parental care in these amphipods from shallow subtidal soft-bottoms, juveniles may also benefit in other ways as is suggested by reports on maternal food-provisioning and grooming. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Parental care is characteristic of a variety of invertebrate species. While relatively little is known about the occurrence and details of parental care in marine invertebrates, extensive studies have been conducted on some groups of terrestrial and freshwater invertebrates. Parental care is found among leeches (Sawyer, 1971), scorpions (Polis, 1990), spiders (e.g. Whitehouse and Jackson, 1998), insects such as cockroaches (Nalepa and Bell, 1997), water bugs (Smith, 1997), beetles (Griffiths and Griffiths, 1983; Reid and Roitberg, 1994; Trumbo, 1994, 1995, 1997; Sato, 1997; Scott, 1998), and many hymenopterans (Wilson, 1975), land crabs (e.g. Diesel, 1989, 1992 Schubart et al., 1998) and isopods (Linsenmair and Linsenmair, 1971; Linsenmair, 1984). Parents of some terrestrial invertebrates provide for their offspring in relatively stable dwellings which they defend against conspecific and foreign intruders. These parental dwellings are important structures for the success of parental care (Wyatt, 1986; Polis, 1990; Reid and Roitberg, 1994; Crespi and Mound, 1997; Crespi et al., 1997; Halffter, 1997; Thorne, 1997; Trumbo, 1997). Yet parental care does not necessarily depend on the existence of a parental dwelling. In some water bugs, males carry developing eggs on their backs (Kight and Kruse, 1992), some scorpion females carry nymphs on their backs (Polis, 1990), and in many spiders females carry egg cocoons from which small spiderlings emerge (Foelix, 1996). In many cases, the presence and behavior of parents substantially enhances offspring survival (Tallamy and Denno, 1981; Reid and Roitberg, 1994; Halffter et al., 1996; Kirkendall et al., 1997; Nalepa and Bell, 1997; Eggert et al., 1998; Scott, 1998).

Parents may feed, groom, hide or defend their offspring (e.g. Wilson, 1975; Clutton-Brock, 1991). One of the most common parental behaviors among terrestrial invertebrates is defense of offspring against parasites, competitors and predators (Wilson, 1975; Tallamy and Wood, 1986). This defense of developing offspring can involve direct encounters between parents and potential invaders. For example, staphylinid beetles defend their larvae against parasites and predators (Wyatt and Foster, 1989a,b), parental burying beetles actively defend food resources against intra- and interspecific competitors (Scott, 1998), male pine engravers defend developing offspring against insect predators (Reid and Roitberg, 1994), spiders defend their brood against predators (Fink, 1984, 1986; Whitehouse and Jackson, 1998), and many hymenopterans chase away intruders much larger than themselves (Heinrich, 1979; Hölldobler and Wilson, 1990). Defense does not necessarily involve direct parent-invader interactions. Some parents avoid direct encounters by burying their developing brood deep in the soil (Halffter, 1997) or by hiding during the parental care period in unpalatable or unreachable dwellings (Crespi and Mound, 1997; Kirkendall et al., 1997).

Thus, terrestrial invertebrate parents achieve effective protection of their offspring by actively defending them against intruders or by hiding them from potential enemies. The question arises whether marine invertebrate parents can achieve similarly effective

protection for their offspring. Unfortunately, the simultaneous occurrence of parents and offspring is often the only indication for parental care among marine invertebrates. Parent–offspring associations occur among a wide variety of tube-dwelling polychaetes, small bivalves and gastropods, large numbers of echinoderm species, and many different crustacean species. Some observations have been made on food provisioning for offspring (Shillaker and Moore, 1987), ventilation of the offspring cradle by parents (Durchon, 1956; Ockelmann and Åkesson, 1990), and active defense of juveniles against intruders or predators (Stephan, 1980; Aoki and Kikuchi, 1991). However, the effects of these parental activities on offspring survival are not known.

The most advanced form of parental care among marine invertebrates is found in peracarid crustaceans such as amphipods and isopods. Parent amphipods and isopods may care for individual offspring for periods of weeks up to several months, and during these periods juveniles may reach more than half adult size (Thiel et al., 1997). While some amphipod parents have been observed to feed or groom their offspring (Stephan, 1980; Shillaker and Moore, 1987), protection from predation has been suspected as one of the most important benefits from parental care in marine amphipods and isopods (Thiel, 1998a). Peracarid crustaceans are very attractive prey items for a diverse armada of marine predators, and thus protective behaviors could be advantageous for them. Parent individuals may be able to protect their offspring at least against some of these predators. Similar to terrestrial invertebrates, two major forms of parental protection can be envisioned for marine peracarids: parents can actively defend offspring against predators, or they may provide indirect protection from predation by providing a safe offspring cradle. Active protection from predation appears likely for epibenthic amphipods that defend their offspring against aggressive conspecifics, i.e. predators of similar sizes as the parents, but much larger than small offspring (e.g. Stephan, 1980; Aoki and Kikuchi, 1991). In endobenthic burrow- or tube-dwelling amphipods and isopods, parents may build an offspring cradle that is not accessible for many marine predators such as fishes and decapods (Conlan and Chess, 1992; Thiel et al., 1997).

Three amphipod species, *Leptocheirus pinguis* (Stimpson 1853), *Casco bigelowi* (Blake 1929) and *Dyopedos monacanthus* (Metzger 1875), that were found to engage in extended parental care, inhabit shallow subtidal soft-bottoms along the Gulf of Maine (Thiel et al., 1997; Thiel, 1997a,b). During the summer and fall, large numbers of epibenthic predators such as fish and decapods are active and abundant on these shallow subtidal soft-bottoms (Embich, 1973; Corey, 1981; Hacunda, 1981; Thiel, 1997a), and soft-bottom dwelling amphipods such as *L. pinguis* are among their most preferred prey items (Tyler, 1972; Hacunda, 1981). Thus, extended parental care in these amphipods may provide protection for small offspring against some of these predators (Thiel et al., 1997). Offspring of some marine amphipods with extended parental care can also survive without parents when kept in experimental conditions without predators (Aoki, 1997; Thiel, 1998a). Previous experiments have demonstrated that in the burrow-dwelling species *L. pinguis* and *C. bigelowi*, survival of orphan juveniles can be very high in a predator-free environment (Thiel, 1998a). In the epibenthic species *D. monacanthus* that lives on self-constructed mud whips, survival of orphan juveniles is comparatively low, even in predator-free environments (Thiel, 1998a). Orphan juveniles of all three amphipod species were very susceptible to epibenthic predators *Crangon*

septemspinosa, and either were preyed upon or emigrated from experimental trays during exposure to these predators (Thiel, 1998a).

In the present study, I examined whether maternal care can provide effective protection from epibenthic predation in these soft-bottom dwelling amphipods.

2. Materials and methods

2.1. Amphipod dwellings

The quality of a parental dwelling can be an important factor determining the success of parental care (e.g. Wyatt, 1986). Herein, I used the depth of the amphipod burrows (for *Leptocheirus pinguis* and *Casco bigelowi*) as a measure for the quality of an amphipod dwelling. This is based on the assumption that individuals with deep burrows are out of the reach of many surface-foraging predators (see e.g. Zwarts and Wanink, 1989; Zaklan and Ydenberg, 1997). For the epibenthic amphipod *D. monacanthus*, previous studies have suggested that space for offspring may become limiting on the mud whips (Thiel, 1997b), and therefore the length of a mud whip can be used to reflect whether an individual female can host many offspring on its dwelling.

Individual burrows of *Leptocheirus pinguis* and *Casco bigelowi* (revealing their existence by the burrow openings) were located in the field and carefully excavated using both hands to remove a sediment plug containing the burrow. Upon retrieval, the sediment plug was gently broken, the burrow depth measured with a ruler and the inhabitants of the burrow collected for later measurements. Burrows of *Leptocheirus pinguis* and their inhabitants were sampled on 24 May 1997 (i.e. during their main reproductive period) at which time parental females (with juveniles in their burrows) could be distinguished from non-parental amphipods (females without juveniles, males and subadults). Burrows of *Casco bigelowi* and their inhabitants were sampled on 7 April 1997, i.e. after their reproductive period, and thus all individuals of this species were non-parental (Thiel, 1997a). For the epibenthic amphipod *Dyopodos monacanthus*, mud whips and their inhabitants were collected monthly between July 1995 and July 1997; those data are presented elsewhere (Thiel, 1998b), but will be referred to in the discussion section of this study.

