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Reproductive biology of a deposit-feeding amphipod, *Casco bigelowi*, with extended parental care

Received: 25 November 1997 / Accepted: 14 April 1998

Abstract The reproductive traits of a deposit-feeding amphipod that engages in extended parental care were examined. At the study site in Lowes Cove, Maine, USA, *Casco bigelowi* (Blake, 1929) occurred in highest densities in soft sediments just below mean low water (MLW). During most months, the sex ratio was ≈ 1 . Many females hosted males in their burrows throughout the summer, but after fertilization of females in September, all adult males disappeared from the study area. In October almost 80% of the females were ovigerous, and in November about the same percentage was parental, i.e. caring for juveniles in their burrows. The females produced only one brood each in late fall which they accommodated in their burrows for 2 mo or longer. The average number of juveniles per female was ~ 20 in November, and continuously decreased until January. Juveniles reached sizes >10 mm length in the maternal burrows. In early December the first juveniles were found in their own burrows, but major recruitment took place in late December and January. It is concluded that for *C. bigelowi*, the delay of recruitment into the winter months with low predation pressure and the large offspring size at this time are major advantages gained by extended parental care. *C. bigelowi* is host to the peritrich ciliate *Cothurnia* sp. on its gills, and during the summer months $>70\%$ of all amphipods had ciliates on their gills. Juveniles still living in their mother's burrows showed infestation rates similar to that of the parent; those of highly infested mothers were more heavily in-

festated than those of "clean" mothers. Facilitated epibiont transmission during intimate and long-lasting (2 mo) parent-offspring associations may be a consequence of extended parental care.

Introduction

In most peracarid crustaceans, fully developed juveniles or highly advanced larval stages emerge from the female's brood pouch. While juveniles of most species leave their mothers immediately after hatching from the brood pouch, in some species they remain with their parents for extended time periods. The latter species spend considerably longer time periods caring for developing offspring than most species in their respective phylogenetic group. Parental care that lasts for time periods extending beyond that commonly found among related species is termed "extended parental care".

Several different peracarid crustaceans offer extended parental care to their growing offspring. This reproductive strategy has been found in epibenthic amphipods such as the Podoceridae (Mattson and Cedhagen 1989) and Caprellidae (Aoki and Kikuchi 1991; Aoki 1997; Thiel 1997a), as well as in endobenthic, burrow-living species (Thamdrup 1935; Shillaker and Moore 1987; Thiel et al. 1997). Extended parental care involving parental feeding, cleaning and defense of fully developed juveniles is not a common reproductive strategy in the marine environment, but the reasons for this are not yet known. From almost any marine invertebrate phylum, a few species with some form of extended parental care are known, suggesting that the low number of species engaging in this reproductive strategy is not a result of phylogenetic, but rather of ecological constraints.

Extended parental care, as found in some marine peracarids (Thiel et al. 1997), is one of the most advanced forms of social behavior encountered among marine invertebrates. Juvenile peracarids may remain with their parents for periods of >50 d, and reach

Communicated by N. Marcus, Tallahassee

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remarkable sizes during this time (see Conlan and Chess 1992; Svavarsson and Davidsdottir 1995; Thiel et al. 1997). During extended parental care, peracarid offspring can gain substantial advantages such as improved growth and survival (Aoki 1997; Thiel 1997b). Shelter from intra- and interspecific predation appears to be one of the most important benefits for juveniles of tube- and burrow-living peracarids that engage in extended parental care (Thiel 1997b). Although it may be advantageous for offspring to remain together with their parents as long as possible (i.e. shortly before reaching reproductive maturity), potential conflicts such as increasing competition among siblings and facilitated parasite transmission may prevent this.

Casco bigelowi (Blake, 1929) is a melitid amphipod which inhabits burrows in muddy sediments from the low intertidal to deeper subtidal waters (<150 m depth) along the Atlantic coast of North America (Wildish 1980, 1984). The amphipods feed on subsurface sediments which they excavate, process and immediately redeposit within their burrow systems (Thiel et al. 1997). *Maera loveni*, another melitid amphipod that occurs in subtidal soft-bottoms along the North Atlantic coasts, has a similar life-style and is sometimes found in large burrow systems containing up to 14 individuals per burrow (Atkinson et al. 1982). *C. bigelowi* is not considered abundant; densities rarely exceed 100 individuals m^{-2} (Wildish 1980, 1984). During the reproductive period, females accommodate their growing offspring in their burrows (Thiel et al. 1997). *C. bigelowi* often occurs in the same habitat together with *Leptocheirus pinguis* (Stimpson 1853) (Wildish 1980, 1984), a filter-feeding endobenthic amphipod that also engages in extended parental care (Thiel 1997c; Thiel et al. 1997).

The aim of the present study was to provide a detailed description of extended parental care in *Casco bigelowi*, to determine the time period when it reproduces, and the duration of parental care in this deposit-feeding amphipod. The peritrich ciliate, *Cothurnia* sp., a common epibiont on marine and freshwater amphipods (Warren and Paynter 1991), was found in large numbers on the gills of *Casco bigelowi*. In close aggregations of conspecifics such as parent-offspring groups, epibiont transmission between individuals can be significantly enhanced (see e.g. Brown and Bomberger Brown 1996). The seasonal occurrence of *Cothurnia* sp. on female, male and subadult amphipods was recorded. Particular attention was given to offspring of females with known loads of peritrichs to determine whether these epibionts are transferred from mothers to their offspring during extended parental care.

