

Epibenthic predation in marine soft-bottoms: being small and how to get away with it

Martin Thiel

Darling Marine Center, University of Maine, Walpole ME 04573, U.S.A.

Present address: Smithsonian Marine Station, 5612 Old Dixie Highway, Fort Pierce, FL 34946, U.S.A.

Accepted 30 May 1997

Key words: extended parental care, soft-bottoms, predation, protection, recruitment, amphipoda

Abstract

In intertidal soft-bottoms, epibenthic predation is one of the most important post-recruitment processes. Small juveniles are particularly susceptible to predation, and they often settle in the high intertidal where predation pressure is relatively low. Growth conditions in the high intertidal are, however, only suboptimal compared to the low intertidal. Juvenile amphipods *Leptocheirus pinguis* usually remain in their mother's burrow for extended time periods growing to average sizes of 4–6 mm during this extended parental care. In laboratory experiments, more juvenile amphipods survived in controls than in predator additions. In the predator treatments, most adult amphipods survived while many juveniles disappeared. Medium-sized juveniles (6–10 mm size) that had already established their own burrows emigrated in large numbers from the predator treatments whereas most of the adult females remained as residents in these trays. Juvenile *L. pinguis* survived periods where they are most susceptible to epibenthic predation in the protected burrows of their mother. Extended parental care enables juvenile amphipods to recruit immediately into the adult habitat with a good survival chance. It is hypothesized that some small soft-bottom infauna find protection in the burrows of other infauna, medium-sized infauna is most likely to engage in escape reactions, whereas large infauna build their own, deep, burrows, safe from epibenthic predators.

Introduction

Predation is an important post-recruitment process in soft-bottom environments (Ólafsson et al., 1994). Many soft-bottom inhabitants are potential prey of various other organisms during their life times. Their susceptibility to predation can vary during their life time. Some species become more attractive with increasing age and size by reaching profitable bite sizes for large predators. Others outgrow their most voracious predators becoming too big to be handled or building deeper burrows where they cannot be reached. Juvenile macrofauna are known to be primarily susceptible to epibenthic predation (Reise, 1985). Various strategies during the early life stages of juvenile macrofauna are attributed to the avoidance of predation. Two major categories of predator avoidance strategies can be identified in benthic marine organisms (Table 1). The first one might be termed separation strategy, where the

potential prey either seeks temporal or spatial separation from its major predators. Prey organisms utilizing the second, the protection strategy, often live in the same general habitat as the predators but avoid predation by either hiding in crevices, burrows or by being untasty to predators (e.g. Reise, 1985; Hay & Fenical, 1996).

Both strategies have advantages and disadvantages. The separation strategy requires prey organisms to adjust their presence or activity to the predator presence. Prey organisms may be restricted to areas which are suboptimal with respect to resource supply (oxygen, food), but relatively safe from predation (see e.g. Beukema & de Vlas, 1989). The protection strategy might allow prey organisms to remain in optimal areas as long as they can avoid being eaten. Organisms able to find protection from predation within an optimal resource environment can achieve high growth rates. Those organisms that segregate from predators

Table 1. Predator avoidance strategies of benthic marine invertebrates.

| Strategy | Prey behaviour | References (selected examples) |
|------------|--|--|
| Seperation | Segregation of activity from predator activity | de Vlas, 1985; Kamermans & Huitema, 1994 |
| | Recruitment to areas with low predator abundances | Günther, 1990; Beukema & de Vlas, 1989 |
| | Preventive emigration in response to predator presence | Armonies, 1994 |
| | Escape in response to immediate predator encounters | Ambrose, 1984; Olafsson & Persson, 1986; Thiel & Reise, 1993 |
| Protection | Production or uptake of untasty substances | Kem, 1985; Hay & Fenical, 1986 |
| | Selection of cryptic habitats | Jormalainen & Tuomi, 1989 |
| | Shelter on, in or with other organisms | Ockelmann & Muus, 1978 |

