Extended parental care in marine amphipods. I. Juvenile survival without parents

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Abstract

Extended parental care is found among a variety of marine peracarid species including endobenthic and epibenthic amphipods. After hatching from the female’s brood pouch, small juveniles enjoy parental care for time periods of several days up to several weeks. This study examined whether small juvenile amphipods can survive without parental care to determine if this reproductive strategy is obligate or facultative. Juveniles of the burrow-dwelling species Leptocheirus pinguis (Stimpson 1853) and Casco bigelowi (Blake 1929) survived well in predator-free trays, indicating that extended parental care in these species is a facultative reproductive strategy — juveniles can survive without their parents. Medium-sized juveniles of the epibenthic, suspension-feeding species Dyopedos monacanthus (Metzger 1875) survived relatively well in predator-free traps, but small juvenile D. monacanthus did not. This low survival rate of small D. monacanthus, even in predator-free trays, demonstrates that extended parental care is obligate for the survival of early juvenile stages in this epibenthic amphipod. When exposed to predators, juveniles of all three amphipod species were susceptible to predation, and reacted by emigration. Most juvenile L. pinguis and C. bigelowi emigrated or disappeared from sand shrimp Crangon septemspinosa treatments, but many remained in hermit crab Pagurus longicarpus treatments. Almost all juvenile D. monacanthus emigrated from both sand shrimp and hermit crab treatments, indicating that this epibenthic amphipod species is very susceptible to epibenthic predation. Survival of juvenile D. monacanthus was lower than that of L. pinguis and C. bigelowi both in predator-free and in predator trays. These results suggest that juveniles of this and other epibenthic peracarids depend on maternal care to a higher degree than juveniles of endobenthic burrow-dwelling species.

Keywords: Reproduction; Extended parental care; Amphipoda; Soft-bottom; Predation

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1. Introduction

Extended parental care is a common reproductive strategy among terrestrial invertebrates (Wilson, 1975; Clutton-Brock, 1991), but at present only few marine invertebrates have been found to engage in this reproductive strategy. Parents provide a suitable offspring habitat (e.g. burying beetles *Nicrophorus* sp. — Trumbo, 1992; or marine isopods *Sphaeroma terebrans* — Messana et al., 1994), they gather food resources for their developing offspring (e.g. most hymenopterans — Wilson, 1975; Heinrich, 1979; some caprellid amphipods — Aoki and Kikuchi, 1991), and they guard and defend their offspring (e.g. the green lynx spider *Peucetia viridans* — Fink, 1986; the pine engraver beetle *Ips pini* — Reid and Roitberg, 1994; or caprellid and podocerid amphipods — Stephan, 1980; Mattson and Cedhagen, 1989; Aoki and Kikuchi, 1991). In many cases, developing offspring cannot survive without parental care or at least its survival chances severely decrease when deprived of parental care (Clutton-Brock, 1991 and references cited therein). Extended parental care is thus an obligate reproductive strategy in these species: juveniles cannot survive without parental assistance. If parental care improves the chance of survival for the offspring, but is not essential, then it should be considered a facultative reproductive strategy. Examples for the latter are species where parental foraging provides additional food resources for growing offspring thus enhancing their survival chances (e.g. Brown and Formanowicz, 1995; Lubin and Henschel, 1996).

Among marine invertebrates, extended parental care is an uncommon reproductive strategy. In many species, developing eggs are provided with some food resources, but then grow and develop without further parental care. Diverse forms of parental care are found in a few species of almost any marine invertebrate phylum, but it is only in peracarid crustaceans (amphipods, isopods, cumaceans, etc.) that in all species embryos and larvae develop in the female brood pouch from which late larval stages or small juveniles emerge. In most peracarid species, juveniles leave their mother immediately after hatching from the brood pouch, and no further parental care for the young offspring is provided. There are, however, several endo- and epibenthic peracarid species that engage in extended parental care. In these species, juveniles remain with their mother after hatching from the brood pouch. In endobenthic species, juveniles live in the mother’s burrow for time periods of several days (Thamdrup, 1935; Goodhart, 1939; Watkin, 1947; Bückle-Ramirez, 1965; Johnson and Attramadal, 1982; Hassack and Holdich, 1987), or several weeks (Shillaker and Moore, 1987a,b; Thiel et al., 1997). In epibenthic species, juveniles either cling to the mother (Aoki and Kikuchi, 1991; Svararsson and Davidsdottir, 1995; Thiel, 1997a) or to structures built by the mother (Mattson and Cedhagen, 1989). During the period of extended parental care, juveniles can grow to more than half adult size (Conlan and Chess, 1992; Thiel, 1997b; Thiel et al., 1997).