2.2. Experiments

Reproductive females were introduced to small trays (900 cm²) in the flowing seawater laboratory (for detailed description of tray set-up see Thiel, 1998a). The experiments were set up in a 2 × 2 factorial design. Experiments were conducted separately for each of the three amphipod species. One group of juveniles was left with their mothers while another group was experimentally separated from their mothers. These two groups (with and without mothers) were subdivided again and one half of each group was exposed to predators while the other half remained predator free.

Ovigerous females *Leptocheirus pinguis* and *Casco bigelowi* were collected from Lowes Cove, Maine. Eight females were introduced to each of 12 trays that contained a

10-cm thick mud layer of natural sediments from the amphipod habitat, while another six mud-filled trays remained without amphipods (Fig. 1). Females built burrows in the trays in which their offspring remained after emerging from the brood pouch. Just before the first juveniles left their mothers' burrows, the contents of six trays that contained amphipods were sieved over a 500- μ m screen, and all juveniles from one tray were introduced to one of the amphipod-free trays. These juveniles were allowed to establish their burrows in these trays for a few days before a screen preventing amphipod emigration was removed from the outflow.

For *Dyopedos monacanthus*, parental females (with juveniles on their mud whips) were transplanted from the field into trays that were filled with a thin layer of mud (3 cm). To each of 12 trays, five parental females were planted together with their mud whips. Both females and juveniles held tightly to the mud whip during transplantation. Immediately before the introduction of predators, females from six trays were carefully removed from their mud whips, so that only juveniles remained on their mothers' mud whips. In the other six trays, females were left on their mud whips. Thus, in this

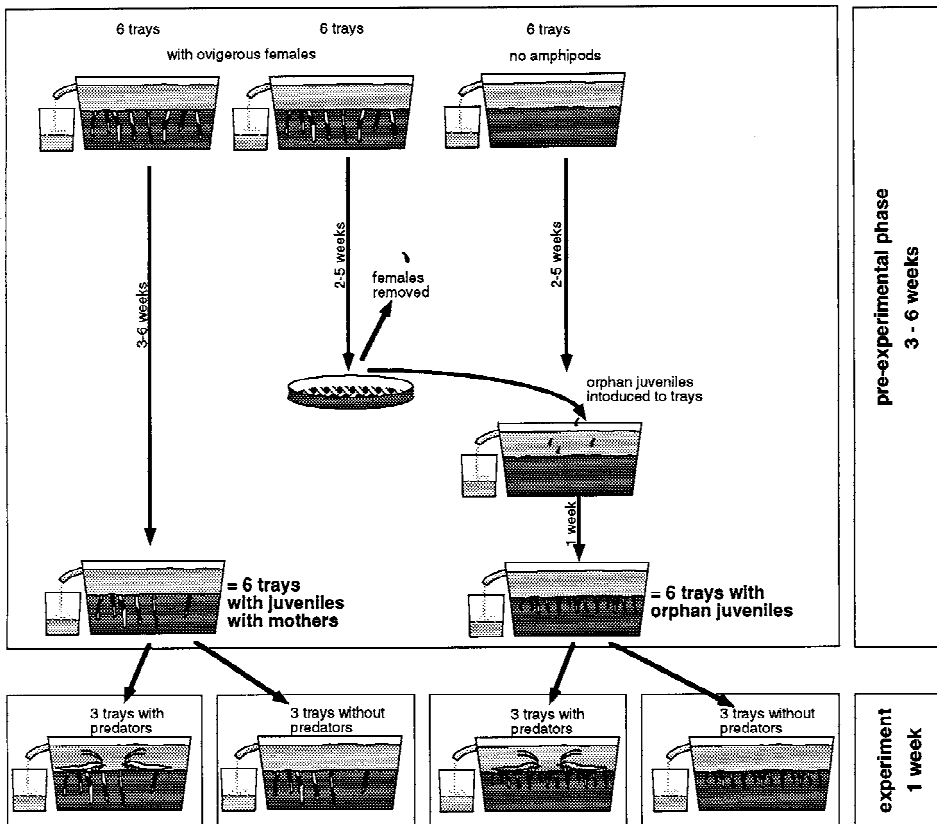


Fig. 1. Schematic set-up of the preparatory treatment of the trays for the two burrow-dwelling amphipods *Leptocheirus pinguis* and *Casco bigelowi*.

experiment orphan juveniles were not removed from their mothers' mud whips as in previous experiments (compare Thiel, 1998a) but were granted the privilege to reside on their mothers' mud whip, albeit without their mother. As in the trays where mothers were left on their mud whips many of these females gave birth to a new brood of small juveniles during the experiment, all new-born juveniles (< 1.2 mm) were excluded from the analysis (newly hatched juveniles typically are 0.8–1.2 mm long; Thiel, 1997b).

In previous experiments, the sand shrimp *Crangon septemspinosa* was found to prey intensively on all three amphipod species (Thiel, 1998a). The sand shrimps were used in the experiments at densities that correspond to their abundance in the natural amphipod habitat during the summer months (Thiel, 1997a). At the beginning of the experimental period, predators (10 sand shrimp *C. septemspinosa* per tray) were introduced to three trays in which juvenile amphipods were with mothers and to three trays in which juveniles were separated from mothers, while the three remaining trays of each group were left predator free (Fig. 1). Following predator addition, all emigrants were collected and preserved daily. The experiment was terminated 7 days after the introduction of the predators and the contents of each tray were sieved over a 500- μ m sieve. For *D. monacanthus*, the maternal mud whips with all their inhabitants were collected and preserved individually from each tray before sieving the remaining contents of the trays.

The numbers of juveniles emigrating during the experiment, of juveniles remaining in the trays as residents (for *D. monacanthus* separated in those on own and those on maternal mud whips), and the total number of surviving juveniles (emigrants + residents) were used to examine the effects of maternal care and predation on juvenile survival. A two-way ANOVA was used after $\log(x + 1)$ transformation of the data.

The females that had been separated from their offspring were used for an experiment that was designed to examine the survival of large adult amphipods. All females taken from 6 trays were introduced to three experimental trays, so that each tray contained 16 (*L. pinguis*, *C. bigelovi*) or 10 (*D. monacanthus*) females, respectively. One week after the introduction of the females, 10 sand shrimp predators were introduced to each tray and left therein for 7 days. The set-up and treatment of each tray was the same as in the other experiments.

2.3. Amphipod measurements

All amphipods were preserved in 5%-formalin, and later transferred to 70% alcohol. The length of the amphipods was measured along their dorsal surface from the rostrum to the telson, using a computer-based image analysis system.

3. Results

3.1. Amphipod dwellings

There was a positive correlation between the length of the amphipods and the depth of their burrows (Fig. 2). Parental females *Leptocheirus pinguis* were relatively large and