and settle in areas with diminished resource supply have relatively low growth rates. Bivalves *Cerastoderma edulis* that were protected from predators by cages in low intertidal soft-bottoms with high predation pressure but optimal food supply grew much faster than their conspecifics in high intertidal soft-bottoms with few predators but only suboptimal food supply (Reise, 1985). Juvenile bivalves are extremely susceptible to epibenthic predators, however they outgrow most of their predators by the time they reach 30 mm in length (Reise, 1985). Many organisms in intertidal or shallow subtidal soft-bottoms seek temporal or spatial separation from the major epibenthic predators during the juvenile stages while small and susceptible. After reaching a certain size, they immigrate into the adult habitat, where growth conditions are usually more favorable than in the juvenile habitat. During these migrations via the water column (e.g. Armonies, 1994), organisms are exposed to other predators and may be misplaced by currents.

The ability to recruit immediately into the adult habitat, thus avoiding long migrations to predator-safe juvenile habitats would present an enormous advantage to recruiting soft-bottom fauna. Yet, few juvenile or small soft-bottom species seem to utilize the protection strategy successfully. A few small bivalve species brood early juvenile stages, and these recruit immediately into the adult habitat after being released from their mother's body (Gallardo, 1993). Some meiofauna organisms (e.g. Reise, 1985; Dittmann, 1996) as well as a variety of other organisms (e.g. Ockelmann & Muus, 1978; Ó Foighil & Gibson, 1984) are found in high numbers in the burrows of larger macrofauna where they might find protection from epibenthic predators. These guests cannot build deep burrows themselves, but rather rely on their hosts. Similarly, early larval and juvenile stages of some polychaetes remain in the relatively well protected burrows of their parents (e.g. *Nereis diversicolor*, Bartels-Hardege

& Zeek, 1990). The juveniles of some amphipods remain in the burrows of their parents for extended time periods (Shillaker & Moore, 1985; Thiel et al., 1997) until they have attained almost half the adult size. We hypothesized that this form of extended parental care provides effective protection for the juvenile amphipods from epibenthic predation (Thiel et al., 1997). The amphipods *Leptocheirus pinguis* inhabit soft-bottoms at MLW (mean low water) where food supply is favorable (Thiel, in press), but epibenthic predators are also very abundant (unpubl. data).

The aim of the present study was to examine whether juvenile amphipods are more susceptible to predation than large adults. Only then would parental care be a useful strategy in avoiding predation. Amphipods were collected in the field to elucidate what sizes of amphipods did successfully establish individual burrows, and how deep these burrows were. The response of juvenile and adult amphipods to epibenthic predators was examined in predation experiments. The results of this study help to answer whether extended parental care can be a successful protection strategy for juvenile macrofauna in marine soft-bottoms.

Materials and methods

Field collection of amphipods Leptocheirus pinguis

In the summer of 1993 juvenile amphipods were collected from their habitat in Lowes Cove, Maine. Juveniles were collected from their mothers' burrows every two weeks from 8th June until 1st September 1993. Additionally, at each sampling date small amphipods were collected from their own individual burrows in order to determine the smallest size of amphipods which recruited into the adult habitat. In August 1996, a possible relationship between amphipod size and the burrow depths was examined. Individual amphipod

burrows were sampled in Lowes Cove, the sediment was broken up along the burrow and the depth of the burrows measured with a ruler. All amphipods were preserved and their size measured with a computer-based video-analysis system along their dorsal surface from the rostrum to the base of the telson.