*Leptocheirus pinguis* (Stimpson 1853) and *Casco bigelowi* (Blake 1929) are common endobenthic amphipods that inhabit burrows in muddy sediments along the Atlantic coast of North America (Bousfield, 1973; Dickinson et al., 1980; Dickinson and Wigley, 1981; Wildish, 1980; Michael, 1987). *L. pinguis* is a filter-feeder living in U-shaped burrows, and *C. bigelowi* is a deposit-feeding species dwelling in irregular burrows. *L. pinguis* is an important prey for a variety of fish (Wigley and Theroux, 1965; Tyler,
1971; Hacunda, 1981; Mahon and Neilson, 1987). In both species, burrows of adults extend 5–10 cm below the sediment surface (Thiel et al., 1997). *Dyopedos monacanthus* (Metzger 1875) is an epibenthic amphipod that constructs mud whips (Mattson and Cedhagen, 1989) which it utilizes as vantage points for suspension-feeding (sensu Moore and Earll, 1985). Female *D. monacanthus* host their offspring on these mud whips for several weeks (Thiel, 1997c). Despite substantial differences in their general biology, all three amphipod species, *L. pinguis*, *C. bigelowi*, and *D. monacanthus*, engage in a progressive form of extended parental care.

In an earlier study (Thiel et al., 1997), we hypothesized that in endobenthic species extended parental care provides shelter from predation, whereas in epibenthic species it is primarily a mechanism to lift small juveniles into water layers with sufficient supply of suspended food. All three amphipod species reach high abundances in soft sediments just at and below mean low water (MLW) (Thiel, 1997b), where predator abundances are high. Juveniles of these amphipods might be particularly susceptible to predation, and extended parental care could be a successful strategy to protect small juveniles from epibenthic predators such as fish, shrimp or conspecifics.

Not all juveniles attain the same age and size during extended parental care. Some individuals of a clutch leave their mothers a few days after birth whereas others remain for weeks or even months (Thiel, 1997c). The question arises whether juveniles that leave their mothers at an early age will have the same survival chances as those that stay longer — i.e. is extended parental care an obligate or a facultative reproductive strategy in these amphipods?

This study examined the survival of juvenile amphipods *Leptocheirus pinguis*, *Casco bigelowi* and *Dyopedos monacanthus* that were separated from their mothers. The major goal was to examine the survival chances of these orphan juveniles both under protected conditions (i.e. free from predation), and under predation pressure.

2. Materials and methods

Experiments were conducted in the flowing seawater facility of the Darling Marine Center, located on the Damariscotta River Estuary, Maine (lat. 43°50’ N, long. 69°37’ W). Seawater is continuously pumped from a depth of about 2 m below MLW, and salinity varies between 29 and 31 ppt, which is similar to conditions that amphipods encounter in the field. Small trays (900 cm²) were established in the laboratory and filled with mud from an adjacent mud flat (a 10-cm thick mud layer for *L. pinguis* and *C. bigelowi* and a 3-cm thick layer for *D. monacanthus*). A constant flow of seawater through trays was maintained for the duration of the experiment. Seawater leaving trays through outflow pipes passed over a screen trapping emigrating juveniles. All emigrants were thus retained in these traps where they could be collected and counted.