Materials and methods

Study area and sampling of amphipods

The study was conducted in Lowes Cove, Damariscotta River Estuary, Maine (43°56'N; 69°35'W). The seasonal water tempera-

tures at the site vary between 0 °C during the winter months and 18.5 °C in August (Thiel unpublished data; see also Wilson and Parker 1996). Individual *Casco bigelowi* (Blake, 1929) were collected at a station 0.3 m below mean low water (MLW). Samples were taken during spring low tides, when the tidal flats were exposed for ~1 h. To collect individual burrows and their inhabitants, a core of 10 cm diam was placed over a burrow, gently pushed into the sediment to a depth of about 15 cm, closed at the top and bottom, and immediately transferred to the laboratory, where the burrow was carefully dissected and its inhabitants collected. In cases where amphipods could not be safely assigned to individual burrows, the samples were discarded. Amphipods were preserved in 4% formalin, later transferred to 70% ethanol, and then measured along their dorsal surface from the rostrum to the base of the telson with a computer-based video-image analysis system. All adult amphipods were sexed, and females were checked for eggs in their brood pouches. The term "parental female" is exclusively used for those females that had juveniles in their burrows. The gills of all adults and juvenile amphipods were examined under a dissecting microscope for the presence of the peritrich ciliate *Cothurnia* sp. Five different infestation categories were distinguished (0, 1 to 10, 11 to 20, 21 to 50 and >50 peritrichs $gill^{-1}$). The amphipods were scored according to the highest infestation category that was found on at least one gill.

To determine amphipod densities, sediment samples of 176 cm^2 surface area were taken to a depth of 15 cm, sieved over a 500 μm -mesh, preserved in 4% formalin, transferred to 70% ethanol, and later sorted under a dissecting microscope. Six replicate samples were taken at each of four stations in spring, summer, fall and winter (May, August, November 1994 and February/March 1995, respectively). Because of low amphipod densities, six additional samples were taken at each of the two stations at MLW and 0.3 m below MLW in November 1994 and February/March 1995. The sediments at all stations consisted of fine muds (60 to 80% porosity). The stations were ~0.3 m above MLW, at MLW, 0.3 m below MLW, and ~2 m below MLW.

Information on numbers of *Casco bigelowi* drifting in the water column were gained by evaluating data from a previously conducted long-term study on macrozooplankton. Plankton nets (750 μm mesh size) were exposed over night for about 6 h at ebbing tide and 6 h at flood tide at three different depths levels (~1, 4 and 14 m below the surface). Each net had a flow meter attached to the center of the net opening to determine filtered water-volume. The data were collected monthly during the periods August 1971 to April 1973 and January 1975 to May 1979 at a station in the Sheepscot River Estuary (43°59'N; 69°39'W) (BJ McAlice and GB Jaeger, Jr unpublished data), which is adjacent (~10 km distant) to the Damariscotta River Estuary.

Results

Population structure of *Casco bigelowi*

From April to September, the sex ratio of *Casco bigelowi* was ≈ 1 . However, in October >97% and in November 100% of all amphipods collected were females (Fig. 1). The first subadults were found in their own burrows at the beginning of December, and their proportion steadily increased during the following months. In February and March 1995, almost the entire population consisted of these newly recruited individuals (Fig. 1). During the summer months, up to 45% of the adult females were hosting male visitors in their burrows (Fig. 2), but the first ovigerous females were not found before September 1994. More than 60% of all females were paired with males, and 26.7% were ovigerous in September 1994. By October 1994, the proportion of

Fig. 1 *Casco bigelowi*. Percentage of females, males and subadults in individual burrows (Nos. on top of bars total number of individuals collected on each sampling date 0.3 m below mean low water in Lowes Cove between May 1994 and May 1995)

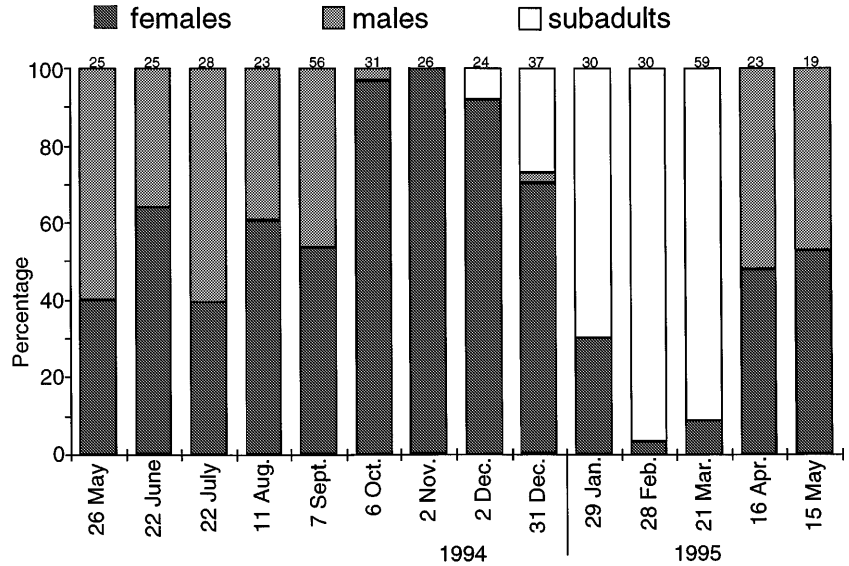
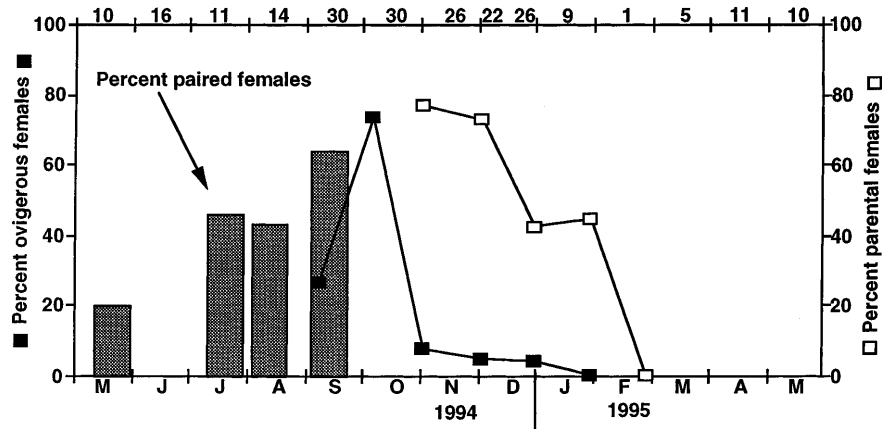


