REPRODUCTIVE BIOLOGY OF AN EPIBENTHIC AMPHIPOD (*DYOPEDOS MONACANTHUS*) WITH EXTENDED PARENTAL CARE

MARTIN THIEL

Darling Marine Center, University of Maine, Walpole, ME 04573, USA.
Present address: Smithsonian Marine Station, 5612 Old Dixie Highway, Fort Pierce, Florida 34946, USA

Dyopedos monacanthus inhabits self-constructed mud whips on marine soft-bottoms. Juveniles stay on the mud whip of their mother for extended time periods after they hatch from her brood pouch. During the main reproductive period in the spring, parental females have been observed in the aquarium and collected from the field. Specimens of *D. monacanthus* have been collected simultaneously from the intake filter from the sea-water laboratory. Several consecutive clutches have been found on the whip of one female. Most juveniles are small (1 mm in size), but they grow to sizes of >2 mm on the whip of their mother. In the aquarium, juveniles usually hatched immediately after the females had been attended by males. They then clung to their mother's whip for about two weeks. Most parental females in the aquarium produced three broods during a time period of about six weeks. In the field an average of 36 parental females m^{-2} were found in April, and an average number of 75 juveniles clung to each female's whip. The average number of juveniles found on the females' whips declined in May and June. Many juveniles appeared in the sea-water intake filter starting in mid April. Most juveniles caught in the intake filter were between 2 and 3 mm in size which corresponds well with their size at leaving the female's whip. In mid May, all amphipods disappeared within a few days from the aquarium, when shrimp *Crangon septemspinosa* started to become more active again. Many big females disappeared in the field at that time too, and in mid June parental females were smaller than in the previous months. The amphipod *D. monacanthus* belongs in the category of epibenthic suspension-feeding amphipods. It is probably very susceptible to epibenthic predation and extended parental care is primarily a mechanism to lift very small juveniles above the viscous sublayer in the benthic boundary layer.

INTRODUCTION

Peracarid crustaceans have a relatively progressive reproductive strategy. In most species, fully developed small juveniles hatch from the female's brood pouch. At least in a few peracarid species, the parents care for growing juveniles after hatching. Species with this extended parental care can be distinguished from the other peracarids which display the common reproductive strategy where the juveniles are released into the environment as soon as they hatch from the female's brood pouch. The amphipod *Dyopedos monacanthus* (Metzger, 1875) belongs in the category of epibenthic peracarids with extended parental care together with the isopods *Astacilla longicornis* and *A. arietina* (Sars, 1899), *Arcturus baffini* (Svavarsson & Davidsdottir, 1994, 1995), the amphipods *Caprella scaura typica* (Lim & Alexander, 1986), *C. monoceros* and *C. decipiens* (Aoki &

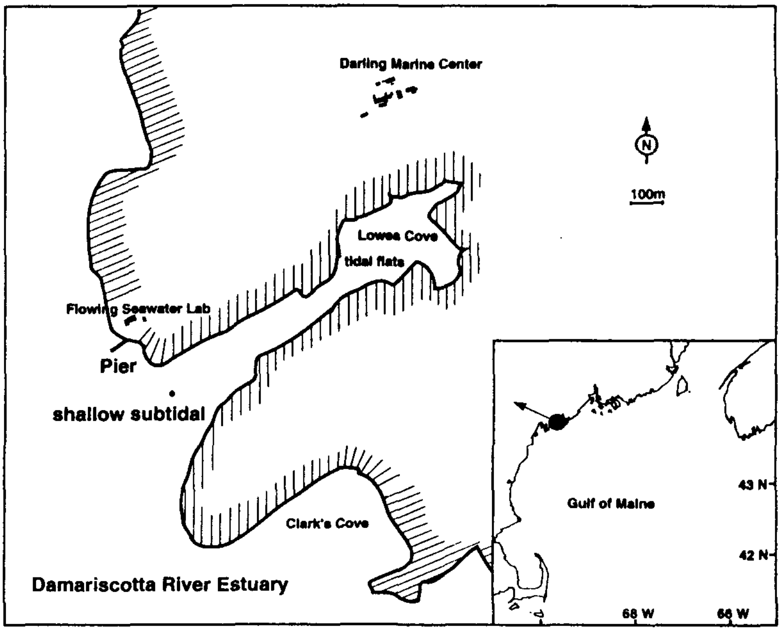

Figure 1. Study area in the Damariscotta River Estuary with the sampling station in the shallow subtidal and the pier with the sea-water intake.