Juvenile amphipods for the experiments were collected from sediments at and below MLW in the Damariscotta River estuary, and after separation from their mothers immediately introduced to the trays. For *L. pinguis* and *C. bigelowi*, burrows of parental females were excavated and all juveniles collected. For *D. monacanthus*, juveniles were taken from mud whips of parental females. A second experiment was conducted for *D.
monacanthus in which juveniles were taken from a culture tank. Some of these juveniles were still living on the maternal mud whips while others had already built their own whips. Juveniles were sorted and equally divided among the different trays where they were allowed to establish burrows or mud whips. During an establishment period of 1–2 weeks, all juveniles that left trays and were caught in the traps were reintroduced to their trays every morning. During a pre-experimental period, 5–10 days up to the commencement of the actual experiment, all juveniles that were caught in traps were counted, but then reintroduced to their trays. Following the introduction of predators to trays, all emigrating juveniles were collected from the traps and preserved. At the end of the experiment (7–11 days after introduction of predators), the entire content of each tray was sieved over a 500-µm-mesh and preserved. All amphipods were sorted from these samples, counted and measured along their dorsal surface from the rostrum to the telson using a computer-based image analysis system.

Two epibenthic predators that are common in the habitat of the amphipods were selected for experiments, the sand shrimp Crangon septemspinosa, and the hermit crab Pagurus longicarpus. Ten sand shrimp were introduced to each of three shrimp trays, three hermit crabs were introduced to each of three hermit crab trays, and three trays were left predator-free as controls. During predation experiments, all trays (including control trays) were covered with a 1-mm-screen to prevent shrimp or hermit crabs from leaving trays. The percentage of juveniles surviving as residents and emigrants was calculated from the number of juveniles initially introduced to each tray. To test whether percentages of survivors differed significantly between treatments (sand shrimp, hermit crabs and controls), percentage values were arcsin-transformed and tested by ANOVA (n = 3 replicate trays for each treatment, df = 2) followed by Fisher’s PLSD post-hoc test.

3. Results

3.1. Emigration of juveniles

Juveniles of all three amphipod species responded to addition of predators by emigrating from trays (Fig. 1). Numbers of Leptocheirus pinguis emigrating from trays were relatively low in the 6 days preceding the introduction of predators (Fig. 1A), and numbers of juveniles emigrating from control trays remained low for the entire duration of the experiment (Fig. 1A). Immediately following the introduction of sand shrimp to the three shrimp trays, large numbers of juveniles emigrated (35.3±10.9 S.E. tray⁻¹ at day 1 — Fig. 1A). In hermit crab trays, about four juvenile L. pinguis emigrated from each tray immediately after introduction of hermit crabs, but during the subsequent days, numbers of emigrants dropped again to less than one amphipod tray⁻¹ day⁻¹. For Casco bigelowi, relatively large numbers of juveniles emigrated during days preceding the addition of predators, but emigration decreased until day 7 in both experimental and control trays (Fig. 1B). A slight increase of C. bigelowi emigrants was noted in predator additions at days following predator introduction (Fig. 1B), yet this emigration response was not as pronounced as for L. pinguis juveniles (compare Fig. 1A). Relatively large
Fig. 1. Mean number (±S.E.) of emigrating juveniles tray⁻¹ day⁻¹ from control, hermit crab and sand shrimp trays for (A) Leptocheirus pinguis, (B) Casco bigelowi, (C) small Dyopedos monacanthus and (D) medium-sized D. monacanthus; time period when predators were present in trays indicated by light shading; trap from each tray was monitored every morning; during the pre-experimental period, emigrating juveniles were counted but then reintroduced to their tray; during the experimental period, all emigrants were collected and preserved; n = 3 trays for each treatment.

numbers of small Dyopedos monacanthus that were separated from their mothers emigrated during the pre-experimental period (Fig. 1C). No strong increase in numbers of small D. monacanthus emigrants was observed after addition of predators, probably due to the low number of small orphan juveniles remaining at that time. Medium-sized juvenile D. monacanthus that had already built their own mud whips immediately constructed new whips after introduction to trays, and few individuals emigrated during the pre-experimental period (Fig. 1D). Few medium-sized D. monacanthus (< 1
juvenile tray\(^{-1}\) day\(^{-1}\) during most days) emigrated from control trays over the entire period of the experiment (Fig. 1D). Immediately following introduction of predators, almost all medium-sized \textit{D. monacanthus} emigrated from predator additions (33.3±7.96 S.E. emigrants tray\(^{-1}\) day\(^{-1}\) from shrimp trays; 43.0±14.36 S.E. emigrants tray\(^{-1}\) day\(^{-1}\) from hermit crab trays) (Fig. 1D).