Fig. 2 *Casco bigelowi*. Percentage of paired females (with male visitors) (histograms), and of ovigerous and parental females (Nos. on top abscissa number of adult females found on each sampling date)



ovigerous females had increased to almost 80%. Most juveniles emerged from the females' brood pouches during the month of October, as indicated by a decrease in ovigerous females to ~7.7% until 2 November 1994, when the majority of females were parental (i.e. caring for juveniles). The percentage of these parental females remained high until early December 1994, when ~80% of all females were parental; it then dropped to about 40% in late December 1994, and remained at this level until the end of January 1995. At the end of February, no more parental females were found (Fig. 2).

Reproductive potential of female *Casco bigelowi*

No significant correlation between the number of eggs and juveniles per female and female size was found (Fig. 3) (Spearman rank-correlation, $p > 0.1$). The smallest ovigerous female was 19.6 mm in length (7 September 1994), and the largest parental female

was 26.4 mm (2 November 1994). Average female length increased to $\approx 21.9 \text{ mm} \pm 0.5$ (mean \pm SE) in June 1994, and remained at this level during the rest of the summer (Fig. 4A). Male *Casco bigelowi* showed a similar trend in size (Fig. 4A). Most males disappeared between September and October, when only one adult male was found (Fig. 4A). Only one other adult male was found, on 31 December 1994. In January 1995, the first subadult males were found in their own burrows. The average length of males increased from $\approx 14.1 \text{ mm} \pm 0.7$ in January 1995 to $20.2 \pm 1.0 \text{ mm}$ in May 1995. The average number of eggs per female was 43.3 ± 4.9 in September and 42.8 ± 2.2 in October (Fig. 4B). The highest number of eggs carried by one females was 69 on 31 December 1994 (Fig 4B). Up to 56 juveniles were found in the burrow of one female *C. bigelowi* (2 November 1994), but some females accommodated only a few juveniles at the time of sampling. The average number of juveniles per female decreased from 20.5 ± 3.5 (2 November 1994) to 5.0 ± 1.7 on 29 January 1995

Fig. 3 *Casco bigelowi*. Number of eggs and juveniles per female as a function of female size. All ovigerous ($n = 27$) and parental ($n = 40$) females collected between May 1994 and May 1995 are pooled

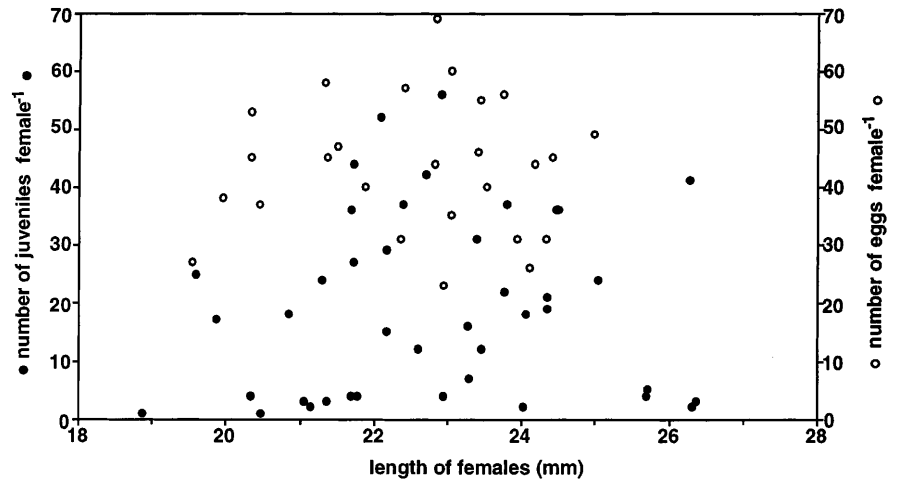
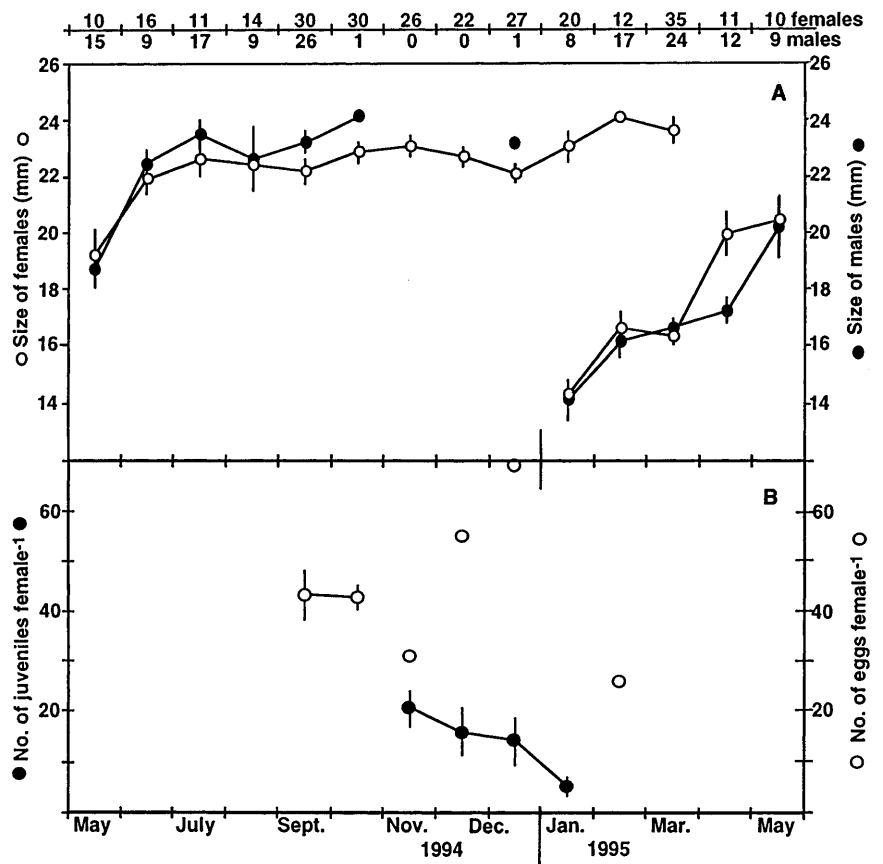