Kikuchi, 1991), *Dyopedos porrectus* (Mattson & Cedhagen, 1989), *Dulichia falcata* (Kanneworff & Nicolaisen, 1973; Stephan, 1980), and *D. rhabdoplastis* (McCloskey, 1970). Burrow and tube inhabiting peracarids have been found to engage in extended parental care (Thamdrup, 1935; Goodhart, 1939; Watkin, 1947; Bückle-Ramirez, 1965; Richter, 1978; Laval, 1980; Johnson & Attramadal, 1982; Borowsky, 1983; Bird & Holdich, 1985; Hassack & Holdich, 1987; Shillaker & Moore, 1987; Conlan & Chess, 1992; Chess, 1993). Based on observational evidence it has been assumed that for these endobenthic species, extended parental care is primarily a mechanism to protect the juveniles from epibenthic predators (Thiel et al., 1997). Most epibenthic peracarids with extended parental care are suspension-feeders which leads to the assumption that the feeding mode of these species has an influence on their reproductive behaviour. Further interpretation suffers from the fact that only little information is available on the numbers of juveniles produced by each female and the size at which they leave the females. These data are provided in this study for the epibenthic amphipod *Dyopedos monacanthus*. The data obtained, together with aquarium observations, are used to discuss the evolution of extended parental care in epibenthic peracarids.

MATERIALS AND METHODS

Study area

The study was conducted in the Damariscotta River Estuary, Maine (43°50′N 69°37′W). Salinities are ~30, and water temperatures vary between -1 and 19°C over the course of the year. Amphipods were collected in the shallow subtidal (~2 m below mean low water) at the mouth of Lowes Cove in the Damariscotta Estuary (Figure 1). The sediment at the sampling station is muddy, the organic matter content of the sediments is ~3·5%, and the water content is ~80%. The surface sediments support a high standing stock of benthic diatoms, and the concentrations of sediment chlorophyll-*a* are high throughout the year (M.T., unpublished data).

Observations on parental females in the aquarium

Dyopedos monacanthus is an epibenthic amphipod that builds 'mud whips' from fine particulate material and sometimes filamentous algae (Mattson & Cedhagen, 1989). Small juveniles have been found on the mud whips of female *D. monacanthus* (Mattson & Cedhagen, 1989). In the following, females with juveniles on their whips were termed 'parental females' to distinguish them from 'non-parental females' which did not host juveniles on their whips.

From mid March to mid May several females were allowed to build mud whips in a big glass aquarium (160 l) with a 3 cm layer of mud from the field site. The females were monitored every morning, the numbers of juveniles were recorded and whether or not males were attending. Very small juveniles were clinging to the mud whips in a close pack so that it was impossible to distinguish and count individual juveniles. Therefore, numbers of small juveniles were estimated, but larger juveniles were counted individually.

Sampling of parental females in the field

From March to June 1995 about 20 parental females were collected monthly from the field. Sampling was done by diver during spring low tide. Collection of individual females on their mud whips involved location of the whip which was then carefully covered with a glass jar (diameter 5 cm, volume 250 ml). The jar was removed with a thin sediment plug, and then the lid was screwed on. In March and April, photographs were taken of each female to confirm that they, their offspring or attending males did not abandon the whip shortly before the jars were put over them. In April, all parental females in 14 0·25 m^2-quadrats were counted to obtain an estimate of the number of parental females in the field. The contents of the jars were sieved over a 300-μm mesh, fixed in 4% formalin, later transferred to 70% alcohol, and females and juveniles sorted from the sample.

Sampling of amphipods Dyopedos monacanthus *from the sea-water intake filter*

The sea-water intake for the flowing sea-water laboratory of the Darling Marine Center is located on a pier extending into the Damariscotta Estuary (Figure 1). The intake opening is ~3 m above the bottom and ~2 m below MLW. Sea-water is pumped through an intake filter-bag with a mesh size of 250-μm at a rate of ~500 l min^{-1}. From mid March until the end of May 1995, the content of the filter-bag was retrieved every morning and amphipods *D. monacanthus* sorted from the material retained in the filter-bag.

Measurement of amphipods

All amphipods were measured with a computer-based image-analysis system along their dorsal side from the rostrum to the base of the telson. Ovigerous females were noted, and if the content of their brood pouch was complete, the eggs were counted.