3.2. Survival of juvenile amphipods

Many juvenile amphipods survived as residents in predator-free control trays, whereas in sand shrimp trays few or no juveniles survived as residents but rather emigrated during experiments (Fig. 2). More than 90% of juvenile \textit{L. pinguis} that were introduced to control and hermit crab trays survived the experiments (Fig. 2A). A relatively large percentage (63.6%) of juvenile \textit{L. pinguis} survived in sand shrimp trays, but less than 10% of these survivors remained as residents, while the majority (50%) emigrated during the experimental period (Fig. 2A). While the percentages of \textit{L. pinguis} survivors did not differ significantly among different treatments (ANOVA, \(P > 0.05\)), significantly

![Graph showing survival rates of juvenile amphipods](image)

Fig. 2. Mean percentage of juveniles surviving in control, hermit crab and sand shrimp trays; for (A) \textit{Leptocheirus pinguis}, (B) \textit{Casco bigelowi}, (C) small \textit{Dyopedos monacanthus} and (D) medium-sized \textit{D. monacanthus}; calculated as percentage of potential survivors; \(n = 75\) juvenile \textit{Leptocheirus pinguis}, \(n = 90\) \textit{Casco bigelowi}, \(n = 55\) small \textit{Dyopedos monacanthus} and \(n = 94\) medium-sized \textit{D. monacanthus} were initially introduced to each tray in the respective experiments; lines indicate significant differences for: top lines — total survivors (= residents + emigrants); middle lines — emigrants and bottom lines — residents (ANOVA with \(n = 3\) replicate trays for each treatment, \(df = 2\); followed by post-hoc Fisher’s PLSD-test; \(P < 0.05\)).
higher percentages emigrated from shrimp trays than from hermit crab and control trays (ANOVA, $P < 0.05$). In total, 77% of juvenile *C. bigelowi* survived in control trays (about 65% as residents), while 58.15% survived in hermit crab additions (37.8% as residents) (Fig. 2B). No juvenile *C. bigelowi* remained in shrimp trays after the experiment, but 30.7% escaped predation by emigrating from trays (Fig. 2B). The percentage of survivors and of residents differed significantly among all treatments (ANOVA, $P < 0.05$), and a significantly higher percentage of juveniles emigrated from shrimp trays than from control trays (ANOVA, $P < 0.05$). Of the small *D. monacanthus* that were separated from their mothers, less than 12% survived ($\pm$ emigrants + residents) in all three types of trays (predator additions and controls). Only 6% of these small *D. monacanthus* remained in control trays at the end of the experiment (Fig. 2C).

In this same experiment, no significant differences in survivorship or emigration of small *D. monacanthus* among different treatments were found (ANOVA, $P > 0.05$), while the few small *D. monacanthus* remaining in control trays were significantly different from hermit crab and sand shrimp trays where no residents remained (ANOVA, $P < 0.05$). In the experiment with medium-sized *D. monacanthus*, many juveniles survived in control trays (>$50\%$ as residents) (Fig. 2D). No medium-sized *D. monacanthus* remained in shrimp trays at the end of the experiment but 37.2% survived as emigrants. Only one medium-sized *D. monacanthus* remained in one hermit crab tray at the end of the experiment, but 48.9% emigrated after introduction of hermit crabs (Fig. 2D). The percentages of total survivors were not significantly different in the three different treatments (ANOVA, $P > 0.05$), but significantly higher percentages of juveniles emigrated from shrimp and hermit crab trays than from control trays (ANOVA, $P < 0.05$).

### 3.3. Sizes of juvenile amphipods surviving in trays

For all experiments, the majority of juveniles originally introduced to trays were of sizes that are typically found in burrows or on mud whips of parental females (Fig. 3).