Fig. 4 *Casco bigelowi*. **A** Average length (± 1 SE) of females and males; **B** average number of eggs or juveniles per ovigerous or parental female, respectively (Nos. on top abscissa number of females and males found on each date)



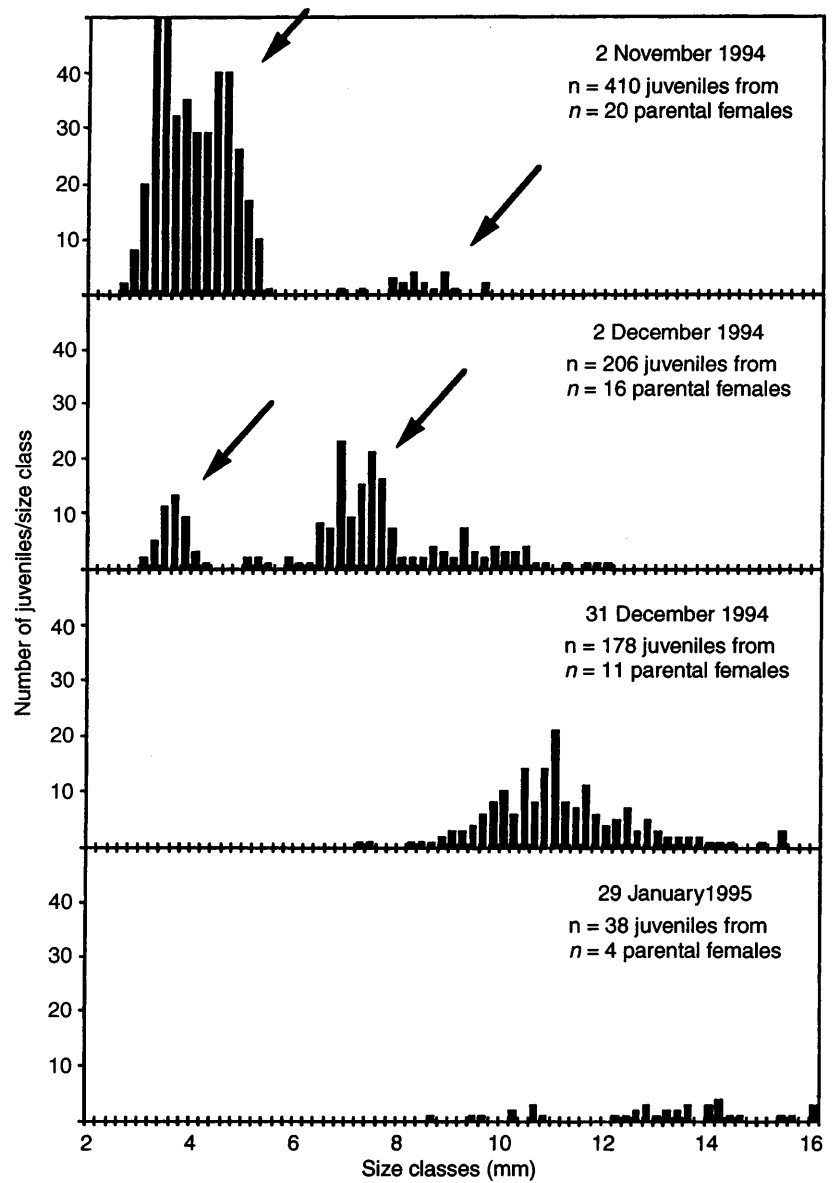
(Fig. 4B). Parental females were never found to be ovigerous, indicating that each female produces only one brood.

