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Population biology of *Dyopedos monacanthus* (Crustacea: Amphipoda) on estuarine soft-bottoms: importance of extended parental care and pelagic movements

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Abstract The suspension-feeding amphipod *Dyopedos monacanthus* (Metzger, 1875) is a common epibenthic amphipod that lives on self-constructed “mud whips” (built from filamentous algae, detritus and sediment particles) in estuaries of the northern North Atlantic Ocean. The population biology of *D. monacanthus* at a shallow subtidal site in the Damariscotta River Estuary (Maine, USA) was examined between July 1995 and July 1997. The resident population at the study site was dominated by adult females during most months of the year. High percentages of subadults were found in late summer/early fall. Often, between 10 and 20% of the adult females were paired with males, and the percentage of ovigerous females varied between 40 and 100%, indicating continuous reproduction. The percentage of parental females varied between 40 and 80% during most months, but dropped to levels below 20% during summer/early fall. The average size of amphipods on their own mud whips was ~4 mm during the summer/early fall, after which it increased continuously to >7.0 mm in March or April, and then dropped again. In March and April, the average number of eggs and juveniles female⁻¹ was ~100 eggs and 55 juveniles, while during the summer/early fall the average number of eggs female⁻¹ was <20 and that of juveniles female⁻¹ was <10. Many juveniles grew to large sizes (>1.4 mm) on their mothers’ whips in winter/early spring but not in the summer/fall. The average number of amphipods at

the study site was low in late summer/early fall (<50 individuals m⁻²), increased steadily during the winter, and reached peak densities of >3000 individuals m⁻² in April 1996 (>1600 individuals m⁻² in May 1997), after which densities decreased again. The decrease of the *D. monacanthus* population at the study site coincided with a strong increase of amphipods found pelagic in the water column. This behavioural shift occurred when temperatures increased and benthic predators became more abundant and active on shallow soft-bottoms, suggesting that *D. monacanthus* at the study site is strongly affected by predation. The effects are direct (by predation on amphipods) and indirect (by reducing duration of extended parental care and enhancing pelagic movements). Both extended parental care and pelagic movements are important behavioural traits of *D. monacanthus* (and other marine amphipods), and significantly affect its population dynamics.

Introduction

The behavioural repertoire of benthic amphipods is highly diverse, and can have important consequences for their population dynamics. Sex-specific assortative grouping can have important consequences on fertilization rates and thus population reproductive success (e.g. Dick and Elwood 1989, 1996; Iribarne et al. 1995). Parental care can positively affect offspring survival (Aoki 1997; Thiel 1997a), and pelagic movements can contribute to dispersal (Sainte-Marie and Brunel 1985; Chevrier et al. 1991), exploitation of resources (see e.g. Boudrias and Carey 1988), and genetic exchange among amphipod (marine invertebrate) populations. Yet most population studies of marine amphipods exclusively focus on quantitative aspects such as abundance, sex ratios, broods per female, eggs produced per female, generation times and growth rates. Although these data can provide important information about the life history and population biology of marine amphipods, they only tell part of the story.

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Drastic and unexplainable changes in local amphipod abundances are usually ascribed to pelagic movements (Mills 1967; Wildish 1980; Collie 1985). In a direct comparison of benthic and pelagic samples, Sainte-Marie and Brunel (1983) confirmed that changes in the benthic density of *Arrhis phyllonyx* result from pelagic movements of this deposit-feeding amphipod. Several other studies on macrozooplankton revealed that large numbers of "benthic" amphipods frequently occur in the water column (Williams and Bynum 1972; Kaartvedt 1989; Chevrier et al. 1991). While pelagic movements are increasingly considered to be an integral component of the life history of many benthic amphipod species, the fact that these amphipods may engage in extended parental care has been largely neglected. Our present knowledge about extended parental care is limited, since commonly employed sampling methods (grab and core samples immediately sieved after retrieval) do not allow the recognition of animal associations such as parent-offspring groups. Herein, I use an individual-centered approach to examine the importance of both extended parental care and pelagic movements for the population dynamics of an epibenthic amphipod, *Dyopodos monacanthus* (Metzger, 1875) (Gammaridea: Podoceridae). An initial study on the reproductive biology of this amphipod pointed to the potential importance of these behavioural traits (Thiel 1997b), but left many questions unanswered.

The suspension-feeding amphipod *Dyopodos monacanthus* inhabits flexible mud whips that it constructs from filamentous algae, detritus and sediment particles (Mattson and Cedhagen 1989; Thiel 1997b). It is a common amphipod on estuarine soft-bottoms along the North Atlantic coasts (Stephan 1980; Mattson and Cedhagen 1989; Thiel 1997b), and has been identified as a major prey item of demersal fish species (Mattson and Cedhagen 1989). *D. monacanthus* and several other epibenthic peracarids (Aoki 1997; Thiel et al. 1997) provide extended parental care for their offspring; juveniles remain and grow on the body of their mother or on structures built by her. Most epibenthic peracarids with extended parental care are suspension-feeders. Epibenthic peracarids are very susceptible to predation (Nelson 1979a, b; Caine 1991), but *D. monacanthus* is a good swimmer that avoids benthic predators by emigrating into the water column (Thiel 1998). Although this escape response may save individual amphipods from immediate death, it leaves them with the necessity to get back to the bottom and build or conquer a new mud whip. As mud whips are important structures for feeding (Moore and Earll 1985) and for reproduction (Mattson and Cedhagen 1989; Thiel 1997b) in *D. monacanthus*, frequent abandonment of mud whips may reduce both the condition and the reproductive potential of an individual. According to Stephan (1980), swimming podocerid amphipods are easy prey for fish predators, and thus leaving the mud whip is a risky option for them. These observations indicate that the escape of *D. monacanthus* into the water column may have important consequences for the population dynamics of

this amphipod. The major goal of this study was to reveal the extent of both extended parental care and pelagic movements in *D. monacanthus*, and the effect of these behaviours on the population dynamics of this epibenthic suspension-feeding amphipod.

Materials and methods

Study area

The study was conducted at the mouth of Lowes Cove, a mud flat in the Damariscotta River Estuary, Maine (Latitude 43°56'N; Longitude 69°35'W). The sampling station is ~2 m below mean low water (MLW), salinities are about 30‰ (McAlice 1993), and annual water temperatures range from 0 to 17 °C (Fig. 1). Sediments at the station are characterized by high standing stocks of benthic microalgae, indicated by high concentrations of sediment chlorophyll *a* throughout the year (Thiel 1997c). High concentrations of chlorophyll *a* in bottom waters show that substantial amounts of the microphytobenthos are regularly resuspended at the sampling site and are available for filter- and suspension-feeding species.