Most juvenile *L. pinguis* originally introduced to trays were between 3 and 7 mm in size, sizes that are commonly found in burrows of parental females (Thiel, 1997d). In control and in hermit crab trays many of these juveniles survived and grew to sizes >5 mm (Fig. 3A). In sand shrimp additions most of the few remaining resident *L. pinguis* were >7 mm (Fig. 3A). The sizes of juvenile *C. bigelowi* introduced to trays are typical for those of juveniles found in the burrows of parental females (Thiel et al., 1997). The majority of juvenile *C. bigelowi* surviving as residents in control and hermit crab trays were <$12$ mm, and thus of a size that usually still enjoys parental care. The juveniles emigrating from control and hermit crab trays were mostly <$10$ mm, but all sizes of juvenile *C. bigelowi* emigrated from shrimp trays (Fig. 3B). In the experiment with small *D. monacanthus* juveniles, all juveniles initially introduced to trays were <$3$ mm (Fig. 3C). Very few of these juveniles survived in either control or predator addition trays (Fig. 3C). In the experiment with medium-sized *D. monacanthus*, 23.4% of juveniles that were initially introduced to trays were >2.4 mm, and thus had already reached sizes at which they normally have left their mother’s mud whip (Thiel, 1997c) (Fig. 3D). All medium-sized juveniles that remained as residents in control trays were
Fig. 3. Size frequency distribution of juvenile (A) Leptocheirus pinguis, (B) Casco bigelowi, (C) small juvenile Dyopedos monacanthus and (D) medium-sized juvenile D. monacanthus surviving as residents (upper dark columns) and emigrants (lower light columns) in the different treatments; shown are resident and emigrant juveniles surviving in sand shrimp trays, hermit crab trays, control trays and juveniles initially introduced to the trays; size range of juveniles that are commonly found to leave their mothers are highlighted by light shading; all juveniles from the three replicate trays for each treatment were pooled; $n$ = number of total survivors (residents + emigrants) from three replicate trays represents 100% for each treatment; $n_i$ = number of initially introduced juveniles per tray represents 100%.
1.4 mm. All size ranges of medium-sized *D. monacanthus* juveniles emigrated from both sand shrimp and hermit crab additions (Fig. 3D). Thus, in this experiment with medium-sized *D. monacanthus*, sizes that are typically found on their own mud whips in the field (Thiel, 1997c) emigrated after addition of predators.

4. Discussion

Juvenile amphipods *Leptocheirus pinguis* and *Casco bigelowi* that had been separated from their mothers survived in large numbers in predator-free trays where they immediately had established their own burrows. In contrast, almost no small juvenile *Dyopedos monacanthus* separated from their mothers survived even when kept in predator-free environments. This indicates that juvenile *D. monacanthus* depend on maternal care to a higher degree than juvenile *L. pinguis* and *C. bigelowi*. Orphan juveniles of all three species were very susceptible to sand shrimp predation, indicating that predation strongly affects juvenile survival in these amphipods with extended parental care.

4.1. Survival of juvenile amphipods without parental care

Several endo- and epibenthic amphipod species provide extended parental care for their developing offspring (Aoki, 1997; Thiel et al., 1997), yet it is not well known whether small juveniles of these species can survive without parents.

In the majority of marine amphipods and other peracarids, juveniles leave their parents immediately after hatching from the female’s brood pouch (Wildish, 1982; see Sainte-Marie (1991) for recent overview). Survival of freshly hatched juveniles is influenced by the availability of habitat and resources (e.g. Shillaker and Moore, 1987a), by competition and predation (e.g. Nelson, 1979; Grant, 1981; Wilson, 1989, 1991), and by abiotic factors such as temperature, salinity and disturbance (Wildish, 1982; Wilson and Parker, 1996). Staying with parents might increase the survival chances of juvenile amphipods because parents can provide resources (see e.g. Richter, 1978a,b; Laval, 1980), protect their offspring from competition and predator encounters (Aoki and Kikuchi, 1991), and mediate the impact of abiotic factors. Observations on parent-offspring interactions by Richter (1978a), (1978b), Lim and Alexander (1986) and Aoki and Kikuchi (1991) suggest improved offspring survival resulting from extended parental care, but it was only recently that Aoki (1997) demonstrated experimentally that juveniles may benefit from parental care.