Size of juveniles in female burrows and of adults and subadults in their own burrows

The size of juveniles found in their mother's burrow varied between 2.7 (smallest juvenile found on

2 November 1994) and 17.8 mm in length (largest juvenile found on 29 January 1995). In each female burrow, only one cohort of juveniles was found, again indicating that only one brood is produced by each female. Even after pooling the juveniles from all females collected at each sampling date, distinct size cohorts can be recognized (arrows in Fig. 5). The majority of juveniles in November 1994 were between 3 and 5 mm in length, but a few had already grown to between 7 and 9 mm. The distinct separation of many small juveniles

Fig. 5 *Casco bigelowi*. Numbers of juveniles of various size classes (length, mm) found in burrows of parental females between November 1994 and January 1995; all juveniles from each sampling date were pooled (Arrows indicate distinguishable cohorts)



and a few large juveniles indicates that the latter were most probably born earlier than the small ones. On 2 December 1994 there was another cohort of small juveniles but the majority of juveniles were ≥ 6 mm in length. On 31 December 1994 most juveniles found were ≥ 10 mm and on 29 January 1995 most juveniles found were ≥ 12 mm. During the rest of the year no juveniles were found in female burrows.

In May 1994 most of the burrow occupants (= recruits + a few adult females) were > 15 mm in length (Fig. 6). These grew quickly to ≥ 18 mm until June 1994; thereafter, they did not grow during the rest of the summer. Even after the majority of females had molted (during oviposition in September), no change in size-frequency distribution was observed (Fig. 6). The first small recruit was found on 2 December 1994, and in the following months the numbers of recruits steadily

increased, while the large mature females disappeared (Fig. 6). The newly recruited individuals grew quickly between February and May 1995. Since many of these new recruits had reached adult size already in April 1995 they could not be distinguished from adults, and it cannot be excluded that some of their mothers survived until May 1995 and possibly later.

Seasonal occurrence of peritrich ciliate on amphipod gills

Most amphipods were hosts to the peritrich *Cothurnia* sp. on their gills (Fig. 7). Some individuals hosted large numbers of this peritrich on their gills (> 50 peritrichs gill^{-1}). During the summer months (June to August 1994), the epibiont load of males was higher than that of