Sampling of amphipods in the field

From July 1995 until July 1997, ~24 mud whips and their inhabitants, *Dyopodos monacanthus*, were collected monthly from the field. Sampling was done by a diver during low tides. Individual amphipods on their mud whips were collected with forceps by carefully pulling the whip out of the sediment and placing it into a glass jar (5 cm diam, 250 ml vol), which was then immediately closed. While amphipods usually clung tightly to their mud whips during collection, on several occasions (May, June and July 1997), they were extremely prone to release their hold on the mud whips. During these periods, jars or small vials (1 cm diam, 5 ml vol) were placed over the amphipods with their mud whips and pushed into the sediment to a depth of about 1 cm. The sediment layer provided an immediate plug to the vials and thereby ensured that amphipods could not escape by leaving their mud whips during sampling. The contents of the jars were sieved over a 300 µm mesh, fixed in 4% formalin and later transferred to 70% alcohol. All amphipods were sorted from the sample, and were measured with a computer-based image-analysis system along their dorsal side from the rostrum to the base of the telson. The length of each mud whip was measured

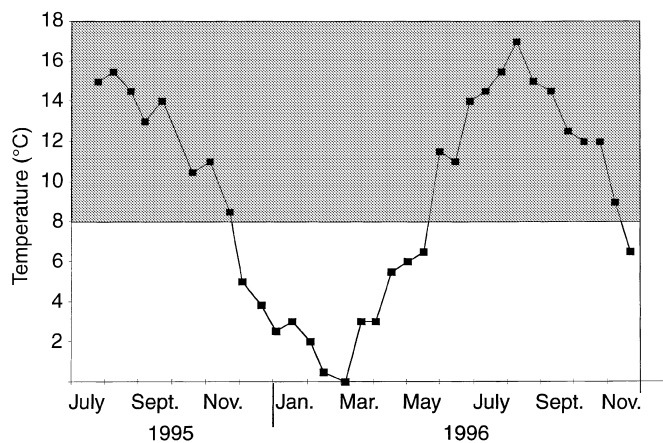


Fig. 1 Water temperatures of bottom waters at study site in Lowes Cove, Damariscotta River Estuary, Maine; sampling was at bi-weekly intervals between July 1995 and November 1996

to test for a relationship between the length of the whips and the size of the amphipods. Eggs of ovigerous females and juveniles of parental females were counted. In the following, females with juveniles on their whips are termed "parental females" to distinguish them from "non-parental females" which did not host juveniles on their whips. Small amphipods still on the maternal mud whips are termed "juveniles", and those on their own mud whips are considered subadults when they could not be clearly identified as adult males (large 2nd gnathopods) or females (eggs in gonads or brood pouch, oosetigers present). As egg production in many amphipods is temperature-related (Steele and Steele 1975; Wildish 1982; Sheader 1983), data on female fecundity (egg numbers female⁻¹) are separated into two time periods, the months during which water temperatures are usually >8 °C (June to November), and those during which they are ≤8 °C (December to May) (Fig. 1).

Pelagic movements of *Dyopedos monacanthus*

Data from a previously conducted long-term study on drifting macrozooplankton were evaluated. The data were collected monthly during the time periods August 1971 to April 1973 and January 1975 to May 1979 at one station in the Sheepscot River Estuary (43°59'N; 69°39'W) (McAlice and Jaeger, unpublished data; for details see Thiel 1997d).

Amphipods were collected from the Darling Marine Center seawater-intake filter (for details see Thiel 1997b) each day for time periods of 5 to 6 d in July, September and November 1995, and in March and June 1996. All collected individuals were preserved and their size measured.

Results

Population structure and life-history traits of *Dyopedos monacanthus*

During most of the year, adult females dominated the population at the study site (Fig. 2). The sex ratio never fell below 2:1 (females:males), and reached highest levels

in September 1995 and August 1996, when <10% of all amphipods were adult males. The highest percentages of subadults in the population were found each year during summer/early fall, when >40% of all amphipods were subadults (Fig. 2). Low percentages of subadults occurred each year during the winter months. Average size of *Dyopedos monacanthus* was ≈4 mm during the late summer/early fall, increasing continuously during the late fall and winter (Fig. 3A). The average size of females increased from 4 mm in October to 7.5 mm in March; it remained at this level only until April, and then dropped sharply. The average size of males increased from 4 mm in October to 6–7 mm in January, but then remained at this level throughout the winter (Fig. 3A). The average number of eggs was low during the summer/early fall (<20 eggs female⁻¹) and started to increase during the fall (Fig. 3B). A continuous increase in egg numbers female⁻¹ was observed throughout the winter; the highest values were reached in March and April (~110 eggs female⁻¹). In the late spring, the number of eggs female⁻¹ substantially dropped. The seasonal development of raised juveniles followed this pattern, but mean numbers never exceeded 65 juveniles female⁻¹ (Fig. 3B).

On most sampling dates, between 10 and 20% of all females were paired with males (Fig. 4A), and no seasonal pattern was discernible. During most of the year, the majority of females were ovigerous (40 to 100%: Fig. 4B). The percentage of parental females usually varied between ~80% and 40%, but reached low values (<20%) each year in summer/fall (Fig. 4B). At any given time, only the largest females were reproductive (Fig. 5). The smallest females in the population were always non-reproductive, but during the summer months females of a size that had been non-reproductive during the winter months were carrying eggs or pro-

Fig. 2 *Dyopedos monacanthus*. Percentage of females, males and subadults on individual mud whips (Nos. on top of bars number of individuals collected on each sampling date 2 m below mean low water in Lowes Cove between July 1995 and July 1997)