The present study demonstrates that juveniles of the burrow-dwelling species *L. pinguis* and *C. bigelowi* survive relatively well without parental care when kept in predator-free environments, while small juveniles of the epibenthic species *D. monacanthus* were less competent under such conditions. In most burrow-dwelling amphipods, small juveniles are thought to establish their own burrows immediately after hatching from their mothers’ brood pouches (e.g. Wildish, 1984; Shillaker and Moore, 1987a,b; Dauvin, 1989; Wilson, 1989; Sudo and Azeta, 1996), yet in some species, juveniles remain in the maternal burrows for several days (Thamdrup, 1935; Goodhart, 1939;
Watkin, 1947; Shillaker and Moore, 1987b). None of the authors that found juvenile amphipods remaining in maternal burrows suggests that this reproductive behavior is obligate. Reports of juveniles that feed on their mothers food (Shillaker and Moore, 1987b) imply some positive effects on the growth potential of juveniles that remain in maternal burrows versus those that leave at an early age and size, however these potential benefits require further investigation. In these (and possibly other) burrow-living amphipods extended parental care can be considered a facultative reproductive strategy: small juveniles are able to survive on their own.

Small juvenile *Dyopedos monacanthus* that were separated from their mothers did not survive whereas medium-sized juveniles, many of which had already built their own mud whips, did. Low survival rates of small juvenile *D. porrecta* and *D. monacanthus* that were separated from their mothers were also observed by Stephan (1980). All these podocerid amphipod species construct mud whips that are used as ‘vantage points’ for suspension-feeding (sensu Moore and Earll, 1985) and vigorously defended against conspecifics (Stephan, 1980; Thiel, 1997c). Suspension-feeding amphipods extend their setose antennae into the water current, and at frequent intervals ingest suspended particles gathered by the antennae. Small juvenile *D. monacanthus* cling to the upper parts of their mothers mud whips, i.e. high in the benthic boundary layer where the feeding environment may be optimal for them (Thiel, 1997c). The low survival rate of small juveniles in the present study indicate that in these podocerid amphipods extended parental care is an obligate reproductive strategy: the early and small juvenile stages depend on maternal care to survive. Small podocerid juveniles may not be able to construct and successfully defend large enough mud whips that are suitable for efficient suspension-feeding.

A similar form of extended parental care, where small juveniles are lifted above the substratum by their mothers, can be seen in several caprellid amphipods (Harrison, 1940; Lim and Alexander, 1986; Aoki and Kikuchi, 1991; Aoki, 1997; Thiel, 1997a). Interestingly, small orphan juveniles of caprellid species with extended parental care had relatively high survival rates in predator-free environments (Aoki, 1997). Containers used in Aoki’s (Aoki, 1997) study provided large areas of suitable clinging substratum for small caprellid juveniles, while the podocerid juveniles in this study were forced to construct their own mud whips. Caprellid amphipods usually inhabit preexisting substrata such as macroalgae and hydroids, whereas most podocerid amphipods construct their own substrate structures in the form of mud whips. Therefore, juvenile podocerids may depend on their mothers (as constructors of a mud whip) to a larger degree than juvenile caprellids. These observations suggest that the availability of suitable clinging substratum influences the survival chances of small juveniles in epibenthic peracarids with extended parental care.

4.2. Effects of predators on the survival of juvenile amphipods

The addition of predators to the trays caused decreased survival of juveniles in all three amphipod species. These results confirm earlier studies that demonstrated the impact of epibenthic predators on soft-bottom dwelling macro- and meiofauna (Reise, 1985; Mattila et al., 1990). Juvenile *L. pinguis* and *C. bigelowi* were less susceptible to
epibenthic predators than juvenile *D. monacanthus*, probably due to the endobenthic life-style of the former two species.

In both *L. pinguis* and *C. bigelowi* a positive relationship exists between the size of amphipods and the depth of their burrows (Thiel, 1997e,f). Large individuals can build deeper burrows in which they are relatively safe from epibenthic predators such as shrimp. Small juvenile *L. pinguis* and *C. bigelowi*, that dwell in shallow burrows close to the sediment surface were susceptible to shrimp predation whereas a high percentage of large adults that build deep burrows survived, even under high predation pressure (Thiel, 1997e). Many burrow-dwelling amphipods are sensitive to epibenthic predators, but often large individuals are preferably taken (due to higher profitability) by predators while small individuals are ignored (see Wilson (1989) and references cited therein).