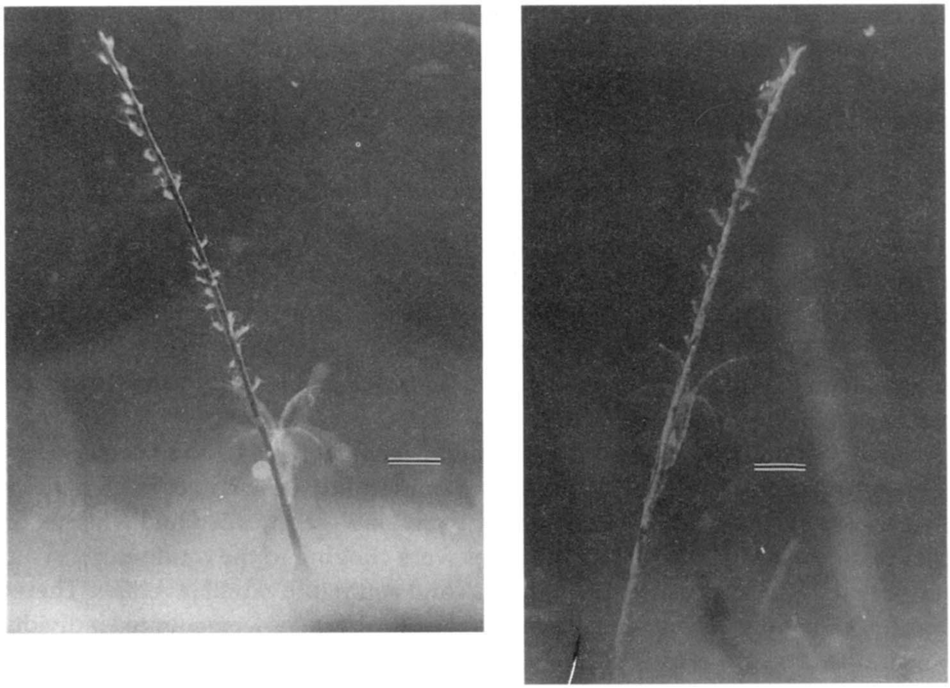

Figure 2. Females *Dyopedos monacanthus* and their juveniles clinging to the females' mud whips; juveniles can be seen clinging to the upper part of the mud whip, females at the base of the whip. Scale bar: 5 mm.

RESULTS

Aquarium observations on Dyopedos monacanthus

Female *Dyopedos monacanthus* readily built mud whips after being introduced to the aquarium. Some established their whips on the glass walls of the aquarium where they could not reach bottom sediments for whip construction. This indicates that whips are built primarily from suspended sediment particles filtered from the water. The females were never observed to leave their whips, but sometimes handled sediment at the base of the whip to which they clung. Usually the parental female sits at the base of the whip, ~2 cm above the bottom (Figure 2). The juveniles are always on the top of the whip. Females actively defended their mud whips against conspecifics which tried to invade the whips from the base. The females vigorously tried to push these intruders down and away from the whip. Large males were sometimes able to invade the whip successfully, and in one case a male was seen between the female and its juveniles. The male tried to push the juveniles away from the whip or to tear them off the whip, but it could not be determined whether the male preyed upon the juveniles. At the time of fertilization, the males usually attended individual females for 1–3 d (Figure 3A). In the aquarium, males were never seen building their own whips. When they were not on female whips, they could be found clinging to epibenthic structures such as algae, pine needles, worm tubes or old abandoned whips. Often, small juveniles hatched immediately after the females had been attended by males (Figure 3A). Intervals

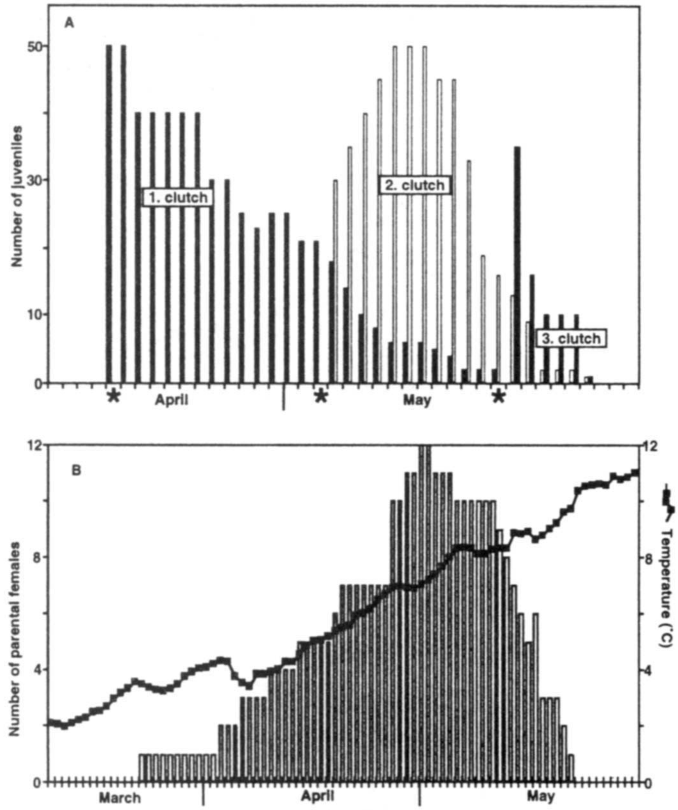

Figure 3. (A) Number of juveniles on the mud whip of one individual female *Dyopedos monacanthus* in glass aquarium; numbers of very small juveniles immediately after their birth were estimated, larger juveniles could be counted; stars indicate days when males were present on the female's mud whip; numbers of amphipods on the whip were controlled every morning. (B) Number of parental females *D. monacanthus* in glass aquarium and water temperatures in the flowing sea-water laboratory.

between successive visits of males varied from 4 to 13 d for individual females. Times from hatching of the first to the following brood varied between 16·5 ±0·65 d (N=7 births between 22 April and 5 May) and 12·4 ±0·67 d (N=10 births between 6 and 19 May).