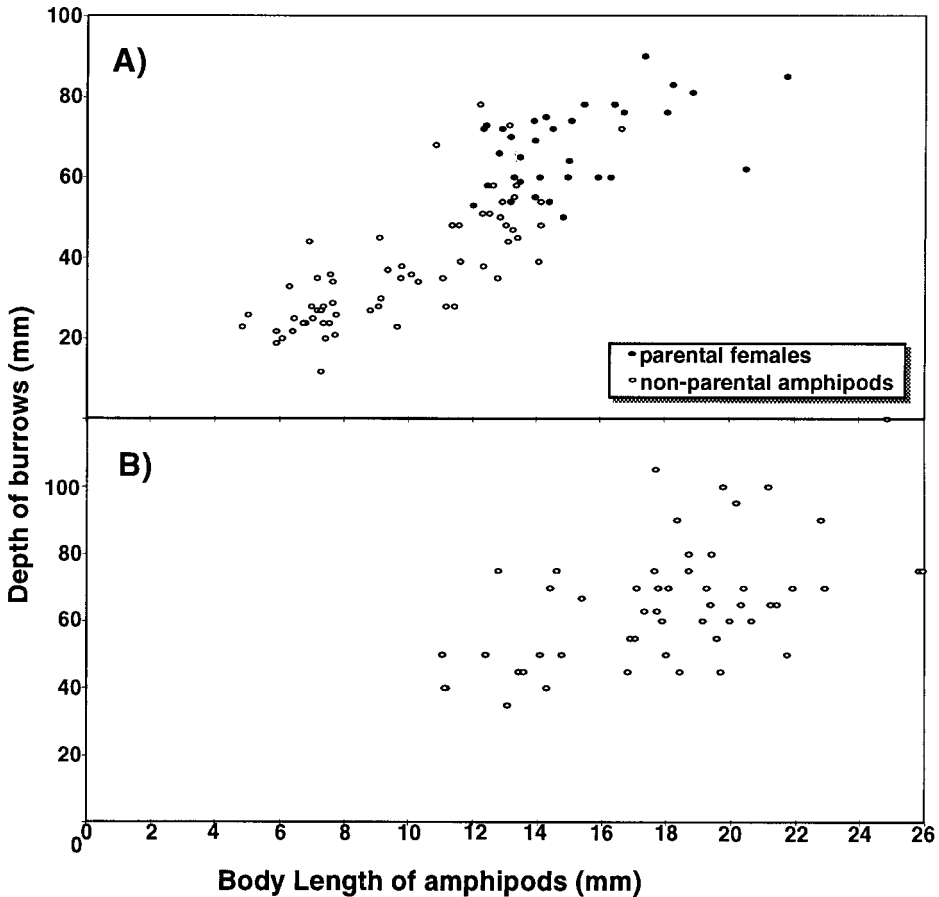


Fig. 2. Relationship between body length of amphipods and the depth of their burrows for (A) *Leptocheirus pinguis* and (B) *Casco bigelowi*; *L. pinguis* were collected on 24 May 1997 (during their spring reproductive period) and *C. bigelowi* on 7 April 1997 (after their annual reproductive period).

inhabited deep burrows. For both parental females and non-parental amphipods, burrow depth was correlated with the length of the amphipods ($y = -4.805 + 4.53x$; where y is burrow depth in mm and x is amphipod body length in mm; $R^2 = 0.726$; $P \leq 0.05$; Fig. 2A). There was a similar correlation between the length of the amphipods and the depths of their burrows for *Casco bigelowi* ($y = 15.829 + 2.758x$; where y is burrow depth in mm and x is amphipod body length in mm; $R^2 = 0.297$; $P \leq 0.05$; Fig. 2B). Thus, in both *L. pinguis* and *C. bigelowi* large (and potentially parental female) amphipods occupied deep burrows.

3.2. Adult survival with predators

Adult females *Leptocheirus pinguis* and *Casco bigelowi* had very high survival rates when exposed to predators *Crangon septemspinosa* (Fig. 3). During a 7-day period, no

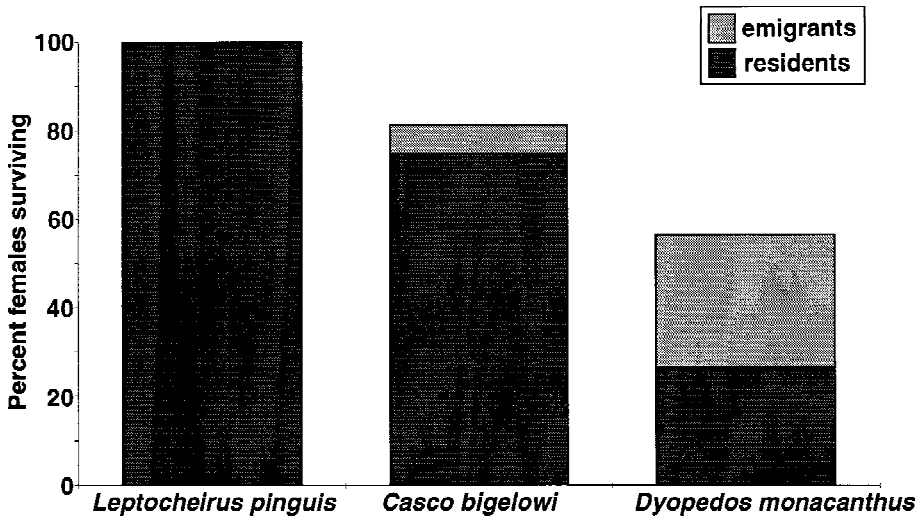


Fig. 3. Mean percentage of adult females *Leptocheirus pinguis*, *Casco bigelowi*, and *Dyopodos monacanthus* surviving in trays with predators; $n = 3$ trays per amphipod species, for *L. pinguis* and *C. bigelowi*, $n = 16$ females per tray, for *D. monacanthus*, $n = 10$ females per tray; for the experimental period of 7 days each tray contained 10 sand shrimp *Crangon septempinosus*.

L. pinguis females disappeared from experimental trays, while about 20% of the introduced *C. bigelowi* females disappeared and about 5% emigrated from the trays during exposure to predators (Fig. 3). About 45% of all *Dyopodos monacanthus* females disappeared from the trays, 30% emigrated, and only 25% survived as residents in the experimental trays (Fig. 3). Female *D. monacanthus* that survived in the trays either had relatively long mud whips or had built their whips at the wall of the trays several cm above the sediment layer.

3.3. Effects of maternal care and predation on the survival of juvenile amphipods

In all three amphipod species, predation had strong effects on the behavior and survival of juveniles that had been separated from their mothers (Fig. 4, Table 1, Table 2, Table 3). In the burrow-living species *Leptocheirus pinguis*, maternal care significantly enhanced juvenile survival (Fig. 4A, Table 1). For resident, emigrant and total surviving juvenile *L. pinguis*, there was a significant interaction between the factors 'mothers' and 'predators' (Table 1), indicating that the effects of predators on juvenile survival are significantly reduced by the presence of mothers. Juveniles that enjoyed maternal care emigrated in much smaller numbers from the predator trays than juveniles that had been separated from their mothers (Fig. 4A). In the other burrow-dwelling species, *Casco bigelowi*, no significant effect of maternal care was detected in the experiments (Fig. 4B, Table 2). Juveniles that were in trays with their mothers remained in slightly higher numbers in the predator trays than juveniles that had been separated from their mothers (Fig. 4B). In the epibenthic amphipod *Dyopodos monacanthus*, no