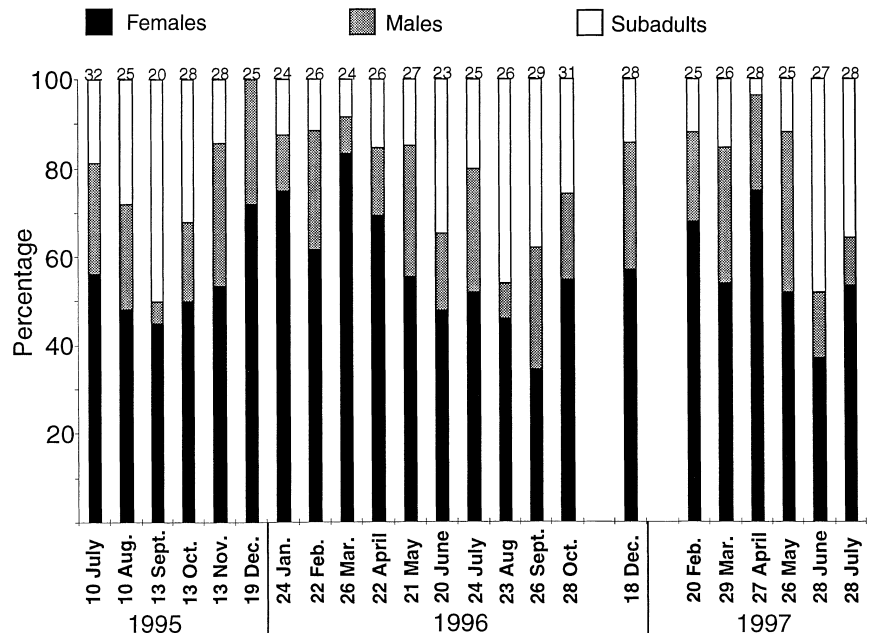


Fig. 3 *Dyopedos monacanthus*. **A** Average length (± 1 SE) of females and males; **B** average numbers of eggs and juveniles per ovigerous and parental female, respectively; note that many parental females are also ovigerous (*Nos. on top of figure number of females and males collected on each sampling date*)

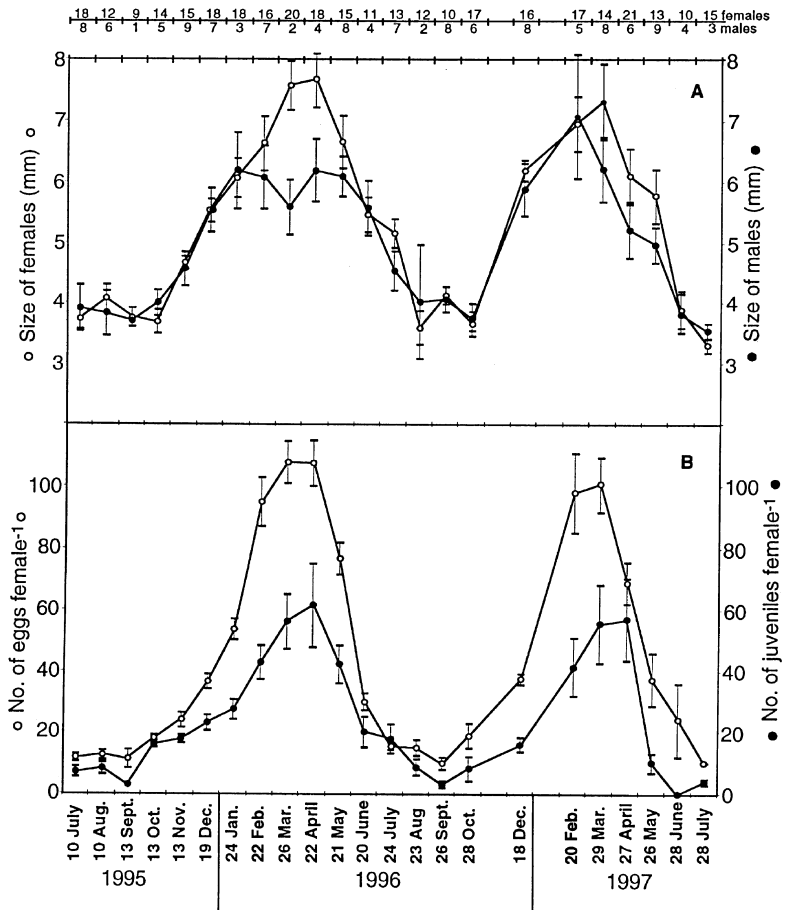
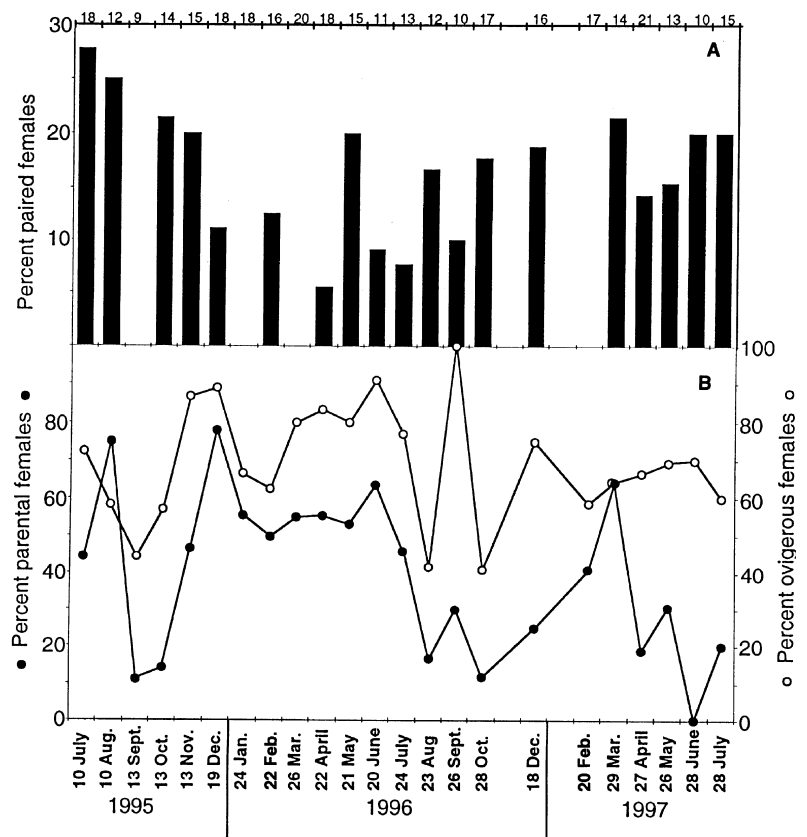


Fig. 4 *Dyopedos monacanthus*. **A** Percentage of paired females (with male visitors); **B** percentage ovigerous and parental females (*Nos. on top abscissa number of females collected on each sampling date*)