Predation experiments

Ovigerous female amphipods *Leptocheirus pinguis* were collected from mudflats in Lowes Cove, Maine. Eighteen females were introduced to each of 6 trays that contained natural sediments collected from the amphipod habitat. Another 18 females were preserved immediately after collection, and their eggs counted in order to determine the reproductive potential. The trays had a size of 900 cm² and the sediment in the trays had a depth of about 10 cm. Fresh seawater was flowing through the trays, and the females were allowed to establish burrows and rear juveniles within the burrows for approximately 5 weeks. During this time, the outflow was covered with a 500 μm screen, confining all amphipods to the trays. When the first juveniles started emerging from their mother's burrows, the screen was removed (=start of experiment), and the outflowing seawater passed through a trap with a 500 μm screen, collecting all organisms emigrating from the trays. For the next seven days, all emigrants were counted each morning, but then reintroduced to their respective trays. At day seven, predators (10 sandshrimp *Crangon septemspinosa* per tray) were introduced to three trays, while the three remaining trays were left predator-free as controls. Following the predator addition, all emigrants (=escapees) were collected and preserved every day. The experiment was terminated on day 14 and the contents of each tray were sieved over a 500 μm sieve. All juvenile and adult amphipods were collected, preserved, and measured.

Results

Sizes of juvenile amphipods *Leptocheirus pinguis* in the field

During the whole sampling period (June–September 1993) the average size of juveniles in their mothers' burrows varied between 4 and 6 mm (Figure 1a). Significant differences between consecutive sampling dates were only observed early in the summer (ANOVA, $p < 0.05$; followed by Scheffé-test, $p < 0.05$). The

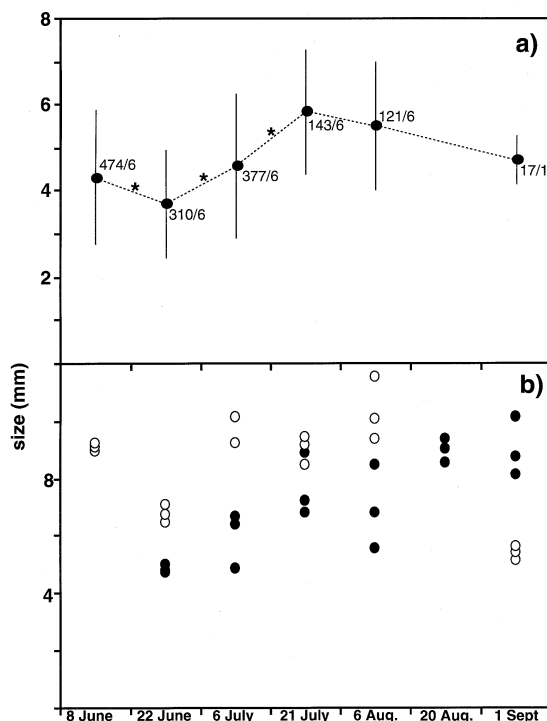


Figure 1. (a) Average size (mm; \pm std err) of juveniles collected from their mothers' burrows in Lowes Cove during the summer of 1993 (n = number of juveniles/ N = number of mothers from which juveniles were collected); significant differences (ANOVA, $p < 0.05$; post-hoc Scheffé test, $p < 0.05$) between consecutive sampling dates marked by *. (b) The three smallest juveniles *Leptocheirus pinguis* found in own burrows (filled dots) and the three largest juveniles in mothers' burrows (open dots) in Lowes Cove in the summer of 1993; no females with juveniles in their burrows were found on 20 August 1993.

size of the smallest juveniles in their own individual burrows slightly increased during the summer (Figure 1b) and most were at least 5 mm in length. There exists a significant correlation between the size of amphipods and the depths of their burrows ($y = 3.662x + 9.546$, $R^2 = 0.424$; t -test, $p < 0.01$) (Figure 2). In August 1996, all amphipods collected were larger than 6 mm; only two individuals inhabited burrows which extended less than 20 mm below the sediment surface. All amphipods larger than 14 mm were found in burrows at least 40 mm deep.