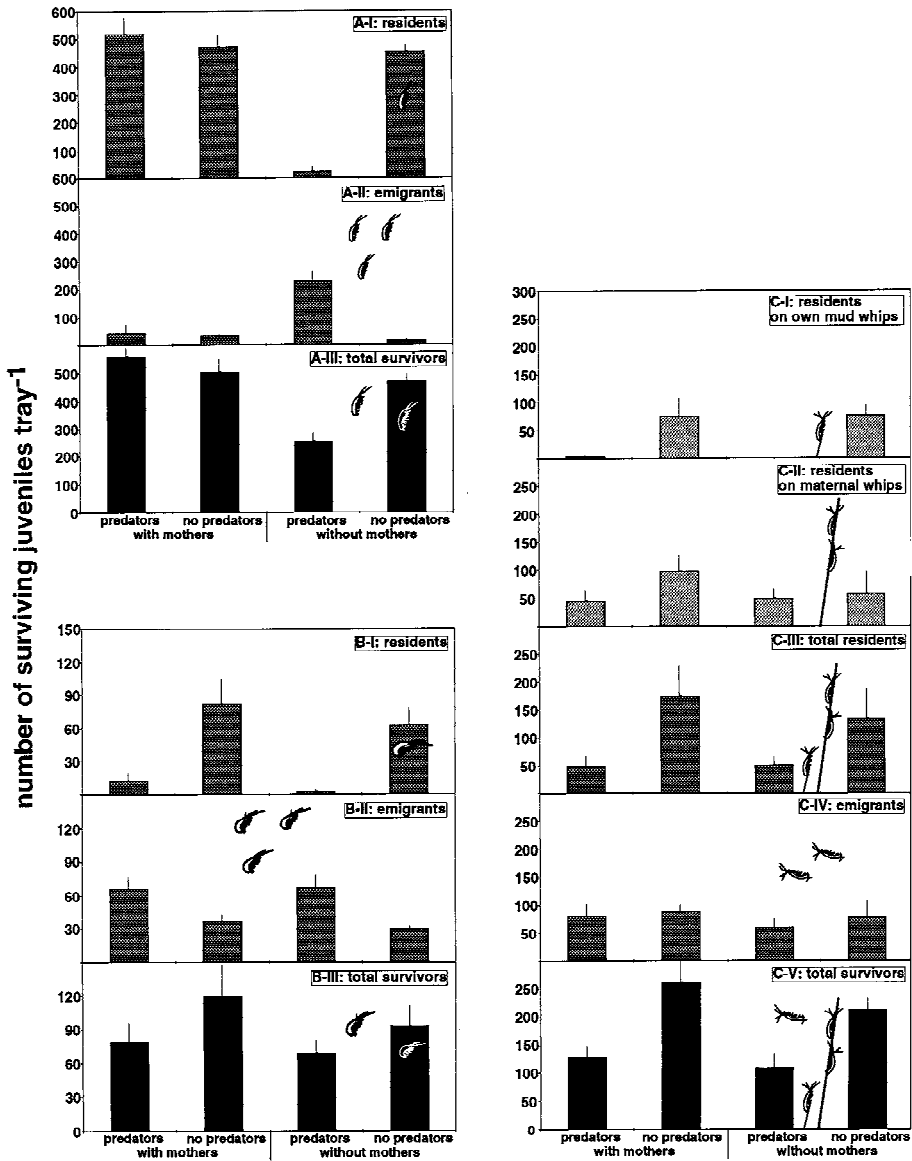


Fig. 4. Mean numbers of juvenile (A) *Leptocheirus pinguis*, (B) *Casco bigelowi*, and (C) *Dyopodos monacanthus* surviving in trays with and without predators; $n = 3$ trays per treatment; for *L. pinguis* and *C. bigelowi*, $n = 8$ ovigerous females per tray, for *D. monacanthus*, $n = 5$ parental females per tray; for the experimental period of 7 days the predator trays contained 10 sand shrimp *Crangon septemspinosus* each; for further details see text and for statistical analysis see Tables 1–3.

Table 1

Two-way ANOVA of numbers of juvenile *Leptocheirus pinguis* residents, emigrants, total survivors with the factors predation and maternal care

Independent variable	Df	MS	F value	P
Dependent variable: juvenile residents at end of experiment				
Mothers (yes/no)	1	1.882	20.664	0.0019*
Predators (yes/no)	1	1.647	18.080	0.0028*
Interaction (mothers × predators)	1	1.816	19.935	0.0021*
Residual	8	0.091		
Dependent variable: juvenile emigrants at end of experiment				
Mothers (yes/no)	1	0.263	2.855	0.1296
Predators (yes/no)	1	0.834	9.059	0.0168*
Interaction (mothers × predators)	1	1.201	13.043	0.0069*
Residual	8	0.092		
Dependent variable: juvenile survivors at end of experiment				
Mothers (yes/no)	1	0.106	28.073	0.0007*
Predators (yes/no)	1	0.037	9.929	0.0136*
Interaction (mothers × predators)	1	0.075	19.959	0.0021*
Residual	8	0.004		

* $p \leq 0.05$

significant effect of maternal care was detected in the experiments (Fig. 4C, Table 3). It should be noted that predators had no significant effect on the number of juveniles remaining on their mothers' mud whips at the end of the experiment despite the absence of mothers from one half of the experiments (Fig. 4C-II, Table 3).

Table 2

Two-way ANOVA of numbers of juvenile *Casco bigelowi* residents, emigrants, total survivors with the factors predation and maternal care

Independent variable	Df	MS	F value	P
Dependent variable: juvenile residents at end of experiment				
Mothers (yes/no)	1	0.236	1.118	0.3212
Predators (yes/no)	1	4.387	20.790	0.0019*
Interaction (mothers × predators)	1	0.089	0.4205	0.5350
Residual	8	0.211		
Dependent variable: juvenile emigrants at end of experiment				
Mothers (yes/no)	1	0.005	0.339	0.5767
Predators (yes/no)	1	0.250	18.598	0.0026*
Interaction (mothers × predators)	1	0.005	0.398	0.5459
Residual	8	0.013		
Dependent variable: juvenile survivors at end of experiment				
Mothers (yes/no)	1	0.106	0.767	0.4067
Predators (yes/no)	1	0.064	3.074	0.1176
Interaction (mothers × predators)	1	0.002	0.106	0.7529
Residual	8	0.021		

* $P \leq 0.05$.

Table 3

Two-way ANOVA of numbers of juvenile *Dyopodos monacanthus* residents, emigrants, total survivors, and residents on own and maternal mud whips with the factors predation and maternal care

Independent variable	Df	MS	F value	P
Dependent variable: juvenile residents at end of experiment				
Mothers (yes/no)	1	0.004	0.035	0.8564
Predators (yes/no)	1	0.763	6.493	0.0343*
Interaction (mothers × predators)	1	0.020	0.172	0.6894
Residual	8	0.118		
Dependent variable: juvenile emigrants at end of experiment				
Mothers (yes/no)	1	0.057	0.773	0.4050
Predators (yes/no)	1	0.011	0.151	0.7082
Interaction (mothers × predators)	1	0.001	0.008	0.9316
Residual	8	0.074		
Dependent variable: juvenile survivors at end of experiment				
Mothers (yes/no)	1	0.018	1.069	0.3314
Predators (yes/no)	1	0.278	16.136	0.0039*
Interaction (mothers × predators)	1	0.001	0.001	0.9755
Residual	8	0.017		
Dependent variable: juv. resdts. on own whips at end of experiment				
Mothers (yes/no)	1	0.060	0.434	0.5283
Predators (yes/no)	1	6.723	48.845	0.0001*
Interaction (mothers × predators)	1	0.203	1.476	0.2591
Residual	8	0.138		
Dependent variable: juv. resdts. on mat. whips at end of experiment				
Mothers (yes/no)	1	0.077	0.538	0.4841
Predators (yes/no)	1	0.075	0.524	0.4898
Interaction (mothers × predators)	1	0.159	1.103	0.3242
Residual	8	0.144		

* $P \leq 0.05$.

3.4. Sizes of juvenile amphipods surviving in trays

In all experiments, the juveniles of the three amphipod species comprised a wide range of sizes. For each amphipod species, the smallest juveniles found at the end of the experiments were of sizes that usually enjoy maternal care in the field, while the largest juveniles were of sizes that can be found on their own in the field (Fig. 5).

In *Leptocheirus pinguis*, only juveniles that had been separated from their mothers and were exposed to predators emigrated in large numbers from the trays (Fig. 5A-III). All sizes of juveniles emigrated from these trays, indicating that juveniles from 1–10 mm in size are very susceptible to predation (Fig. 5A-III). Juveniles of similar sizes which still enjoyed maternal care remained in large numbers in the predator trays (Fig. 5A-I).

In *Casco bigelowi*, many juveniles emigrated from the trays (Fig. 5B), but in the predator-free trays juveniles of all sizes remained as residents in the trays (Fig. 5B-II and Fig. 5B-IV). When exposed to predators, only very few juveniles remained in the trays after 7 days (Fig. 5B-I and Fig. 5B-III). In trays in which juveniles were together with their mothers, some small juveniles remained as residents in the predator trays (Fig.