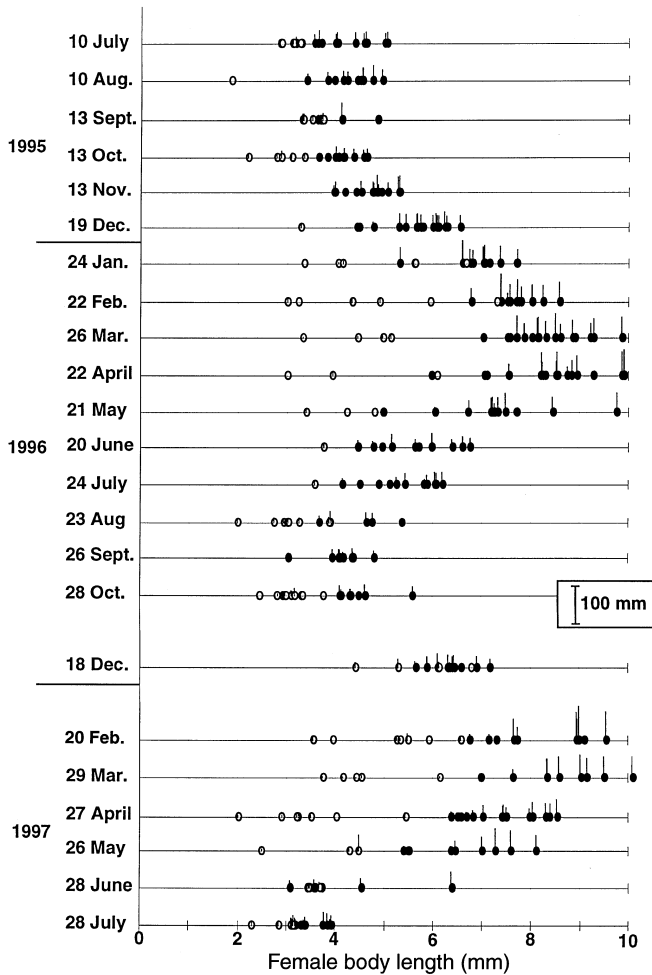


Fig. 5 *Dyopodos monacanthus*. Sizes of reproductive (●) and non-reproductive (○) females at each sampling date; length of ticks represents length of mud whip of each female; reproductive females either had embryos in their brood pouch or juveniles on their mud whips, non-reproductive females had neither embryos nor juveniles

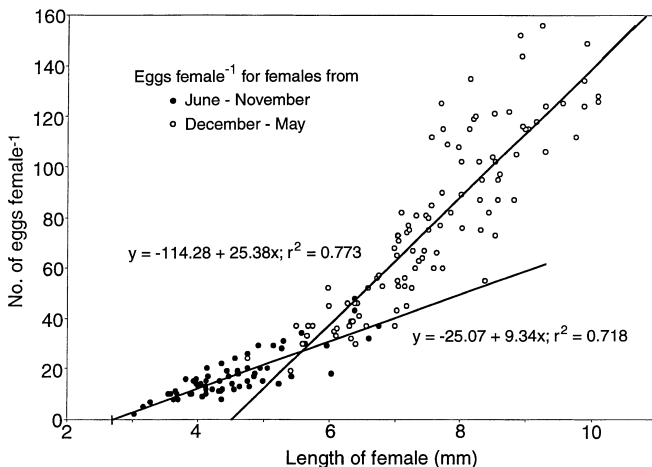


Fig. 6 *Dyopodos monacanthus*. Relationship of body length of females and number of eggs in their brood pouch during periods June to November ($n = 64$) and December to May ($n = 103$); all females from the respective months are pooled regardless of year (1995, 1996 or 1997) in which they were collected

viding for offspring (Fig. 5). The number of eggs female⁻¹ was significantly correlated with the size of the females (Fig. 6), but the slope of this relationship differed significantly between the warm time-period (June to November, water temperatures > 8 °C) and the cold time-period (December to May, water temperatures ≤ 8 °C) (Fig. 6) (F -test; $P < 0.01$).

Almost all amphipods collected at the sampling site inhabited mud whips. Some individuals were sitting on pine needles or other exposed substrates. The majority of mud whips was at least 5 mm long. Mud whips of large non-parental amphipods were only slightly larger than those of small individuals (Fig. 7), whereas a strong positive correlation was found between the size of parental females and the size of their mud whips ($P < 0.01$; Fig. 7); i.e. large females can build and defend larger mud whips than small females. The slopes of the two regression lines (parental females versus non-parental individuals) were significantly different (F -test; $P < 0.01$). The smallest mud whip was 1 mm short, while the longest mud whip was 91 mm long.

Juveniles on maternal and adults/subadults on their own mud whips

Most juveniles on their mothers' mud whips were ~1 mm in size, but many of them also reached larger sizes (Fig. 8). During the main reproductive period in late winter/early spring, large numbers of juveniles were > 1.4 mm, while during the summer months almost no juveniles reached sizes > 1.4 mm on the maternal mud whips (Fig. 8). Correspondingly, there were always a few subadults < 2.0 mm on their own mud whips during the summer months, while during the winter months amphipods < 2.0 mm were rarely found on their own mud whips (Fig. 9). The size-frequency distribution of amphipods on their own mud whips shifted towards larger size between October and February and back towards smaller size between April and June each year (Fig. 9). Thus, the population is dominated by small individuals during the months June to November and by large individuals during the months December to May in each year (Fig. 9).

Densities of *Dyopodos monacanthus* on shallow subtidal soft-bottom and in water column

The densities of *Dyopodos monacanthus* at the study site were low during the summer and fall, began to increase in the winter, and reached maximum values during the spring (Fig. 10). Following peak densities of > 3000 individuals m⁻² in April 1996 (> 1600 individuals m⁻² in May 1997), a steady decline was observed during the summer and fall culminating in minimum densities of 2.8 ± 1.0 SE individuals m⁻² in October 1995 and 2.4 ± 1.3 individuals m⁻² in October 1996 (Fig. 10). The numbers of drifting individuals (data from the ad-

adjacent Sheepsfoot River Estuary 1971 to 1979) reached high values during late spring/summer, but, numbers were low during the rest of the year (Fig. 11). The size-frequency distribution of drifting amphipods collected in the Damariscotta River Estuary indicates that during the summer and fall primarily small individuals are found drifting, whereas the few pelagic individuals collected in March were relatively large (Fig. 12).

Discussion

Both extended parental care and pelagic movements are important behavioural traits of the epibenthic amphipod *Dyopetos monacanthus*. The extent to which the population at the study site engages in these two behaviours changes seasonally. Juveniles grow to large sizes under parental care during the winter months, but not during the summer months. Pelagic movements of *D. monacanthus* occur less frequently during the winter months than during the summer months. A major focus during the following discussion will be on the effect of parental care and pelagic movements on the population dynamics of *D. monacanthus*.