Newly-hatched juveniles crowd together on the female whip, but after a few days spread out over the whole whip. Two clutches of juveniles are sometimes found on one female whip (Figure 3A). It is not clear what induces the juveniles to leave the whip. The females have never been observed pushing their juveniles off. However, on two occasions (due to a male intruding in one case, and due to a sand shrimp *Crangon septemspinosa* in another case), small juveniles just let go of the whip and drifted away with the water currents.

At the beginning of May, 12 parental females were present in the aquarium (Figure 3B). Towards the end of the aquarium observations, with increasing water temperatures, several sand shrimp *C. septemspinosa* in the aquarium became more active. On one occasion a sand shrimp was seen raiding a whip with juveniles. At the same time mud whips with juveniles, but no females, were observed. A few days after these observations,

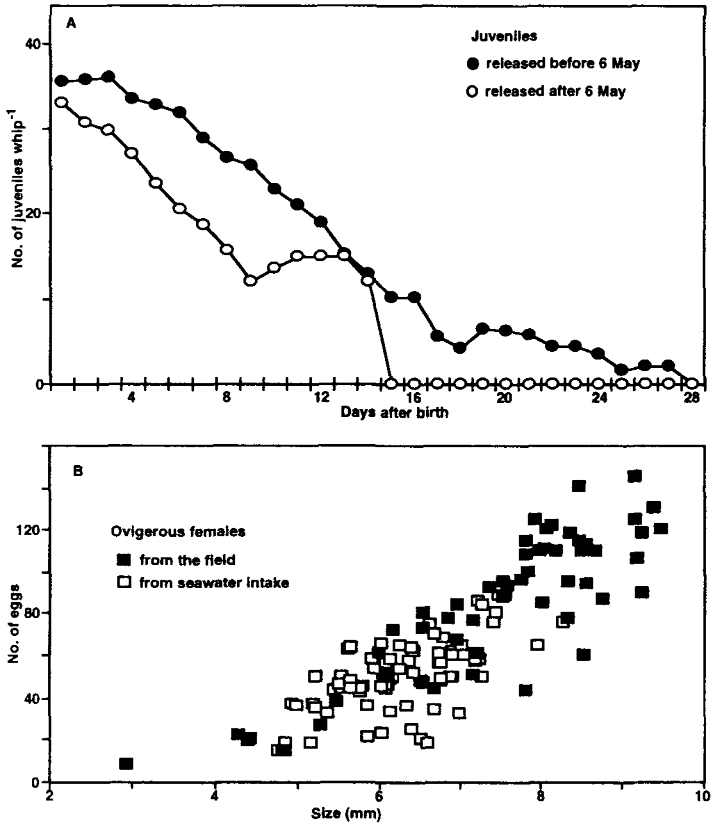

Figure 4. (A) Average numbers of juveniles *Dyopedos monacanthus* remaining on mud whip of their mothers at days after their release from the brood pouch; for juveniles released from brood pouch before 6 May 1996 (●) and after 6 May 1996 (○). (B) Relationship between number of eggs in brood-pouches of female *D. monacanthus* and their size for females collected as parental females in the field (■) and adult females from the sea-water intake (□).

no more amphipods were seen in the aquarium (Figure 3B). Juveniles released from the brood pouch before 6 May remained up to 27 d on the mud whips of their mothers, but juveniles released after 6 May stayed no longer than 15 d on their mother's whip (Figure 4A). Juveniles of both groups (released from brood pouch before and after 6 May) steadily disappeared from their mother's whips. About 14 d after hatching, ~50% of the original number of juveniles remained on the mother's whip (Figure 4A).

Reproductive stage and size of female Dyopedos monacanthus

Parental females in the field

Between March and May 1995 parental females averaged 8 mm in size, but in June this dropped to ~5 ±0·246 mm (N=20) (Figure 5A). In April, the mean number of parental females in the field was 36·57 ±6·61 females m^{-2} (N=14 plots counted). Usually ~20% of the parental females were attended by males on their whips, and >80% of them were ovigerous. The number of eggs in the brood pouch of the females was strongly correlated with their size (Figure 4B; y=6·041x$10^{0\cdot141x}$, R=0·61, for N=83 females