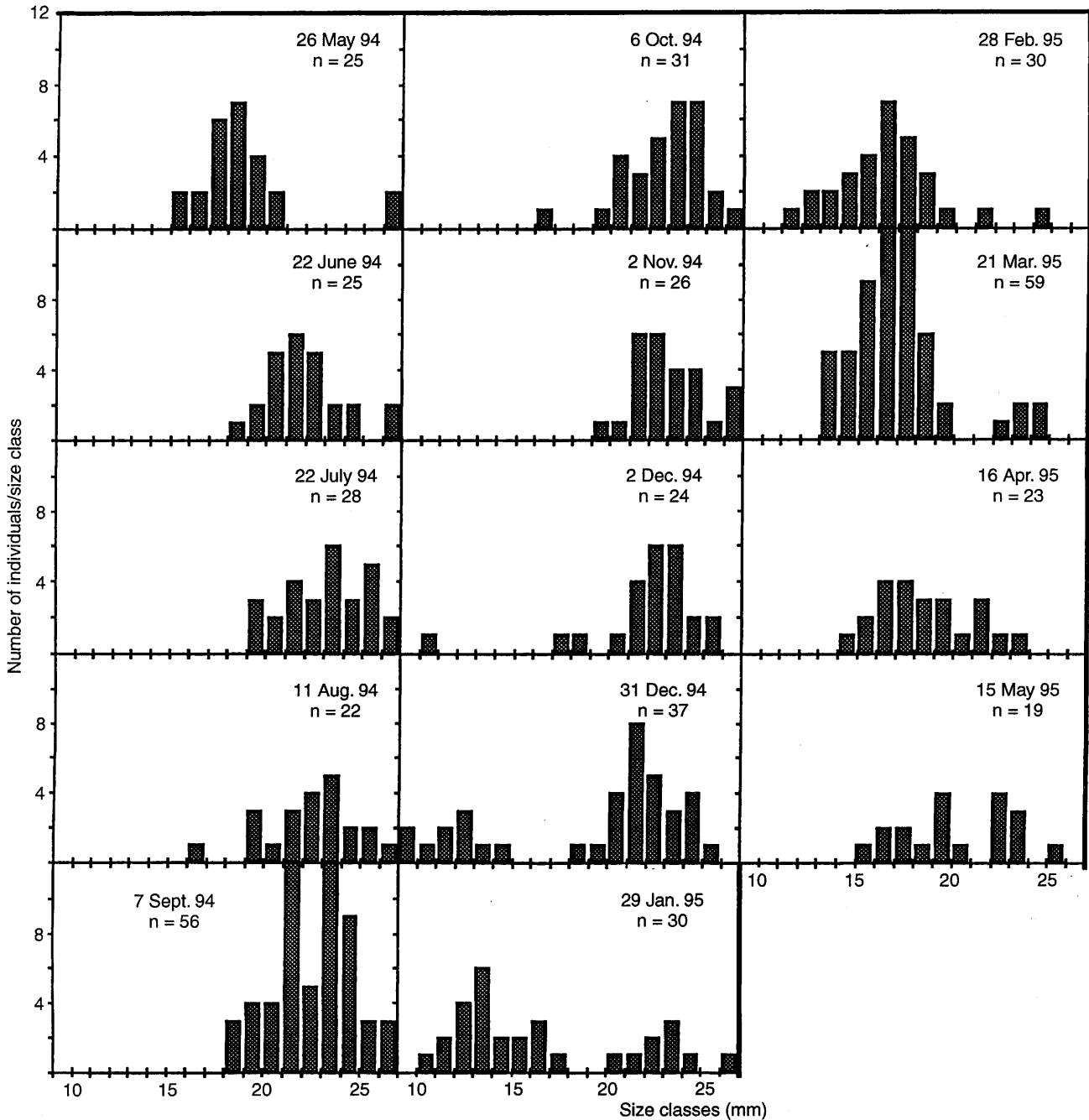


Fig. 6 *Casco bigelowi*. Numbers in various size classes (length, mm) collected in their own individual burrows; burrow-sharing females and males (= pairs) are also included

tation rates than juveniles of mothers with low numbers of *Cothurnia* sp. on their gills (Fig. 8).

the females (always > 50% of the males had at least one gill with > 20 peritrichs). The epibiont infestation of females decreased during September/October, when many females shed their old exoskeleton during the reproductive molt. The prevalence of peritrichs on newly recruited subadults was relatively low, but already on 31 December 1994 and on 29 January 1995 some subadults were hosts to peritrichs on their gills (Fig. 7C). Juveniles of mothers that were heavily infested had higher infes-

Seasonal abundance of *Casco bigelowi* in sediments and drifting in water column

The highest densities of *Casco bigelowi* were found in sediments just below MLW, but the densities in the study area never exceeded 120 individuals m^{-2} (Fig. 9). No *C. bigelowi* were found at MLW and 0.3 m above MLW. Few *C. bigelowi* were found drifting in the Sheepscot River Estuary, and all drifters were caught during the fall months. The numbers never exceeded 10

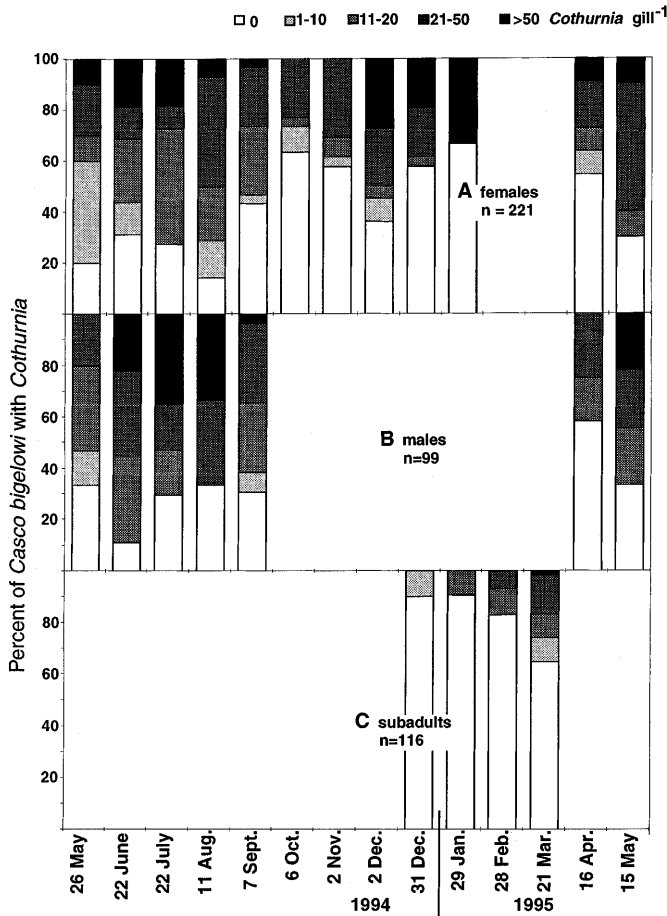


Fig. 7 *Casco bigelowi*. Percentages of females, males, and subadults with peritrich ciliate *Cothurnia* sp. on their gills (Key shows grades of infestation)

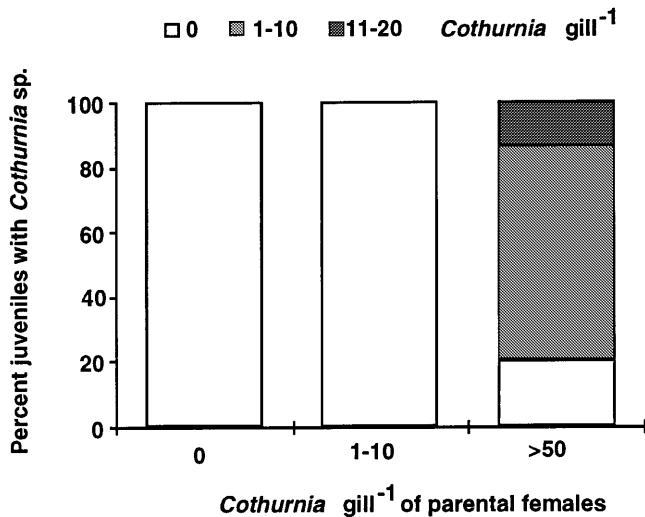


Fig. 8 *Casco bigelowi*. Percentage of juveniles infested with peritrich ciliate *Cothurnia* sp. from parental females with no (0), few (1-10) and many (>50) *Cothurnia* sp. [Key shows grades of juvenile infestation (109 juveniles from 8 females)]