Life history of *Dyopetos monacanthus*

The life history of *Dyopetos monacanthus* is characterized by distinct seasonal changes in female fecundity, extent of parental care and pelagic movements. During the cold months (water temperatures ≤ 8 °C: December to May) amphipods grow to large sizes, females produce many eggs; they raise their juveniles to large sizes on their mud whips and pelagic movements are rare. During the warmer months (water temperatures > 8 °C: June to November) the opposite occurs. Despite these strong seasonal changes, reproduction appears to be continuous in *D. monacanthus*, as indicated by the high percentages of ovigerous females present throughout the year. This reproductive pattern is unusual for amphipods from temperate waters, most of which have one or two distinct reproductive periods each year (Mills 1967; Wildish 1980, 1984; McBane and Croker 1984; Morgan and Woodhead 1984; Collie 1985; Donn and Croker 1986; Highsmith and Coyle 1991; Wilson and Parker 1996; Thiel 1997d). The reproductive periods of these amphipods often are closely coupled with the availability of food resources (Wildish 1982; Bethune 1995). *D. monacanthus* is found in large numbers in an area just below mean low water, where high concentrations of benthic microalgae occur year-round and are frequently resuspended (Thiel 1997c) making them available for suspension-feeding organisms. Thus, continuous availability of food resources may enable *D. monacanthus* to reproduce year-round. Sheader (1983) described continuous reproduction (except in June, July) for the mobile species *Gammarus duebeni*, an omnivorous species that can feed on a variety of food resources that are

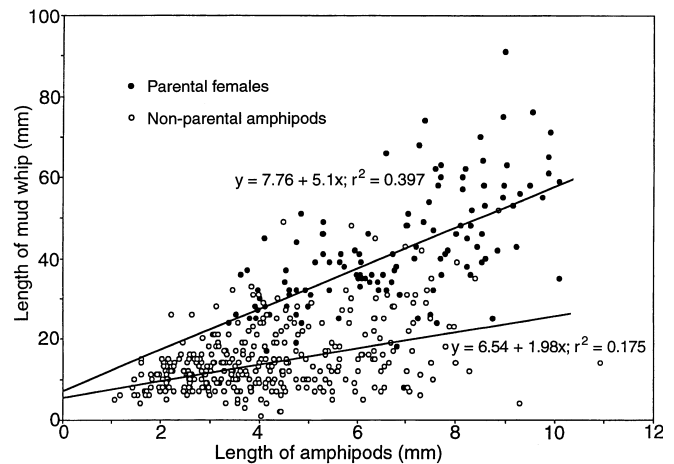


Fig. 7 *Dyopetos monacanthus*. Relationship of body length of amphipods and length of their mud whips (*Parental females* females with juveniles, $n = 122$; *Non-parental amphipods* subadults, females without juveniles, and males, $n = 348$)

available throughout most of the year. Although *D. monacanthus* reproduces continually, there are seasonal changes in the number of eggs produced. The fecundity of small females *D. monacanthus* that dominate the adult population during the warm months (> 8 °C) is relatively low, while that of large females which are most abundant during the cold months (≤ 8 °C) is comparatively large. This trend has also been observed in a variety of other epibenthic and endobenthic amphipods, and is thought to be directly driven by temperature (Nelson 1980; McBane and Croker 1984; Highsmith and Coyle 1991). Nelson (1980) suggested that for epibenthic amphipods the lower fecundity and possibly faster developmental rates during the summer months could be a strategy to reduce predation risk for embryos and juveniles. Predators that select for large amphipods (Caine 1989), may play a direct role in driving populations of benthic amphipods towards small, less fecund females during the summer months.

Not only fecundity but also the extent of parental care provided by female *Dyopetos monacanthus* varies between summer and winter. During summer months, juveniles never grew much larger than 1.4 mm on their mother's mud whip, while during the winter and spring months many such juveniles attained sizes > 1.4 mm. The fact that many juveniles leave their mothers at small sizes during summer/fall is reflected by the finding that during that time amphipods < 2 mm inhabited their own mud whips but not during winter/early spring (Fig. 9). The limited extent of parental care in *D. monacanthus* during the summer months is possibly a result of frequent escape movements caused by predator activities. *D. monacanthus* responds to benthic predators, such as decapod shrimp, by immediate escape into the water column (Thiel 1998), a behavioural reaction typical for benthic amphipods (Ambrose 1984; Ólafsson and Persson 1986; Thiel and Reise 1993; Thiel 1997e). Frequent encounters with benthic predators during the