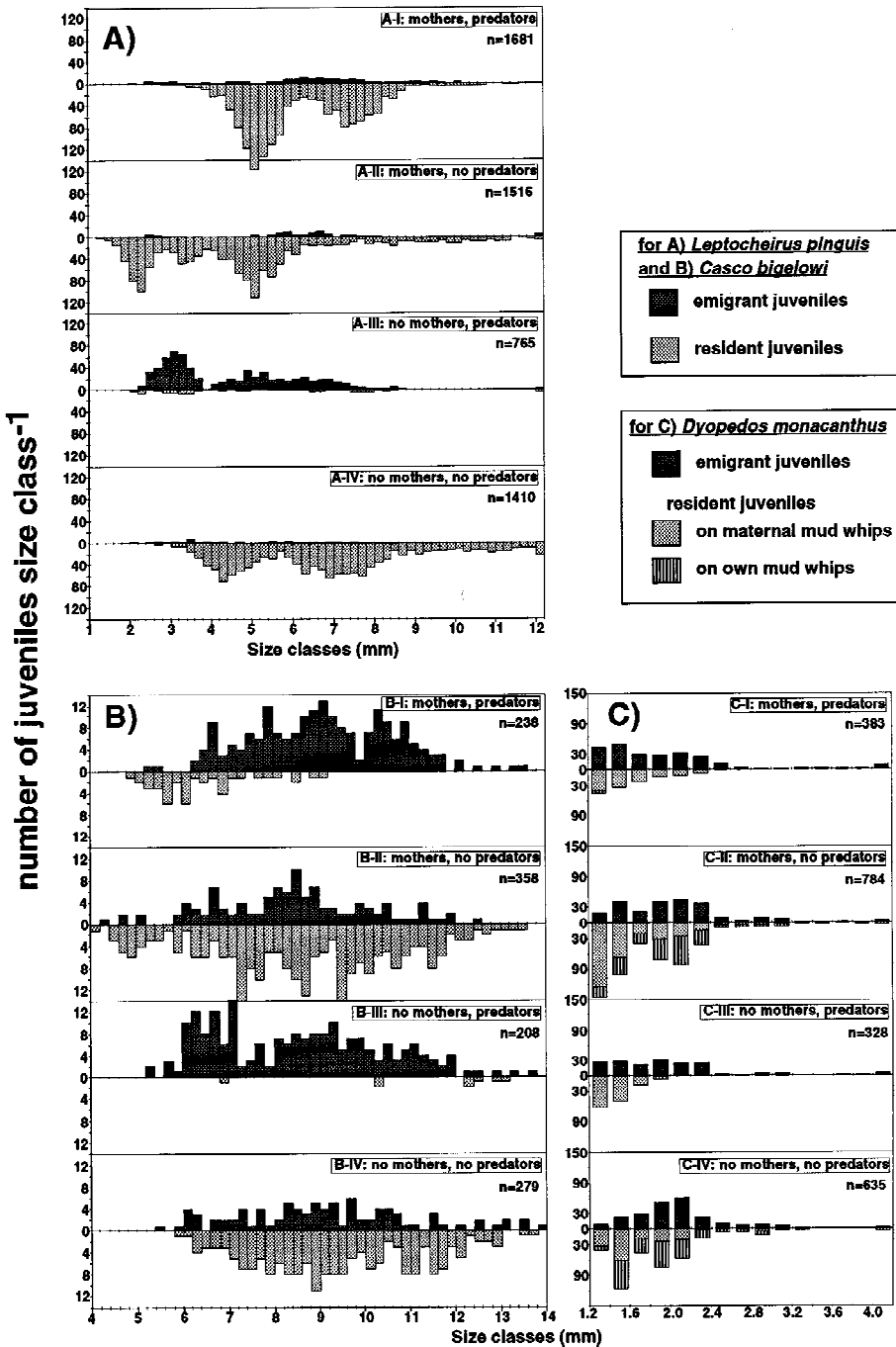


Fig. 5. Size frequency distribution of juvenile amphipods (A) *Leptocheirus pinguis*, (B) *Casco bigelowi* and (C) *Dyopedes monacanthus* surviving in trays with and without predators; all juveniles from the three replicate trays for each treatment were pooled; n = number of total survivors (residents + emigrants) for each n = 3 trays from each treatment.

5B-I). In trays with orphan juveniles, a few large juveniles remained as residents in the predator trays (Fig. 5B-III).

In *Dyopedos monacanthus*, the numbers and sizes of juveniles emigrating from trays are relatively similar in all the different treatments (Fig. 5C). Also, the numbers and sizes of juveniles remaining on maternal mud whips are very similar among the different treatments. In contrast, many juvenile *D. monacanthus* were found on their own mud whips in trays without predators, but not in predator trays (Fig. 5C).

4. Discussion

The experimental results have shown that maternal care can provide protection from predation for juvenile amphipods. However, the maternal effects as revealed by the present experiments varied among the three amphipod species. In the following, I first discuss the potential reasons for this variation in maternal effects. In the second section of the discussion, I examine how amphipods may provide protection for their offspring, and in which other ways marine invertebrates that engage in parental care may enhance the survival of their offspring.

4.1. Amphipod dwellings and maternal protection from predation

Large individuals of *Leptocheirus pinguis* and *Casco bigelowi* inhabited deeper burrows than small or medium-sized individuals. Macrofaunal organisms that inhabit deeper sediment layers are usually less susceptible to epibenthic predators than those that live close to the sediment surface (Reise, 1985; Zaklan and Ydenberg, 1997). Thus, large parental females *L. pinguis* and *C. bigelowi* are well out of the reach of common epibenthic predators such as shrimp and fish. Most parental females have sizes that allow them to build burrows >50 mm deep, providing an optimal shelter against many epibenthic predators. Both *L. pinguis* and *C. bigelowi* spend most of their time at the bottom of their burrows where they feed (Thiel et al., 1997). They rarely come to the sediment surface to maintain their burrows, and are thus relatively safe from most epibenthic predators. Hosting offspring in these deep burrows would thus provide optimal protection for small juveniles against these predators.

The *L. pinguis* experiment strongly demonstrated that mothers are able to provide effective protection from predation. Many more juveniles survived predator additions in their mothers' burrows than in their own burrows. However, there was no significant maternal effect revealed in the *C. bigelowi* experiment. This does not necessarily mean that female *C. bigelowi* cannot provide protection for their offspring, but may rather reflect problems during the experiment. The most important precondition for this experiment was to be able to compare the survival of orphan juveniles with that of juveniles still experiencing parental care. However, many juvenile *C. bigelowi* were leaving their mothers' burrows and had begun establishing their own burrows just before and during the experiment (see also large numbers of emigrants in all treatments, Fig. 4). Thus, during the experimental period there were only a few small juveniles left that were

still enjoying parental care while predators were in the trays. A closer look at the sizes of juveniles *C. bigelowi* that survived as residents in trays with mothers (Fig. 5B-I) revealed that these resident juveniles were substantially smaller (5–7 mm) than the emigrating juveniles (8–12 mm in length). These small juveniles survived the predation experiments safely in the deep burrows of their mothers while their conspecifics that had already built their own burrows suffered from heavy predation and died or emigrated during exposure to predators. A few very large orphan juveniles also remained as residents in the predator treatments, indicating that they were already able to build deep burrows safe enough from sand shrimp predators. Under natural conditions, large size classes of *C. bigelowi* juveniles (up to 16 mm) can be found in maternal burrows (Thiel, 1997a). Laboratory conditions might have caused juveniles to leave their mothers' burrows prematurely. Thereby higher numbers and more vulnerable individuals were subjected to predation than it would naturally be the case. Hence, the protective effect of maternal care in relation to predation is probably underestimated by the *Casco*-experiment.

Unexpectedly, large numbers *Dyopodos monacanthus* survived the predator additions, even in trays from which mothers were removed. This result is surprising since in previous experiments on juvenile survival, most juveniles died or emigrated from predator trays (see Thiel, 1998a). While in the previous study orphan juveniles had been forced to build their own mud whips (Thiel, 1998a), in the present study they were left on the maternal mud whip (albeit without mother) where many of them remained and survived the presence of predators. This result indicates the importance of maternal mud whips, which are significantly longer than mud whips of non-maternal *D. monacanthus* (Thiel, 1998b). Thus, long maternal mud whips may not only represent a tool to lift small juveniles high up in the benthic boundary layer (Thiel, 1997b), but also to keep them out of the immediate foraging range of important benthic predators such as sand shrimp. Supporting the latter interpretation are results by Ambrose and Irlandi (1992) who found that juvenile bivalves that were about 5 cm above the bottom had lower mortality rates than those at the bottom due to reduced predation effects at those heights above the bottom. Observations by Primavera (1997) also indicate that predators oriented towards benthic prey may overlook prey that hides on structures a short distance above the bottom. While life on a mud whip may render *D. monacanthus* and other podoceric amphipods extremely susceptible to fish predators (Stephan, 1980; Mattson and Cedhagen, 1989), it may provide some protection from true benthic predators such as nemertines, polychaetes and sand shrimp.