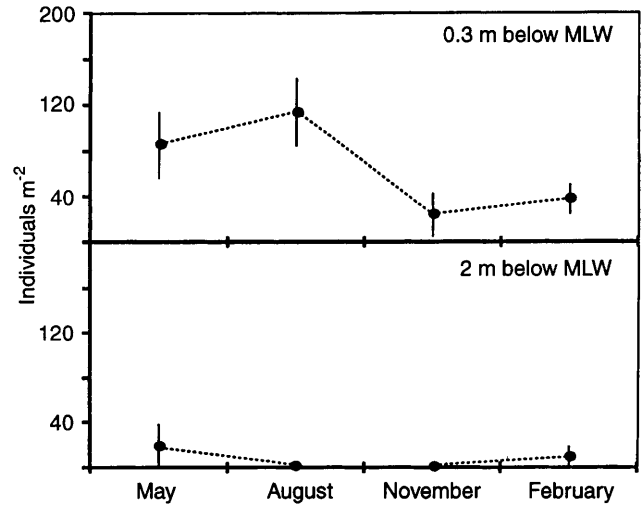


Fig. 9 *Casco bigelowi*. Average densities (means \pm SE) at two different tidal levels in Lowes Cove, in May, August and November 1994 and February/March 1995; juveniles in burrows of parental females were not included. At each tidal level, six cores (176 cm² surface area each) were taken on each sampling date; in November 1994 and February/March 1995, six additional cores were taken at each tidal level because of low densities of amphipods

individuals 1000 m⁻³ (1 individual on 2 November 1972; 2 on 23 September 1975; 1 on 17 November 1977; 1 on 18 November 1977; 8 on 14 December 1977; 1 on 20 September 1978).

Discussion

Casco bigelowi reproduces during the fall, and each reproductive female produces only one brood. After hatching from the female's brood pouch, the juveniles stay in the maternal burrow until they have reached more than half adult size. Two other amphipod species that inhabit the same area as *C. bigelowi* at and just below MLW (*Leptocheirus pinguis* and *Dyopedos monacanthus*) also engage in extended parental care (Thiel 1997d). They invest less time in individual broods than *C. bigelowi* and, in contrast to *C. bigelowi*, they produce several consecutive broods during their reproductive periods (Thiel 1997c, e). The long-lasting maternal care seen in *C. bigelowi* results in specific advantages (large offspring size), but also carries potential threats (facilitated epibiont or parasite transmission). These factors have important implications for the population biology of crustacean (and other marine invertebrate) species that engage in extended parental care and advanced social behavior.

Life history of *Casco bigelowi*

In the Damariscotta River Estuary, *Casco bigelowi* is an annual species, as was also found by Wildish (1984) for a population in the Bay of Fundy. In the fall, juveniles are

born into the female's burrows in which they stay for periods of 2 to 3 mo (Thiel 1997b). Most juveniles leave the female burrows in December, January and February, and many recruit immediately into the adult habitat. Between February and June, these subadult recruits grow quickly, reaching adult size by June. During the summer months, they live in simple burrows, grow little, and steadily decline in numbers (Wildish 1980). Many female and male *C. bigelowi* share one burrow throughout the summer, although fertilization of the females does not occur until September. Females and males may remain together whenever they meet, because this may enable males to avoid potentially risky searches for females in late summer when predation pressure at MLW is very high (Thiel 1997b). Fertilization of the females in September is followed by a rapid disappearance of the males. Whether males die after reproduction or emigrate from the area at MLW is not known. The densities of adult *C. bigelowi* at MLW are low (< 40 individuals m^{-2}) in October, shortly before the juveniles are born. During their stay in the maternal burrows (November to January), juveniles reach more than half adult size. With increasing size of juveniles within the female burrows, the females increase the burrow system, and burrows can have multiple openings (Thiel et al. 1997). The lack of other large and strong burrowers and the low numbers of burrowing conspecifics in the soft sediments at and below MLW (Thiel 1997b) allows *C. bigelowi* to build and maintain extensive burrow systems during its extended parental care. The sediments below MLW contain large amounts of water, and porosity values frequently exceed 80% (Thiel unpublished data). With increasing burrow size, the possibility of collapsing burrows can easily result in the separation of females and their offspring (Thiel personal observation; see also Atkinson et al. 1982), forcing juveniles to build their own burrows.

Casco bigelowi usually is not a very abundant amphipod, with densities rarely exceeding 100 individuals m^{-2} . It is therefore not surprising that it is rarely mentioned as a prey item of demersal fish predators (Wigley and Theroux 1965; Tyler 1971; Hacunda 1981; Mahon and Neilson 1987). In only one of these studies was *C. bigelowi* frequently found as prey item in fish stomachs during winter and spring months, and then it was of but minor importance compared with other amphipod species (e.g. *Leptocheirus pinguis*, *Maera loveni* and *Unciola leucopsis*) (Tyler 1971).