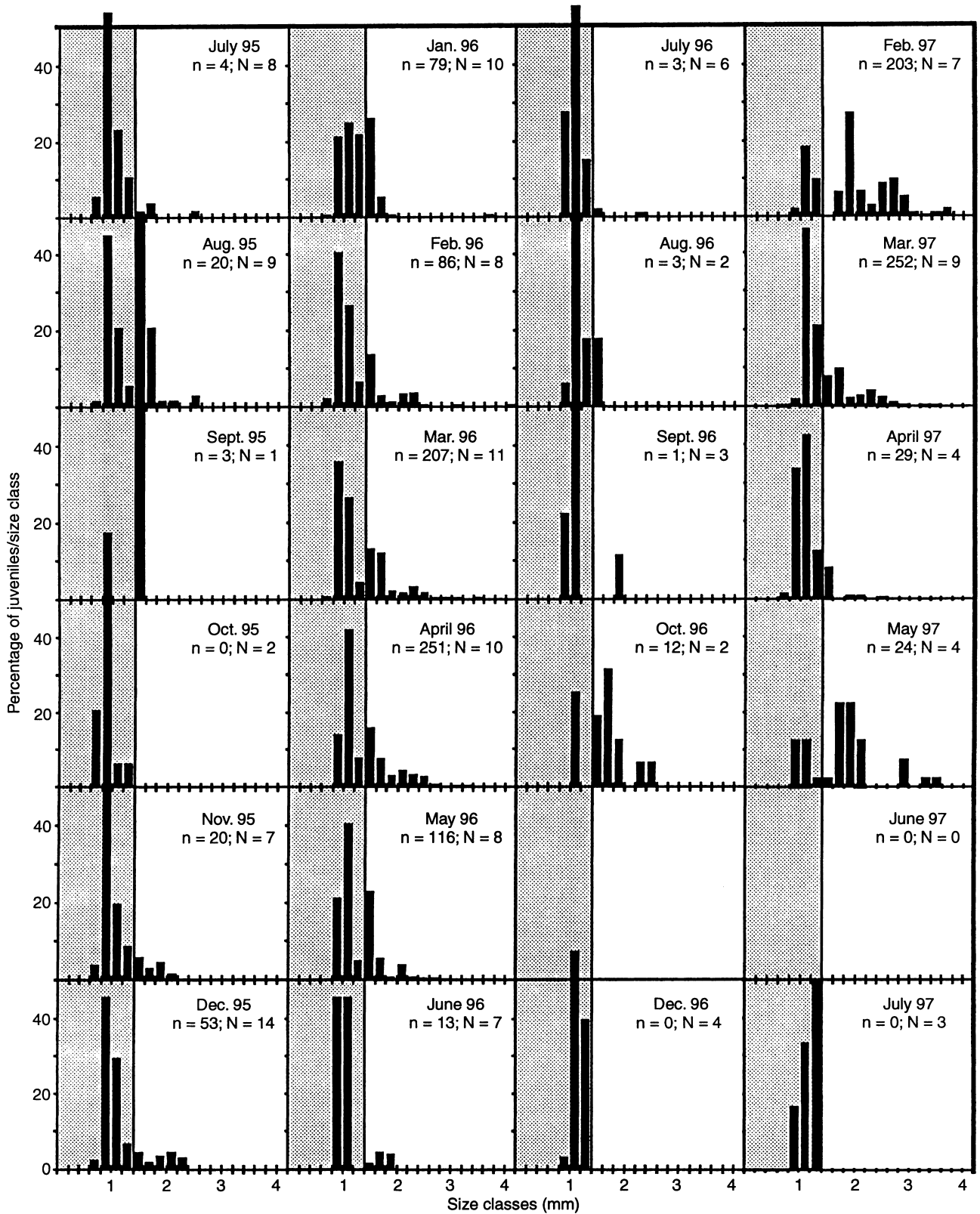


Fig. 8 *Dyopodos monacanthus*. Numbers of juveniles in respective size classes found on mud whips of parental females between July 1995 and July 1997; all juveniles from each sampling date were pooled (*n* number of juveniles > 1.4 mm; *N* total number of parental females found on each sampling date)

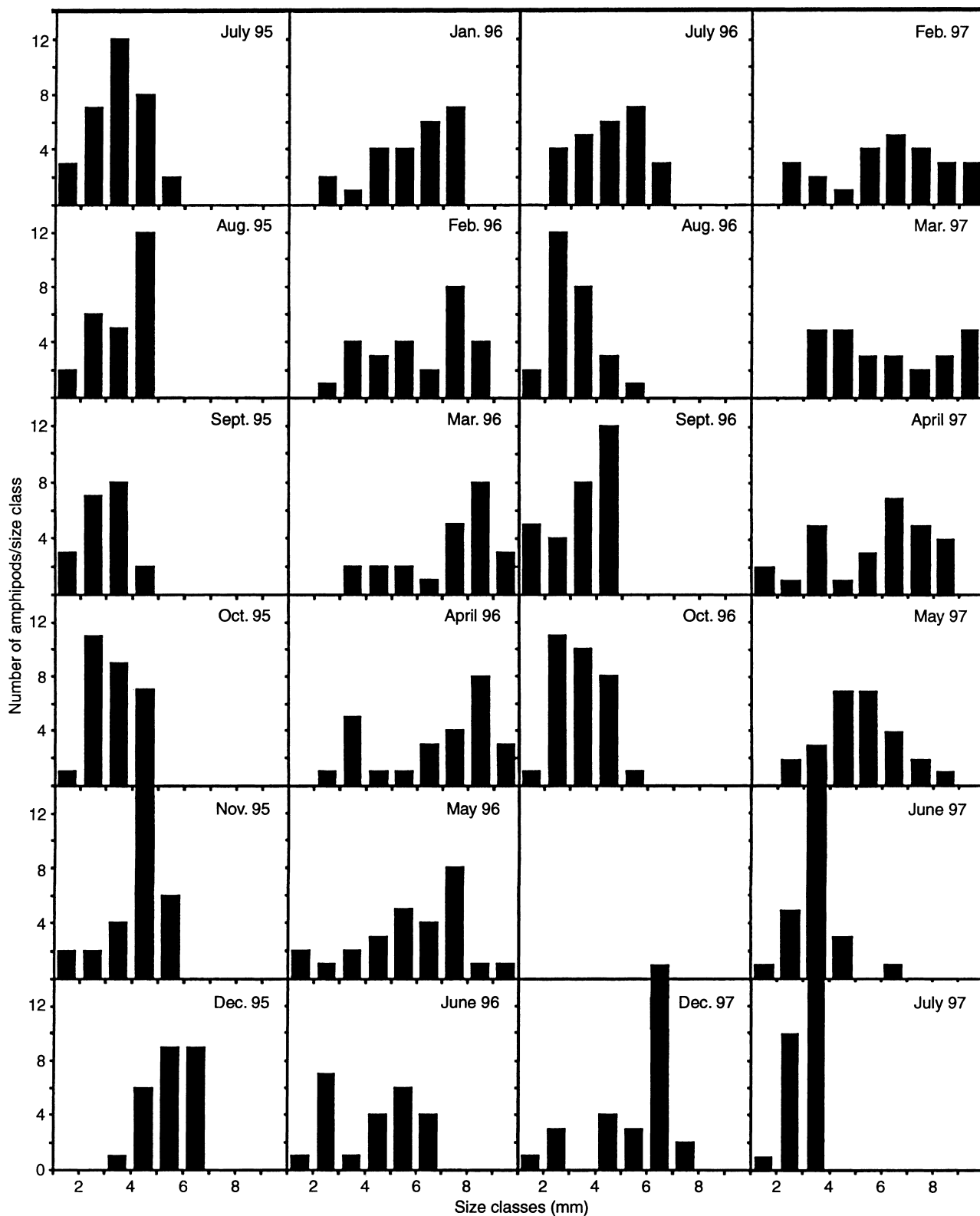


Fig. 9 *Dyopodos monacanthus*. Number of amphipods in respective size classes collected on their own mud whips between July 1995 and July 1997; whip-sharing females and males (= pairs) also included

Fig. 10 *Dyopodos monacanthus*. Average densities (individuals $m^{-2} \pm 1$ SE) 2 m below mean low water between October 1995 and July 1997; 10 to 20 plots were counted on each sampling date