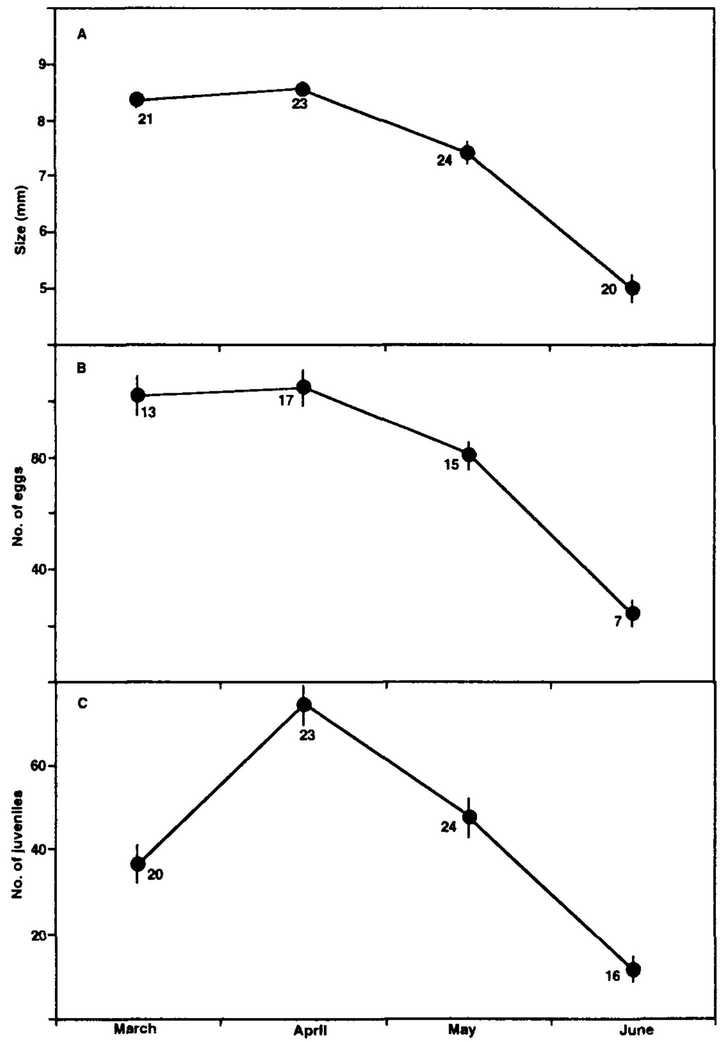

Figure 5. Parental females *Dyopedos monacanthus*: (A) average size (±1 SE) of parental females; (B) average number of eggs (±1 SE) of ovigerous parental females; (C) average number of juveniles (±1 SE) of individual parental females. Numbers indicate N of females collected at each sampling date.

from sea-water intake; $y=4{\cdot}57\times10^{0{\cdot}162x}$, R=0·88, for N=54 parental females from the field). In March and April, parental females had on average 103 eggs in their brood pouch, but with decreasing size of the parental females towards June this value also decreased (Figure 5B). Up to 119 juveniles have been found on the whip of one female *D. monacanthus*, but there were also females which only hosted two juveniles at the time of sampling. The average number of juveniles on their mother's whip increased from 36·7 ±4·45 (N=20) in March 1995 to 74·61 ±4·61 (N=23) in April and 47·54 ±4·69 (N=24) in May, but then dropped sharply to 11·625 ±3·04 (N=16) as a result of smaller females and smaller brood size in June (Figure 5C).

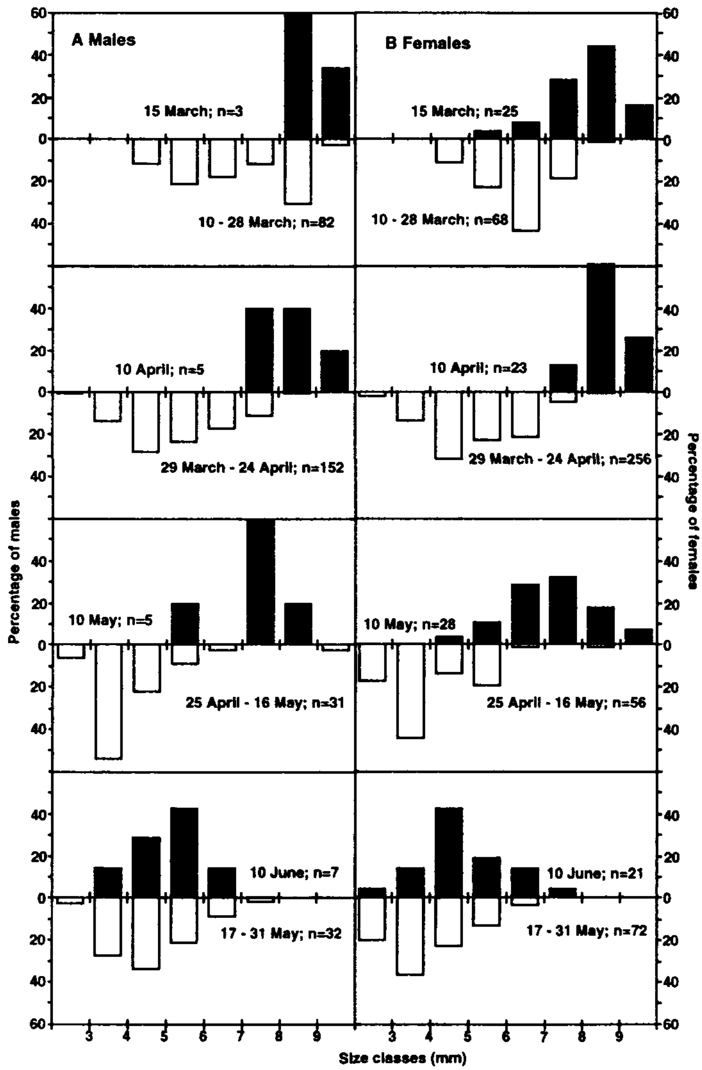

Figure 6. (A) Size frequency distribution of males *Dyopedos monacanthus* collected as male visitors to mud whips of parental females (upper columns, dark shading) and from the sea-water intake (lower columns, light shading). (B) Size frequency distribution of females *D. monacanthus* collected as parental females from mud whips (upper dark columns) and from the sea-water intake (lower light columns).