Predation experiment

The 18 female *Leptocheirus pinguis* preserved at the beginning of the experiment contained on average 64 eggs in their brood pouch (mean \pm s.e.: 63.67 \pm 3.71)

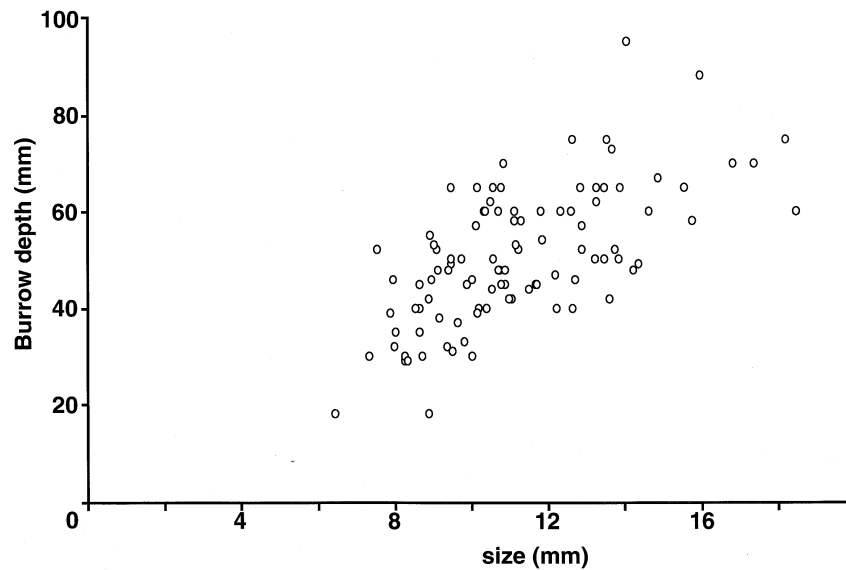


Figure 2. Relationship of the size (mm) of individual amphipods *Leptocheirus pinguis* and the depth of their burrows (mm) in Lowes Cove in August 1996.

resulting in a total reproductive potential of about 1150 juveniles for each tray (18 females \times 64 eggs). The percentage of surviving juveniles in the controls (81.8%) was significantly higher than that of the predator treatments (61.6% surviving juveniles) (Mann-Whitney U-test, $p < 0.05$). In the control trays without predators, an average of 941 juveniles survived at the end of the experiment (= 81.8% of the total reproductive potential per tray) (Figure 3a). Those include 408 emigrants (= 35.4% of total reproductive potential) and 533 residents per tray (= 46.4%). In the predator treatment 584 emigrants (50.8%) and 124 resident juveniles (= 10.8%) per tray escaped from predation, adding up to 708 survivors (= 61.6% of total reproductive potential). The percentages of females surviving in predator treatments and controls were not significantly different (Mann-Whitney U-test; $p > 0.1$). Of the 18 large females in each tray an average of 100% survived in the control and an average of 78% survived in the predator treatment. No females emigrated from the controls, while about 20% escaped from the predator treatment (Figure 3b). Thus, in the predator treatment almost 60% of the large females but only 10% of the potential 1150 juveniles remained in the trays at the end of the experiment. A higher percentage of juveniles emigrated from the predator treatments (50%) than from the controls (30%).

Most juveniles between 6 mm and 10 mm size remained as residents in the predator-free control (Fig-

ure 4a). About 50% of each size class of the small juveniles (2–6 mm body size) emigrated from the predator-free control trays, but the other 50% immediately recruited to, and were residents in, the trays. The addition of predators resulted in a strong escape response in all juvenile sizes, particularly the large ones (6–10 mm body size) (Figure 4b). In the predator treatments, a relatively high percentage of small juveniles (2–6 mm body size) remained as residents in the trays (20 to >40% of each size class) (Figure 4b).

Discussion

Juvenile amphipods *Leptocheirus pinguis* are more susceptible to epibenthic predation than large adults. They spend at least part of the time during which they are particularly susceptible to predation in the protection of their mother's burrow. Juvenile amphipods in their own burrows react to epibenthic predators with a strong emigration response, whereas large adults remain in their deep burrows, indicating that the behavioral response of amphipods *L. pinguis* to these predators changes with size.