The major advantage which *Casco bigelowi* gains from extended parental care is the remarkably large size of recruiting juveniles. In many other endobenthic amphipods, juveniles are thought to establish their own burrows or tubes at sizes of 2 to 6 mm in length (Mills 1967; Klein et al. 1975; Sheader 1977; Morgan and Woodhead 1984; Collie 1985; Dauvin 1989; Sudo and Azeta 1996; Wilson and Parker 1996), while *C. bigelowi* juveniles only leave their mothers and build their own burrows when they are about 10 to 15 mm. Compared to most other soft-bottom dwelling amphipods, *C. bige-*

lowi is also relatively large. Reproductive female and subadult *C. bigelowi* usually live deeper than 5 cm below the sediment surface (Thiel 1997b) well out of the reach of most epibenthic predators. A further advantage of extended parental care in *C. bigelowi* is the delay of recruitment into the winter months. With the onset of cold temperatures, the most important predators in shallow waters (sand shrimp *Crangon septemspinosa*, other decapod crabs and juvenile fish) leave the estuaries (Thiel unpublished data; Embich 1973; Corey 1981; Hacunda 1981), or are less active (most fish stomachs are empty during the winter months: Tyler 1971, 1972). The majority of juvenile *Casco bigelowi* recruit to their own burrows in late December/January, when water temperatures are below 2 °C. Thus, they establish their own burrows at a time when their habitat is relatively free from active, epibenthic predators. After recruiting to their own burrows, subadult *C. bigelowi* continue to grow and, by June, when most epibenthic predators return to shallow waters, recruits have reached adult size; this renders them relatively safe from predation (Thiel 1997b).

Benefits and potential consequences of long-lasting parental care

Extended parental care allows juvenile *Casco bigelowi* to remain in the deep, safe burrows of their mothers (> 10 cm deep: Thiel et al. 1997) at times when major predators are still abundant and active. With the onset of cold temperatures and the departure of most epibenthic predators, juvenile amphipods leave their mothers' burrows to recruit at sizes and at times that are most advantageous for survival in environments with high predation pressure. Many juveniles immediately recruit into the adult habitat at MLW, and it is not known whether dispersal movements commonly occur in these recruits. Numbers of *C. bigelowi* found drifting in the water column were extremely low, suggesting that dispersal may be limited in this species. Two other amphipod species (*Leptocheirus pinguis* and *Dyopodos monacanthus*) that engage in extended parental care in the same habitat as *C. bigelowi*, were found drifting in large numbers during the spring and summer months (Thiel 1997c, e). Our present knowledge of pelagic movements in *C. bigelowi*, *L. pinguis*, and *D. monacanthus* is based on a relatively old data set (1970 to 1979, BJ McAlice and GB Jaeger Jr. unpublished data), and future studies should investigate whether long-lasting parental care can result in limited dispersal and potential genetic isolation.

The duration of extended parental care in *Casco bigelowi* is long compared to that of other amphipod species with this reproductive strategy (Thamdrup 1935; Stephan 1980; Lim and Alexander 1986; Shillaker and Moore 1987; Aoki and Kikuchi 1991; Aoki 1997). The duration of parental care in *C. bigelowi* may only be surpassed by cold-water arcturid isopods (e.g. *Arcturus*

baffini), in which the temporal extent of parental care is most probably >2 mo (Svavarsson personal communication; see large offspring sizes recorded by Svavarsson and Davidsdottir 1995) Epibiont infestation rates of adult *A. baffini* (90%: Svavarsson and Davidsdottir 1995) are similar to values reported here for *C. bigelowi* (see Fig. 7), and in both species, juveniles that enjoy maternal care were already infested with epibionts. Thus, the long duration of parental care in these two peracarid species and epibiont transmission from adults to offspring during this time (Svavarsson and Davidsdottir 1995; present study) might be responsible for the high infestation rates of the adult population. Similarly, in group-living synalpheid shrimp, Duffy (1992), observed a higher incidence of epicaridean isopod infestation in shrimp from large groups than in those from smaller groups. Studies on other crustaceans have indicated that the transmission of epibionts does not require a very close association of infected and uninfected individuals (Bierhof and Roos 1976; Xu and Burns 1991; Willey and Threlkeld 1995). Juvenile *C. bigelowi* move freely in their mother's burrow (Thiel et al. 1997), and fast peritrich transmission is most probably responsible for the high infestation rates of juveniles from heavily infested mothers. At present, it is not known whether the *Cothurnia* sp. epibionts have a negative effect on *Casco bigelowi*, but several other studies indicate that crustacean epibionts can affect the performance and survival of their hosts (Green 1974; Stephan 1980; Kankaala and Eloranta 1987; Bauer 1989; Pohle 1989; Willey et al. 1990; Gannon and Wheatly 1992; Threlkeld and Willey 1993; Weissman et al. 1993; Carman and Dobbs 1997).

Ectoparasites can present a serious threat to communal organisms (Brown and Bomberger Brown 1996), and marine crustaceans can be heavily infested by epibionts and ectoparasites (for most recent overviews see Becker and Wahl 1996; Carman and Dobbs 1997). As a particularly high prevalence of epibionts/ectoparasites is reported for group-living crustaceans (Duffy 1992; Svavarsson and Davidsdottir 1995; present study), future studies on social behavior in marine crustaceans should examine the occurrence of epibionts/ectoparasites and their transmission among group members. At present it appears that in the soft-bottom dwelling amphipod *Casco bigelowi* the benefits gained from extended parental care (decreased predation risk) outweigh the possible consequences of this reproductive strategy (facilitated epibiont transmission).

Acknowledgements I am thankful to J. Dineen, L. Mayer, K. Reise, I. Voparil and L. Watling and two anonymous reviewers for constructive discussions and comments. I was supported by graduate fellowships from the Center for Marine Studies and the Graduate School at the University of Maine. Additional support was received from the Association of Graduate Students at UMaine, SigmaXi, the American Museum of Natural History and an Urda McNaughton scholarship.

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