Compared to many other burrow-dwelling amphipods (compare Sainte-Marie, 1991) adults of both *L. pinguis* and *C. bigelowi* are relatively large (18–20 mm and 20–26 mm, respectively), and therefore they are probably relatively safe from epibenthic predation in their deep burrows, whereas juveniles in shallow burrows are not.

Sand shrimp also had a very strong effect on the survival of juvenile *D. monacanthus*. This epibenthic amphipod is particularly susceptible to epibenthic predators and all individuals quickly disappeared from the trays. Caine (1979) and Aoki (1988) noticed an immediate disappearance of epibenthic caprellid amphipods in field surveys following the appearance of demersal fish species. Similarly, Nelson (1979) observed that in eelgrass beds, epibenthic amphipods are least abundant during the summer and fall when predators are most active. The fact that only one individual *D. monacanthus* remained in the trays with hermit crabs underscores their susceptibility to epibenthic predation. Stephan (1980) noted caprellids *Phitsica marina*, several polychaete species and even ophiurids *Ophiura albida* as important predators of *Dyopedos* sp., indicating that podocerid amphipods are susceptible to a wide variety of epibenthic predators.

In summary, juvenile *L. pinguis* and *C. bigelowi* are only susceptible to specific predators (here: sand shrimp), whereas juvenile *D. monacanthus* appear susceptible to a suite of epibenthic predators (here: sand shrimp and hermit crabs).

### 4.3. Reaction of juvenile amphipods to epibenthic predators

All three amphipod species reacted to the addition of common estuarine predators by emigration from the trays. This escape-migration has proven a successful strategy for potential survival of at least 30% of all juveniles initially introduced to trays (except in the experiments with small juvenile *D. monacanthus*, see above). The relatively weak emigration-response of juvenile *C. bigelowi* after the introduction of sand shrimp (see Fig. 1B) is probably responsible for their relatively low survival (only about 30% of all juveniles) compared to more than 60% survival in *L. pinguis* (compare Fig. 2).

Escape-migration as a response to predators is relatively common for a variety of soft-bottom dwelling amphipods (Ambrose, 1984; Rönn et al., 1988; Thiel and Reise, 1993) and other soft-bottom macro- and meiofauna (Armonies, 1989, 1994). These escape-migrations are induced by immediate predator encounters, and therefore might occur during times unfavorable for survival of drifting amphipods. Amphipods that have escaped from their burrows or their mud whips in response to predators are drifting in
the water column where they can become easy prey to visual predators. Furthermore, these escapees are faced with finding a new habitat and constructing a new dwelling. Thus, escape-migration via the water column can only be viewed as a last and potentially costly resort. The ability to avoid predators and subsequent escape-migrations might significantly enhance the survival chances of soft-bottom infauna. Extended parental care in burrow-dwelling amphipods may be an effective strategy to avoid epibenthic predators.

5. Conclusions

The results of this study suggest that extended parental care is a facultative reproductive strategy in endobenthic marine amphipods while it is obligate for small juveniles in epibenthic podocerid amphipods but apparently not in epibenthic caprellid amphipods (Aoki, 1997). Although in *L. pinguis* and *C. bigelowi* extended parental care is not considered an obligate reproductive strategy, it might be highly essential for the survival of offspring in environments with high predation pressure, such as shallow coastal waters. Extended parental care is obligate for small juvenile *D. monacanthus*. Following the establishment of their own mud whips, all size classes in this species (including adults) remain susceptible to epibenthic predators which is probably the reason why its major reproductive period is during winter/early spring when predator densities and activities on estuarine soft-bottoms are low. Small juvenile *L. pinguis* and *C. bigelowi*, that are usually found in their mothers burrows, are rarely found in their own burrows in the field (Thiel et al., 1997; Thiel, 1997f), and small and medium-sized juvenile *D. monacanthus* are often found drifting in the water column (Thiel, 1997c). These observations indicate that in their natural habitat where predation pressure is high (e.g. Reise, 1985; Thiel, 1997f), predation may substantially affect the survival of these juvenile amphipods in the field. In a future study, it will be examined whether parental protection can indeed positively affect juvenile survival in an environment with high predation pressure.

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