In this and in a previous laboratory study (Thiel, 1998a), many orphan juveniles survived predation by emigration. While this may be a useful option for small soft-bottom fauna to avoid the immediate risk of benthic predation (see also Ambrose, 1984; Thiel and Reise, 1993; Armonies, 1994), it may nevertheless expose these emigrants to water column predators. Swimming amphipods constitute an easy target for fish predators, as is indicated by their high frequency of occurrence in fish stomachs (Hacunda, 1981; Mahon and Neilson, 1987). The overall survival chances of juvenile amphipods can be enhanced if risky emigration into the water column can be avoided, e.g. by parental protection against predation.

4.2. Protection of juveniles and other benefits of extended parental care in marine amphipods

Protection from predation appears to be one of the major benefits that small juveniles gain from extended parental care. This effect is particularly pronounced in tube- and burrow-dwelling species such as *L. pinguis* and *C. bigelowi*. Many more tube- and burrow-dwelling amphipods and isopods are known, and many of them occur in coastal habitats where predation pressure is often very high (e.g. Sheader, 1998). It would thus appear advantageous for these species to host their offspring in their burrows whenever possible. Indeed, a wide variety of other tube-/burrow-dwelling peracarids provide extended parental care for offspring (e.g. Thamdrup, 1935; Watkin, 1947; Johnson and Attramadal, 1982; Mendoza, 1982; Bird and Holdich, 1985; Shillaker and Moore, 1987; Messana et al., 1994), and it is not unlikely that other species will be found to engage in this reproductive behaviour in the future.

The present study indicates that successful protection of juveniles from predation is closely linked to parental dwellings. It is not known whether the construction of these parental dwellings constitutes a major cost to parental amphipods. Usually, individual *Dyopededos monacanthus* cling tightly to their mud whips indicating that the latter is an important resource for them. It is likely that the same is true for deep burrows of *L. pinguis* and *C. bigelowi*. Adults may compete for dwellings in the field, resulting in aggressive interactions among conspecifics (for *D. monacanthus*, e.g. Stephan, 1980; for tube- /burrow-dwelling peracarids, e.g. Shillaker and Moore, 1978; Borowsky, 1983). Thus, in species in which the dwelling represents a valuable resource, parents may also protect small juveniles against intraspecific aggression.

Another form of intrusion that amphipods (and other crustaceans) have to cope with is epibionts. These are frequently found growing on almost all exoskeletal surfaces of crustaceans and sophisticated grooming mechanisms have evolved in many long-lived crustaceans. Parental grooming of juveniles is reported from a variety of epibenthic amphipods with extended parental care (e.g. Stephan, 1980; Lim and Alexander, 1986; Aoki and Kikuchi, 1991), and it may substantially enhance the survival chances of these small juveniles. At present no experimental studies have examined the importance of parental grooming for the survival of juvenile amphipods or other peracarid crustaceans that usually enjoy parental care.

While protection against various intruders may be an important benefit of extended parental care in marine amphipods, the presence and activity of the parents may have other positive effects on offspring survival and growth. Results of an earlier study (Thiel, 1998a) showed that even in predator-free environments, small juvenile *D. monacanthus* could not survive on their own after being separated from their mothers' mud whips. In addition to protection from predation and intraspecific aggression, life on their mothers mud whip may enable small juveniles to acquire optimal food resources. For two caprellid amphipod species, *Caprella monoceros* Mayer 1890 and *C. scaura* Templeton 1836, Aoki (1997) showed that juveniles that experience maternal care have higher growth rates than conspecific juveniles without parental care. Increased growth rates in these two species may be a result of improved feeding conditions or active food

transfer from the mother to her offspring, as has been reported for other caprellid amphipods (e.g. Harrison, 1940). Parental provision of food resources for growing offspring has also been observed in other amphipod species with extended parental care (Richter, 1978; Shillaker and Moore, 1987). In the filter-feeding amphipod *Leptocheirus pinguis*, the female produces a strong current through her burrow, and juveniles may benefit from the pumping activity and efficiency of their mother. In the deposit-feeding amphipod *Casco bigelowi*, juveniles do not actively excavate consolidated sediments, but appear to rely on their mother to provide these resources (unpubl. laboratory observations). These examples indicate that active food provision for growing offspring may not be uncommon in marine amphipods with parental care. Juveniles that enjoy maternally provided food resources may grow faster than juveniles that have to acquire these resources without maternal assistance.

4.3. Conclusions

In marine amphipods, as in some terrestrial invertebrates, parental care can serve to protect developing offspring against predation. For the three amphipods examined in this study it was shown that the parental dwelling is an important requisite for effective parental care. Often, parent individuals increase the size of these dwellings, possibly in order to accommodate more offspring (see Chess, 1993) or to render it safer from potential intruders. Following the period of parental care, offspring may even inherit the parental dwelling, as is suspected for marine amphipods that inhabit ascidians (Thiel, 1999). Yet not all marine invertebrate parents care for their offspring in a dwelling (e.g. Aoki, 1997). While there is increasing evidence that parental care with (this study) or without a dwelling (Aoki, 1997) can improve the survival chances of juvenile amphipods, little is known about the behavioural interactions of parents and their offspring. Detailed studies on the behaviour of marine invertebrate parents will help to reveal whether protection against intruders is one of the major benefits that marine invertebrate juveniles gain from parental care, and whether other parental activities such as food-provisioning or grooming also improve the survival chances of their offspring.

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References

- Ambrose, Jr. W.G., 1984. Increased emigration of the amphipod *Rhepoxynius abronius* (Barnard) and the polychaete *Nephtys caeca* (Fabricius) in the presence of invertebrate predators. J. Exp. Mar. Biol. Ecol. 80, 67–75.
- Ambrose, Jr. W.G., Irlandi, E.A., 1992. Height of attachment on seagrass leads to trade-off between growth and survival in the bay scallop *Argopecten irradians*. Mar. Ecol. Prog. Ser. 90, 45–51.
- Aoki, M., 1997. Comparative study of mother-young association in caprellid amphipods: is maternal care effective?. J. Crust. Biol. 17, 447–458.
- Aoki, M., Kikuchi, T., 1991. Two types of maternal care for juveniles observed in *Caprella monoceros* Mayer, 1890 and *Caprella decipiens* Mayer, 1890 (Amphipoda: Caprellidae). Hydrobiologia 223, 229–237.
- Armonies, W., 1994. Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. Helgoländer Meeresunters. 48, 299–320.
- Bird, G.J., Holdich, D.M., 1985. A remarkable tubicolous tanaid (Crustacea: Tanaidacea) from the Rockall Trough. J. Mar. Biol. Assoc. UK 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*. Mar. Biol. 77, 257–263.
- Chess, J.R., 1993. Effects of the stipe-boring amphipod *Peramphithoe stypotrurpetes* (Corophioidea: Amphithoidea) and grazing gastropods on the kelp *Laminaria setchellii*. J. Crust. Biol. 13, 638–646.
- Clutton-Brock, T.H., 1991. The Evolution of Parental Care. Princeton University Press, New Jersey.
- Conlan, K.E., Chess, J.R., 1992. Phylogeny and ecology of a kelp-boring amphipod, *Peramphithoe stypotrurpetes*, new species (Corophioidea: Amphithoidea). J. Crust. Biol. 12, 410–422.
- Corey, S., 1981. The life history of *Crangon septemspinosa* Say (Decapoda, Caridea) in the shallow sublittoral area of Passamaquoddy Bay, New Brunswick, Canada. Crustaceana 41, 21–28.
- Crespi, B.J., Mound, L.A., 1997. Ecology and evolution of social behavior among Australian gall thrips and their allies. In: Choe, J.C., Crespi, B.J. (Eds.), The Evolution of Social Behavior in Insects and Arachnids. Cambridge University Press, Cambridge, UK, pp. 166–180.
- Crespi, B.J., Carmean, D.A., Chapman, T.W., 1997. Ecology and evolution of galling thrips and their allies. Annu. Rev. Entomol. 42, 51–71.
- Diesel, R., 1989. Parental care in an unusual environment: *Metopaulias depressus* (Decapoda: Grapsidae), a crab that lives in epiphytic bromeliads. Anim. Behav. 38, 561–575.
- Diesel, R., 1992. Maternal care in the bromeliad crab, *Metopaulias depressus*: protection of larvae from predation by damselfly nymphs. Anim. Behav. 43, 803–812.
- Durchon, M., 1956. Mode de reproduction et développement de *Nereis (Ceratonereis) costae* Grube (Annelide Polychète) à Alger. Archives de Zoologie Experimental et Generale (Paris) Series 5, 93, 57–69.
- Eggert, A.-K., Reinking, M., Müller, J.K., 1998. Parental care improves offspring survival and growth in burying beetles. Anim. Behav. 55, 97–107.
- Embich, T.R., 1973. Ecology of the sand shrimp, *Crangon septemspinosa* Say, 1818, in the Penobscot River Estuary, Maine. Unpubl. M.Sc. Thesis, University of Maine, Orono.
- Fink, L.S., 1984. Venom spitting by the green lynx spider, *Peucetia viridans* (Araneae, Oxyopidae). J. Arachnol. 12, 372–373.
- Fink, L.S., 1986. Costs and benefits of maternal behaviour in the green lynx spider (Oxyopidae, *Peucetia viridans*). Anim. Behav. 34, 1051–1060.
- Foelix, R.F., 1996. Biology of Spiders. Oxford University Press, New York, pp. 1–330.
- Griffiths, C.L., Griffiths, R.J., 1983. Biology and distribution of the littoral rove beetle *Psamathobledius punctatissimus* (Le Conte) (Coleoptera: Staphylinidae). Hydrobiologia 101, 203–214.
- Hacunda, J.S., 1981. Trophic relationships among demersal fishes in a coastal area in the Gulf of Maine. Fish. Bull. 79, 775–788.