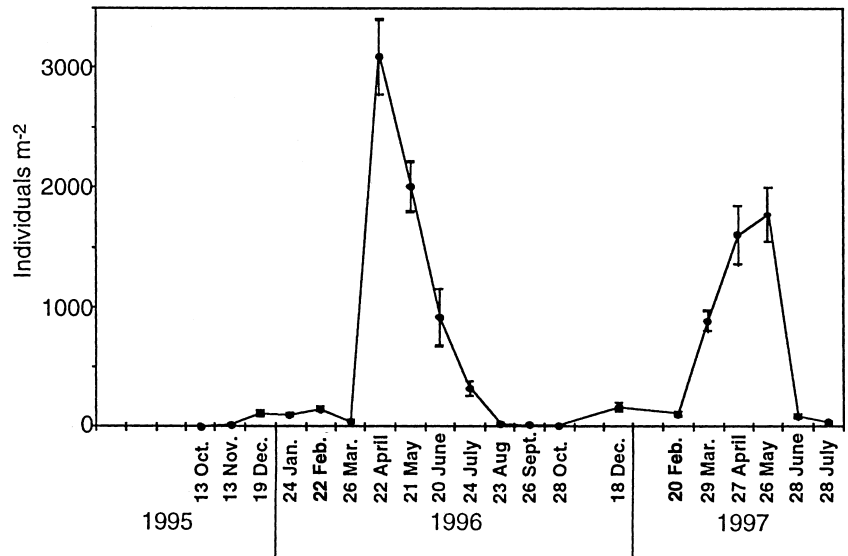
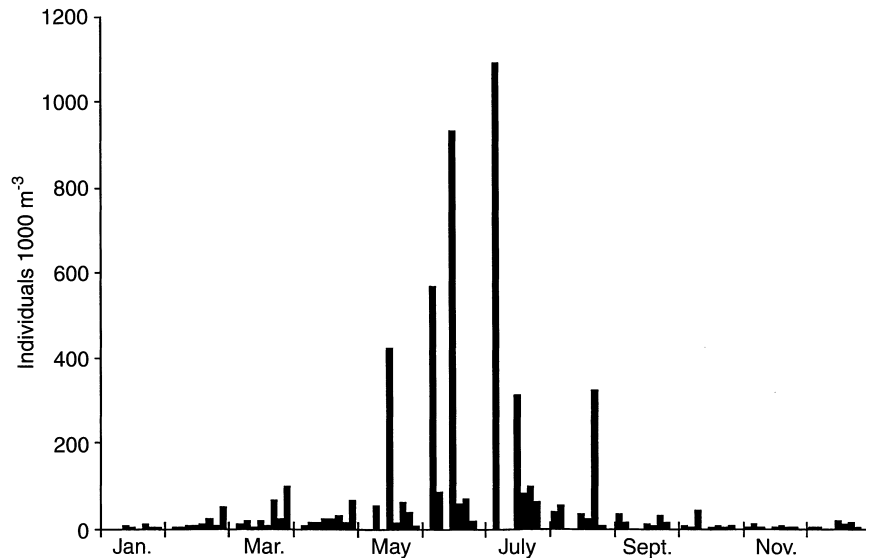


Fig. 11 *Dyopodos monacanthus*. Average densities (individuals $1000 m^{-3} \pm 1$ SE) in water column in Sheepscot River Estuary. Numbers from three different depth levels and ebb and flood tides were pooled; columns for each month represent, from left to right, the years 1970, 1971, 1972, 1973, 1975, 1976, 1977, 1978 and 1979



summer months may cause small juveniles and their mothers to release their hold on the maternal mud whips in order to escape via the water column. This assumption is further underlined by the large numbers of *D. monacanthus* found in the water column during the summer months, when predator abundance and activity is highest.

Juveniles gain two major advantages from spending their first weeks on their mother's mud whip: they are protected from intraspecific aggression and they are lifted into water layers with a good food supply. Offspring survival in *Dyopodos monacanthus* is substantially enhanced when juveniles can remain on the maternal mud whip until they are > 1.4 mm (e.g. Thiel 1998), at which size they are large enough to build relatively long mud whips which they also may successfully defend against intraspecific competitors. In the field, some

D. monacanthus in the size range 2 to 3 mm already occupied their own, > 20 mm-long, mud whips, while no individuals < 2 mm were found on mud whips of that length.

The length of mud whips of parental females is positively correlated with parental female size, reflecting the fact that large females produce many offspring that have to be cared for on the maternal mud whip. Mud whips of parental *Dyopodos monacanthus* were usually > 30 mm long, while those of non-parental individuals were mostly between 7 and 30 mm long. Thus, small juveniles that live on the maternal mud whip feed in water layers above the rest of the amphipod population. This may be a method of avoiding intraspecific competition, particularly during late winter/early spring when abundances of *D. monacanthus* on shallow subtidal soft-bottoms are high.

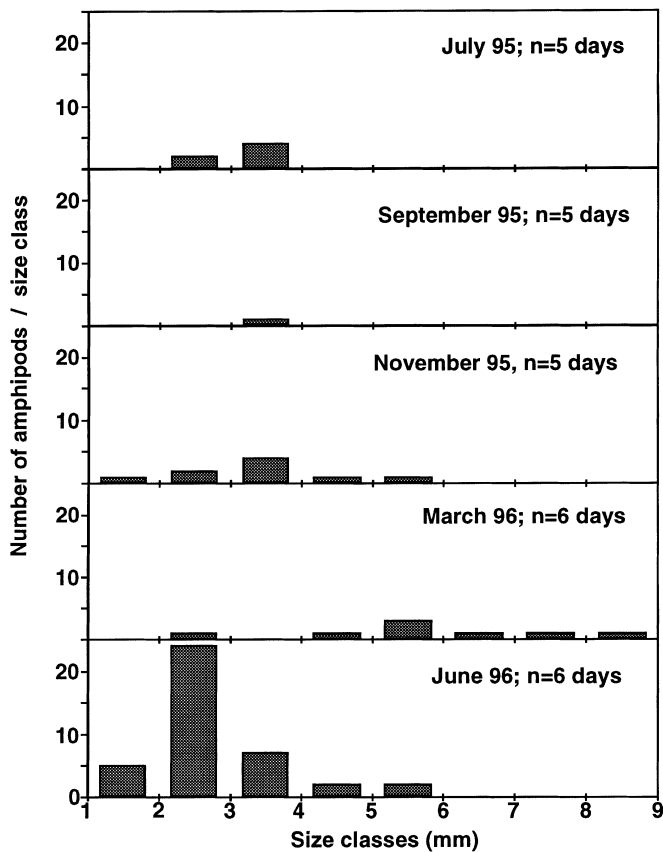


Fig. 12 *Dyopodos monacanthus*. Number of amphipods in respective size classes trapped in seawater intake filter of Darling Marine Center between July 1995 and June 1996; all amphipods collected during *n* days were pooled

Male *Dyopodos monacanthus* have a much more motile life-style than females. Similar to many endobenthic amphipods (see Borowsky 1983), female *D. monacanthus* remain on their mud whips while males roam to find receptive females. Often > 50% of male *D. monacanthus* were found on female mud whips, where they may stay for several days until a female molts and its eggs can be fertilized (Thiel 1997b). The fact that at a given time only the largest females were reproductive (ovigerous or parental) suggests that males select for large females which usually also occupy the largest mud whips. Other studies have experimentally demonstrated that males of the highly mobile amphipods *Eogammarus oclairi*, *Gammarus pulex* and *G. duebeni celticus* select for larger females (Iribarne et al. 1995; Dick and Elwood 1989, 1996). In *D. monacanthus*, females may among themselves compete for long mud whips (e.g. Thiel 1997b), which are important tools for raising large numbers of juveniles to large sizes.