Male Dyopedos monacanthus *from females' whips and from sea-water intake*

Some males were attending parental females on their whips. The sizes of males collected from females' whips decreased from March to June (Figure 6A). Similarly, the sizes of males caught in the sea-water intake decreased between March and May 1995 (Figure 6A).

Non-parental females from the sea-water intake

Females from the sea-water intake were always slightly smaller than the parental females (Figure 6B). Their size continuously decreased between March and May 1995

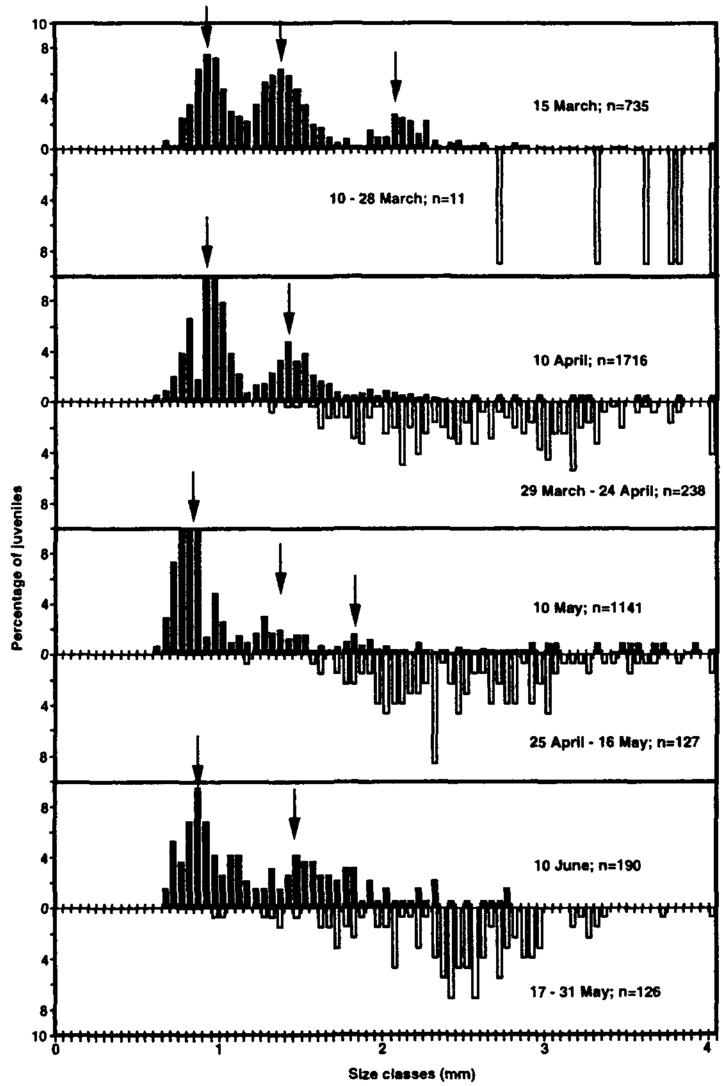

Figure 7. Size frequency distribution of juvenile *Dyopedos monacanthus* from the mud whips of parental females (upper dark columns) and from the sea-water intake (lower light columns); juveniles from all parental females are pooled for the respective sampling dates, and all juveniles collected from the sea-water intake during respective sampling periods are pooled.

(Figure 6B). The number of eggs in the brood pouch of females from the sea-water intake also decreased towards May.

Juvenile Dyopedos monacanthus *from females' whips and from sea-water intake*

Juveniles on their mothers' mud whips in the field. The smallest juvenile found on its mother's whip was 0·58 mm and the largest 4·58 mm but the majority were ~1 mm in length (Figure 7). The size frequency data of the juveniles from females' whips indicate that the juveniles are released at a size between 0·8 and 1 mm (see major peak at all sampling dates; arrows in Figure 7). Some juveniles then moult on their mother's whip