- Halfpter, G., 1997. Subsocial behavior in Scarabaeinae beetles. In: Choe, J.C., Crespi, B.J. (Eds.), *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge University Press, Cambridge, UK, pp. 237–259.
- Halfpter, G., Huerta, C., Lopez-Portillo, J., 1996. Parental care and offspring survival in *Copris incertus* Say, a sub-social beetle. *Anim. Behav.* 52, 133–139.
- Harrison, R.J., 1940. On the biology of the Caprellidae. Growth and moulting of *Pseudoprotella phasma* Montagu. *J. Mar. Biol. Assoc. UK* 24, 483–493.
- Heinrich, B., 1979. *Bumblebee Economics*. Harvard University Press, Cambridge.
- Hölldobler, B., Wilson, E.O., 1990. *The Ants*. Harvard University Press, Cambridge.
- Johnson, S.B., Attramadala, W.G., 1982. Reproductive behaviour and larval development of *Tanais cavolinii* (Crustacea: Tanaidacea). *Mar. Biol.* 71, 11–16.
- Kight, S.L., Kruse, K.C., 1992. Factors affecting the allocation of paternal care in waterbugs (*Belostomatidae*). *Behav. Ecol. Sociobiol.* 30, 409–414.
- Kirkendall, L.R., Kent, D.S., Raffa, K.F., 1997. Interactions among males, females and offspring in bark and ambrosia beetles: the significance of living in tunnels for the evolution of social behavior. In: Choe, J.C., Crespi, B.J. (Eds.), *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge University Press, Cambridge, UK, pp. 181–215.
- Lim, S.T.A., Alexander, C.G., 1986. Reproductive behaviour of the caprellid amphipod, *Caprella scaura typica*, Mayer 1890. *Mar. Behav. Phys.* 12, 217–230.
- Linsenmair, K.E., 1984. Comparative studies on the social behaviour of the desert isopod *Hemilepistus reaumuri* and of a *Porcellio* species. *Symp. Zool. Soc. Lond.* 53, 423–453.
- Linsenmair, K.E., Linsenmair, Ch., 1971. Paarbildung und Paarzusammenhalt bei der monogamen Wüstenassel *Hemilepistus reaumuri* (Crustacea, Isopoda, Oniscoidea). *Z. Tierpsychol.* 29, 134–155.
- Mahon, R., Neilson, J.D., 1987. Diet changes in Scotian Shelf haddock during the pelagic and demersal phases of the first year of life. *Mar. Ecol. Prog. Ser.* 37, 123–130.
- Mattson, S., Cedhagen, T., 1989. Aspects of the behaviour and ecology of *Dyopetos monacanthus* (Metzger) and *D. porrectus* Bate, with comparative notes on *Dulichia tuberculata* Boeck (Crustacea: Amphipoda: Podoceridae). *J. Exp. Mar. Biol. Ecol.* 127, 253–272.
- Mendoza, J.A., 1982. Some aspects of the autecology of *Leptochelia dubia* (Krøyer, 1842) (Tanaidacea). *Crustaceana* 43, 225–240.
- Messana, G., Bartolucci, V., Mwaluma, J., Osore, M., 1994. Preliminary observations on parental care in *Sphaeroma terebrans* Bate 1866 (Isopoda, Sphaeromatidae), a mangrove wood borer from Kenya. *Ethol. Ecol. Evol. (special issue)* 3, 125–129.
- Nalepa, C.A., Bell, W.J., 1997. Postovulation parental investment and parental care in cockroaches. In: Choe, J.C., Crespi, B.J. (Eds.), *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge University Press, Cambridge, UK, pp. 26–51.
- Ockelmann, K.W., Åkesson, B., 1990. *Ophryotrocha socialis* n. sp., a link between two groups of simultaneous hermaphrodites within the genus (Polychaeta, Dorvilleidae). *Ophelia* 31, 145–162.
- Polis, G.A., 1990. *The Biology of Scorpions*. Stanford University Press, Stanford.
- Primavera, J.H., 1997. Fish predation on mangrove-associated penaeids—The role of structures and substrate. *J. Exp. Mar. Biol. Ecol.* 215, 205–216.
- Reid, M.L., Roitberg, B.D., 1994. Benefits of prolonged male residence with mates and brood in pine engravers (Coleoptera: Scolytidae). *Oikos* 70, 140–148.
- Reise, K., 1985. *Tidal Flat Ecology*. Ecological Studies 54. Springer-Verlag, Berlin.
- Richter, G., 1978. Beobachtungen zu Entwicklung und Verhalten von *Phronima sedentaria* (Forsk.) (Amphipoda). *Senckenbergiana Maritima* 10, 229–242.
- Sato, H., 1997. Two nesting behaviours and life history of a subsocial African dung-rolling beetle, *Scarabaeus catenatus* (Coleoptera: Scarabaeidae). *J. Nat. History* 31, 457–469.
- Sawyer, R.T., 1971. The development of brooding behaviour in the Hirudinea. *Hydrobiologia* 37, 197–204.
- Schubart, C.D., Diesel, R., Hedges, S.B., 1998. Rapid evolution to terrestrial life in Jamaican crabs. *Nature* 393, 363–365.
- Scott, M.P., 1998. The ecology and behavior of burying beetles. *Annu. Rev. Entomol.* 43, 595–618.
- Shedden, M., 1998. Grazing predation on a population of *Ampelisca tenuicornis* (Gammaridae: Amphipoda) off the south coast of England. *Mar. Ecol. Prog. Ser.* 164, 253–262.