The results indicate that in *Dyopodos monacanthus* a cascade of intraspecific competitive interactions (females for long mud whips, males for large females) results in selection for prolonged parental care throughout the cold time-period. This intraspecific selection is counter-balanced by interspecific predation, which selects against

long-lasting parental care in *D. monacanthus* during the warm time-period, since long mud whips with large numbers of juveniles are susceptible to epibenthic predators.

Population biology of *Dyopodos monacanthus*

The population development of *Dyopodos monacanthus* at the shallow subtidal study site is characterized by high abundances in late winter/early spring followed by a steep decline and low abundances in summer/fall. This pattern is also typical for other epibenthic peracarids (Nelson 1979b; Aoki 1988). Predation is thought to be responsible for the steep decline in numbers of epibenthic amphipods early in the spring season (Nelson 1979b; Aoki 1988; Caine 1991). *D. monacanthus* is an important prey item for demersal fish (Mattson and Cedhagen 1989) and shrimp (Thiel own observation), and it seems likely that these predators feast on the conspicuous epibenthic amphipods when they return to shallow estuaries in spring/early summer. The low abundance of *D. monacanthus* during the summer/early fall is most probably a combination of factors such as the high degree of pelagic movements, the low reproductive potential of small females, and the low numbers of juveniles growing to > 1.4 mm on the maternal mud whips. These factors may directly (pelagic movements) or indirectly (female fecundity, extent of parental care) be affected by the strong predation pressure on shallow subtidal soft-bottoms during the summer months. With predation pressure lasting throughout the summer, pelagic movements remain at a high intensity while female fecundity and extent of parental care remain low. Large individuals of *D. monacanthus* are the first to disappear in late spring/early summer, but a few small individuals remain at the study site throughout the summer. Despite the high predation pressure, some of these small females successfully "sneak in" a few offspring during the summer months. If predators select for large *D. monacanthus*, as has been shown for other epibenthic amphipods (Caine 1989), then small females may have a good chance to produce a few offspring during the summer. These "summer"-females probably are highly motile, and apparently can only care for their offspring for short time periods. Nevertheless, a few of these offspring may survive and contribute to the slow increase of the local population in the fall. When water temperatures decrease in the fall, most predators leave the shallow parts of temperate estuaries and become increasingly inactive (Tyler 1971; Embich 1973; Corey 1981; Hacunda 1981). With the main predators gone, the ability of *D. monacanthus* to build and occupy mud whips for long time periods increases, as indicated by increasing numbers at the study site. The slow increase of the benthic population during the fall is accompanied by decreasing numbers of amphipods in the water column.

Reasons for pelagic movements of benthic amphipods include search for mates, dispersal, migration be-

tween seasonal habitats, catastrophic migrations and avoidance of deteriorating conditions (Mills 1967; Grant 1980; Sainte-Marie and Brunel 1985; Essink et al. 1989; Kaartvedt 1989; Chevrier et al. 1991; Sudo and Azeta 1992; Johansson 1997). When occurring, pelagic movements can result in substantial emigration losses or immigration gains to local benthic populations (Watkin 1947; Mills 1967; Sainte-Marie and Brunel 1983; Collie 1985). The time period when many *Dyopodos monacanthus* disappear from the shallow subtidal soft-bottoms coincides with a strong increase of their numbers in the water column. In the Sheepscot and Damariscotta River estuaries, most pelagic *D. monacanthus* are found during the summer months when benthic predators are abundant and active in these shallow estuaries. Numbers of *D. monacanthus* on shallow subtidal soft-bottoms and in the water column decrease continuously throughout the summer, possibly as a consequence of intense predation pressure from both benthic and pelagic predators. At present it is not entirely clear whether the pelagic *D. monacanthus* remain in the estuaries and simply exhibit a highly motile life style during the summer months, or whether they move towards deeper waters. *D. monacanthus* is also common on deep subtidal soft-bottoms (Dickinson et al. 1980; Dickinson and Wigley 1981) where pelagic movements are also frequently observed during the summer months (Chevrier et al. 1991).

In shallow estuaries along the northern North Atlantic, *Dyopodos monacanthus* and other epibenthic amphipods constitute important prey items for commercially important fish species (e.g. Mattson and Cedhagen 1989). Herein, it has been shown that an estuarine population of *D. monacanthus* reaches high abundances during winter/early spring, much earlier than many endobenthic amphipods such as *Ampelisca agassizi* (Bethune 1995), *Unciola inermis* (Morrison 1993), *Corophium volutator* (Wilson and Parker 1996) and *Leptocheirus pinguis* (Thiel 1997d). Thus, estuarine populations of *D. monacanthus* (and other epibenthic amphipods) may constitute the first available food for demersal fish returning to shallow estuaries early in the summer.

Extended parental care and pelagic movements substantially improve the survival chances of juvenile and subadult *Dyopodos monacanthus*. In an experimental study, Aoki and Kikuchi (1991) demonstrated that juvenile survival was significantly higher in an epibenthic amphipod with extended parental care than in a similar species not engaging in this reproductive strategy. Despite its potential implications for the population dynamics of benthic amphipods, few studies have thoroughly examined the occurrence of extended parental care (for exception see Shillaker and Moore 1987). Even in well-studied species such as *Corophium volutator*, extended parental care (see Thamdrup 1935) has rarely been taken into account in recent studies of its population dynamics (Murdoch et al. 1986; Jensen and Kristensen 1990; Wilson and Parker 1996) or genetic

population structure (Wilson et al. 1997). Many studies mention that local amphipod populations can appear or almost completely vanish over short time periods, and this is usually attributed to pelagic movements (Watkin 1947; Mills 1967; Collie 1985). Pelagic movements are important behavioural traits of benthic amphipods, and survival of local populations may depend on individuals that successfully escape benthic predators by emigrating via the water column. Therefore, future studies on population dynamics of benthic amphipods should examine both pelagic movements and extended parental care.

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