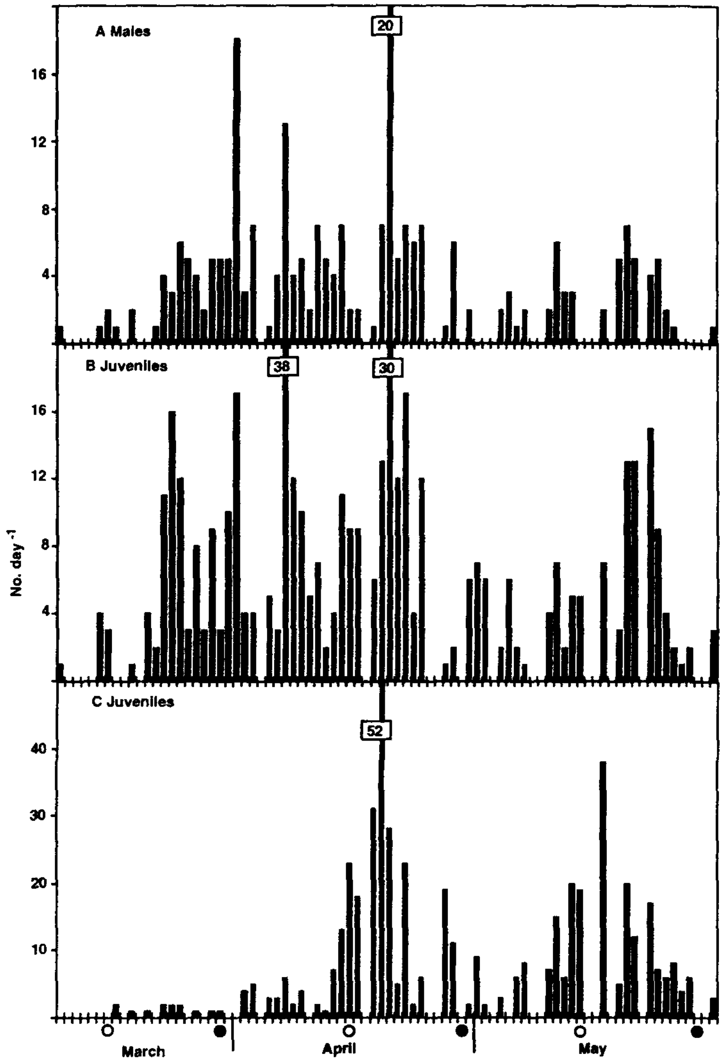

Figure 8. Numbers of *Dyopedos monacanthus* collected daily from the sea-water intake to the flowing sea-water laboratory; intake is located on the pier ~3 m above the bottom; flow through is 500 l min^{-1}, mesh size is 250-μm; amphipods were separated in adult males (A), adult females (B) and juveniles (C); ○ = full moon, ● = new moon.

and grow into a larger size range (see second peak at ~1·5 mm; Figure 7). A few juveniles even undergo a second moult on their mother's whip and grow into a third size group (arrows in Figure 7).

Juveniles from the sea-water intake. The smallest juveniles caught in the sea-water intake were ~1 mm in length but most were between 2 and 3 mm (Figure 7). At lengths of 2–4 mm *D. monacanthus* started to mature and become recognizable as adults. During March 1995 very few juveniles were caught in the sea-water intake but their numbers sharply increased by about mid April (Figure 8C). Highest numbers of juveniles were caught during the full moon spring tides in April and May, whereas numbers were low during new moon spring tides (Figure 8C). The numbers of juveniles caught follow a clear lunar pattern which is not very obvious for adult male and female *D. monacanthus* (Figure 8A,B). Commonly, females were more abundant in the sea-water intake than males.

DISCUSSION

The details of extended parental care in the epibenthic amphipod *Dyopedos monacanthus* are described. Small juveniles live on the mud whip of their mother for extended time periods. During the peak reproductive period, the juveniles which disappear from the mud whips appear in large numbers in the water column.

Reproductive biology of Dyopedos monacanthus

During the main reproductive period of *D. monacanthus* which is in the spring/early summer, each female produced several consecutive broods. As typical for peracarids the reproductive output per individual female strongly corresponds with body size, smaller females producing fewer offspring than larger ones. In April and May, when big females produced large numbers of juveniles, many juveniles were caught in the sea-water intake. This indicates that a large proportion of juveniles recruit via the water column. After settling to the bottom, they build a mud whip. Parental females vigorously defended their mud whips, which can be up to 87 mm long. The aquarium observations indicate that only those females that were long-term occupants of whips reproduced successfully. The fact that adult females and males caught in the sea-water intake are always slightly smaller than the ones occupying whips in the field might indicate that at any particular time only the largest adults reproduce successfully. An average density of 36 parental females m^{-2} does not seem to be a density where intraspecific competition should prevent smaller females from reproducing successfully, but large mud whips might be an important resource for which intraspecific competition exists. After the large females have disappeared (both in the aquarium and in the field starting in May), small females reproduced successfully, but because of their low fecundity their reproductive potential was low.