- Shillaker, R.O., Moore, P.G., 1978. Tube building by the amphipods *Lembos websteri* Bate and *Corophium bonnellii* Milne Edwards (Crustacea: Amphipoda). J. Exp. Mar. Biol. Ecol. 33, 169–185.
- Shillaker, R.O., Moore, P.G., 1987. The biology of brooding in the amphipods *Lembos websteri* Bate and *Corophium bonnellii* Milne Edwards. J. Exp. Mar. Biol. Ecol. 110, 113–132.
- Smith, R.L., 1997. Evolution of paternal care in the giant water bugs (Heteroptera: Belostomatidae). In: Choe, J.C., Crespi, B.J. (Eds.), The Evolution of Social Behavior in Insects and Arachnids. Cambridge University Press, Cambridge, UK, pp. 116–149.
- Stephan, H., 1980. Lebensweise, Biologie und Ethologie eines sozial lebenden Amphipoden (*Dulichia porrecta*, *Dulichia monacantha* und *Dulichia falcata*—Crustacea, Malacostraca). Unpubl. Ph.D. Thesis, University of Kiel, Kiel, 326 pp.
- Tallamy, D.W., Denno, R.F., 1981. Maternal care in *Gargaphia solani* (Hemiptera: Tingidae). Anim. Behav. 29, 771–778.
- Tallamy, D.W., Wood, T.K., 1986. Convergence patterns in subsocial insects. Annu. Rev. Entomol. 31, 369–390.
- Thamdrup, H.M., 1935. Beiträge zur Ökologie der Wattenfauna auf experimenteller Grundlage. Meddr. Kommn Danm. Fisk. og. Havunders. (Ser: Fiskeri) 10, 1–125.
- Thiel, M., 1997a. Extended parental care in estuarine amphipods. Unpubl. Ph.D. Thesis, University of Maine, Orono, p. 188.
- Thiel, M., 1997. Reproductive biology of an epibenthic amphipod with extended parental care, *Dyopedos monacanthus*. J. Mar. Biol. Assoc. UK 77, 1059–1072.
- Thiel, M., 1998a. Extended parental care in marine amphipods. I. Juvenile survival without parents. J. Exp. Mar. Biol. Ecol. 227, 187–201.
- Thiel, M., 1998b. Population biology of *Dyopedos monacanthus* (Crustacea: Amphipoda) on estuarine soft-bottoms—the importance of extended parental care and pelagic movements. Mar. Biol. 132, 209–221.
- Thiel, M., 1999. Host-use and population demographics of the ascidian-dwelling amphipod *Leucothoe spinicarpa*—indication for extended parental care and advanced social behaviour. J. Nat. Hist., in press.
- Thiel, M., Reise, K., 1993. Interaction of nemertines and their prey on tidal flats. Neth. J. Sea Res. 31, 163–172.
- Thiel, M., Sampson, S., Watling, L., 1997. Extended parental care in two endobenthic amphipods. J. Nat. History 31, 713–725.
- Thorne, B.L., 1997. Evolution of eusociality in termites. Annu. Rev. Ecol. Syst. 28, 27–54.
- Trumbo, S.T., 1994. Interspecific competition, brood parasitism, and the evolution of biparental cooperation in burying beetles. Oikos 69, 241–249.
- Trumbo, S.T., 1995. Nesting failure in burying beetles and the origin of communal associations. Evol. Ecol. 9, 125–130.
- Trumbo, S.T., 1997. Parental care in Invertebrates. Adv. Study Behav. 25, 3–51.
- Tyler, A.V., 1972. Food resource division among northern, marine, demersal fishes. J. Fish. Res. Bd. Canada 29, 997–1003.
- Watkin, E.E., 1947. The yearly life cycle of the amphipod *Corophium volutator*. J. Anim. Ecol. 10, 77–93.
- Whitehouse, M.E.A., Jackson, R.R., 1998. Predatory behaviour and parental care in *Argyrodes flavipes*, a social spider from Queensland. J. Zool. 244, 95–105.
- Wilson, E.O., 1975. Sociobiology: the New Synthesis. Belknap Press, Cambridge.
- Wyatt, T.D., 1986. How a subsocial intertidal beetle, *Bledius spectabilis*, prevents flooding and anoxia in its burrow. Behav. Ecol. Sociobiol. 19, 323–331.
- Wyatt, T.D., Foster, W.A., 1989. Parental care in the subsocial intertidal beetle, *Bledius spectabilis*, in relation to parasitism by the ichneumonid wasp, *Barycnemis blediator*. Behaviour 110, 76–92.
- Wyatt, T.D., Foster, W.A., 1989. Leaving home: predation and the dispersal of larvae from the maternal burrow of *Bledius spectabilis*, a subsocial intertidal beetle. Anim. Behav. 38, 778–785.
- Zaklan, S.D., Ydenberg, R., 1997. The body size-burial depth relationship in the infaunal clam *Mya arenaria*. J. Exp. Mar. Biol. Ecol. 215, 1–17.
- Zwarts, L., Wanink, J.H., 1989. Siphon size and burying depth in deposit- and suspension- feeding benthic bivalves. Mar. Biol. 100, 227–240.



Erratum

Extended parental care in marine amphipods II. Maternal protection of juveniles from predation [J. Exp. Mar. Biol. Ecol. 234 (1999) 235 – 253][☆]

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The publisher regrets that Fig. 5 in the above paper was printed incorrectly. The corrected version of the figure appears on the following page.

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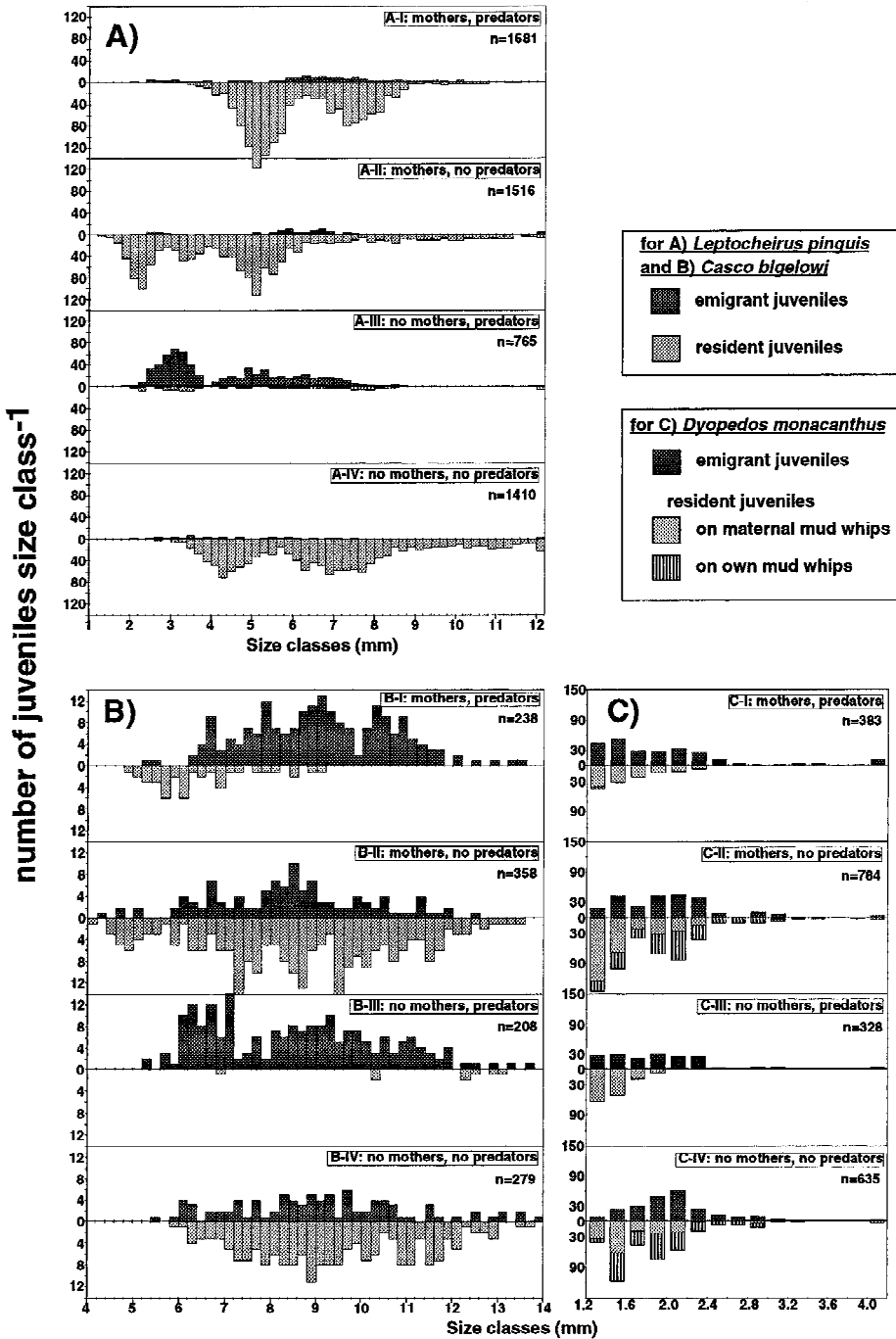


Fig. 5. Size frequency distribution of juvenile amphipods (A) *Leptocheirus pinguis*, (B) *Casco bigelowi* and (C) *Dyopedos monacanthus* surviving in trays with and without predators; all juveniles from the three replicate trays for each treatment were pooled; n = number of total survivors (residents + emigrants) for each N = 3 trays from each treatment.