The relatively clear separation into three size cohorts among the juveniles found on the females' mud whips (Figure 7) indicates that some juveniles may remain for two moults on the whips of the females. The majority of juveniles, however, leave after the first juvenile moult on their mothers' whip. The aquarium observations and the size measurements of juveniles from the females' mud whips revealed that most juveniles leave the whip as medium sized individuals of ~2 mm body length. Older juveniles usually leave when another clutch of juveniles has hatched and starts spreading along the whip. Many juveniles were caught in the sea-water intake during full moon spring tides which indicates that reproduction in *D. monacanthus* is closely coupled to the lunar cycle. The aquarium observations show that each female produces one clutch of juveniles about every 14 d. It remains unclear why peaks of juveniles drifting in the water column occur only every 28 d and not every 14 d.

The data presented here strongly indicate that a major reproductive period for *D. monacanthus* is during the spring months, at a time when the settling spring bloom provides a good food supply for benthic suspension-feeders. For many marine invertebrates the release of larvae or juveniles is tightly coupled with the occurrence of food delivery events, such as plankton blooms (Giese & Pearse, 1974).

Extended parental care in Dyopedos monacanthus

Female *D. monacanthus* provide a strong and long mud whip to accommodate their growing offspring. During the time period of extended parental care, the females continuously clean and improve their whips, and they frequently check and groom the growing juveniles on the whip (Stephan, 1980). *Dyopedos monacanthus* has been observed to prey on small conspecifics, and the parental females defend their brood against intraspecific intruders to their whips (Stephan, 1980). Active intraspecific defence of the offspring is also reported for other epibenthic peracarids with extended parental care (Harrison, 1940; Lim & Alexander, 1986; Aoki & Kikuchi, 1991).

Thus extended parental care might provide some protection for small juveniles against male or immature conspecific prowlers. All sizes of *D. monacanthus* seem susceptible to epibenthic predation as can be concluded from the aquarium observations. Mattson & Cedhagen (1989) identified *Dyopedos* spp. as important prey organisms of demersal fish species. They remarked that '24% of the total number of *Dyopedos* specimens eaten were <3 mm long' (thus ~75% of the individuals eaten would be ≥3 mm long), further supporting the assumption that all sizes of *Dyopedos* specimens are susceptible to epibenthic predation. Juveniles grow larger during extended parental care, but as all sizes of *D. monacanthus* are susceptible to epibenthic predation, this reproductive strategy does not seem to be an effective mechanism to reduce the predation pressure on juveniles substantially. At present there is no reason to assume that larger juveniles would be less susceptible to epibenthic predation than small juveniles.

Mattson & Cedhagen (1989) speculate that the mud whip might reduce the attractiveness of *Dyopedos* specimens as prey items to demersal fish, but they give little attention to another important function of the mud whip: 'as vantage points for suspension-feeding' (Moore & Earll, 1985). *Dyopedos monacanthus* is a passive suspension-feeder, depending entirely on water currents for the delivery of food particles. The mud whip is a structure built by this relatively small amphipod to reach high enough within or above the benthic boundary layer into a zone with enough current to receive sufficient food. Very small individuals on relatively small whips would be limited to heights above the bottom where suspended material is of low nutritional value and fluxes are low (Muschenheim, 1987). Life on their mother's whip during the period of extended parental care is probably a mechanism in this suspension-feeding amphipod to lift the small juveniles into water layers with sufficient food supplies. Thus the mud whip is most likely not a very effective deterrent against epibenthic predators (e.g. fish) as was suggested by Mattson & Cedhagen (1989), but rather a tool for *D. monacanthus* to overcome the physical limitations of a small suspension-feeding amphipod in the benthic boundary layer. Extended parental care thus enables the small juveniles of this passive suspension-feeding amphipod to reach water layers with an optimal food supply. The juveniles only leave their mother's mud whip when they can build their own mud whips large enough to reach water layers within the benthic boundary layer with sufficient food supply.

Extended parental care in epibenthic peracarids

Extended parental care is reported from a variety of epibenthic peracarids where the juveniles live exposed on the body of the female or attached to an epibenthic structure built by the female (Thiel et al., 1997). These presocial peracarids are leading an exposed epibenthic lifestyle above the bottom. They are very susceptible to predation (Caine, 1991), and not surprisingly many of the species within this group are disguised or live in highly cryptic environments. With increasing size they can be more easily attacked by predators (Caine, 1989) and it can be assumed that female-offspring clusters are more obvious to predators than small individuals. Thus advantages resulting from extended parental care must be more important than occasional losses due to interspecific predation. The most obvious advantages are protection from intraspecific predation (Harrison, 1940; Lim & Alexander 1986; Aoki & Kikuchi, 1991) and lifting small juveniles into water layers with sufficient food-supply. The latter argument has never been discussed as an important factor favouring the evolution of extended parental care in aquatic invertebrates. The validity of this argument has not been examined here, but theoretical considerations and observations made by Stephan (1980) make it appear quite reasonable. If extended parental care is a mechanism to lift small juveniles above or at least high enough within the benthic boundary layer, other passive suspension-feeders could be identified as likely candidates for extended parental care.

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