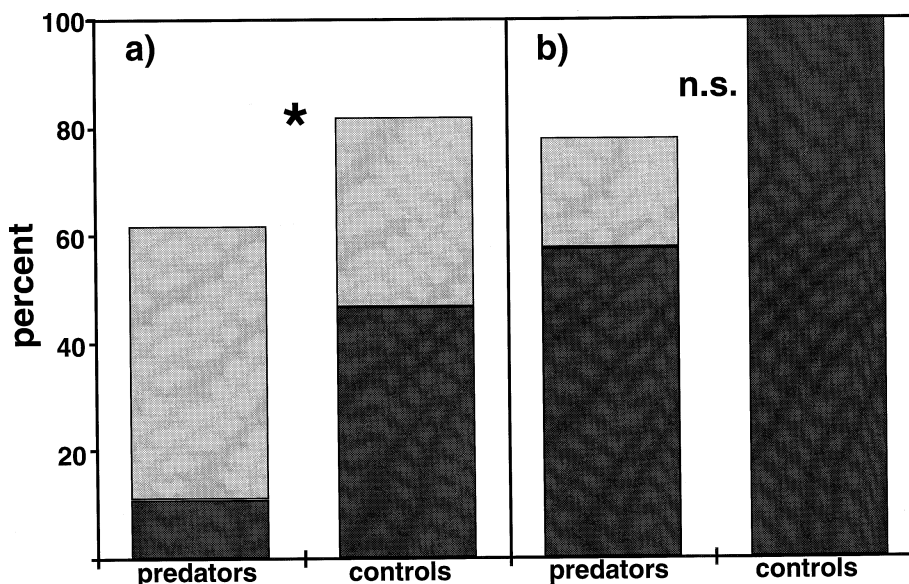


Figure 3. (a) Percentage of juveniles remaining as residents (dark shading) or emigrating (light shading) from experimental trays without (=controls) and with predators; $n = 1150$ potential juveniles each in $N = 3$ controls and $N = 3$ predator treatments. (b) Percentage of females remaining as residents (dark shading) or emigrating (light shading) from experimental trays without and with predators; $n = 18$ females each in $N = 3$ controls and $N = 3$ predator treatments.

Parenting mothers provide protection from epibenthic predators

Extended parental care provides some juvenile amphipods *L. pinguis* with the opportunity to grow to remarkable sizes in the burrow of their mother. The largest juveniles commonly found in females' burrows are between 6 mm and 10 mm in size. At these sizes the juveniles start to build their own burrows, but they are still susceptible to epibenthic predators: the escape of all sizes of juveniles in the experimental predator additions indicates that even large juveniles (6–10 mm) do not gain sufficient protection from epibenthic predation in their own burrows.

Unexpectedly, not all adult females survived in the predator treatments and some emigrated. The high numbers of recruiting juveniles that built their own burrows in the trays may have caused repeated destruction of the upper parts of female burrows. As a consequence, large females frequently had to come to upper sediment layers to repair their burrows thereby exposing themselves to predation. High burrow repair activity of large females in the experiments might thus have resulted in their unexpected disappearance and emigration from predator treatments. Nevertheless, large

females are less affected by predator addition than their offspring, indicating that they are relatively safe from epibenthic predators in their deep burrows. These large females can provide a safe habitat for their offspring in their deep burrows, but many juveniles leave their mothers' burrows at a size still susceptible to epibenthic predation. With increasing size of the juveniles, overcrowding and increasing competition in their mother's burrows (there can be more than 100 juveniles in one female's burrow: Thiel et al., 1997) might cause some juveniles to emigrate, resulting in relatively high numbers of emigrating small juveniles (4–6 mm) in both, control and predator treatments (Figure 4). Before overcrowding effects occur, juveniles are much better off staying with their mothers than going out on their own. Extended parental care by the female (providing a protected burrow, maintaining and irrigating the burrow) enables small juveniles to survive in a habitat with high predation pressure (see e.g. Figure 4b).

Escape reaction of small juveniles during predator encounters

Juvenile *Leptocheirus pinguis* spend their first weeks in the protected burrow of their mother. After leaving

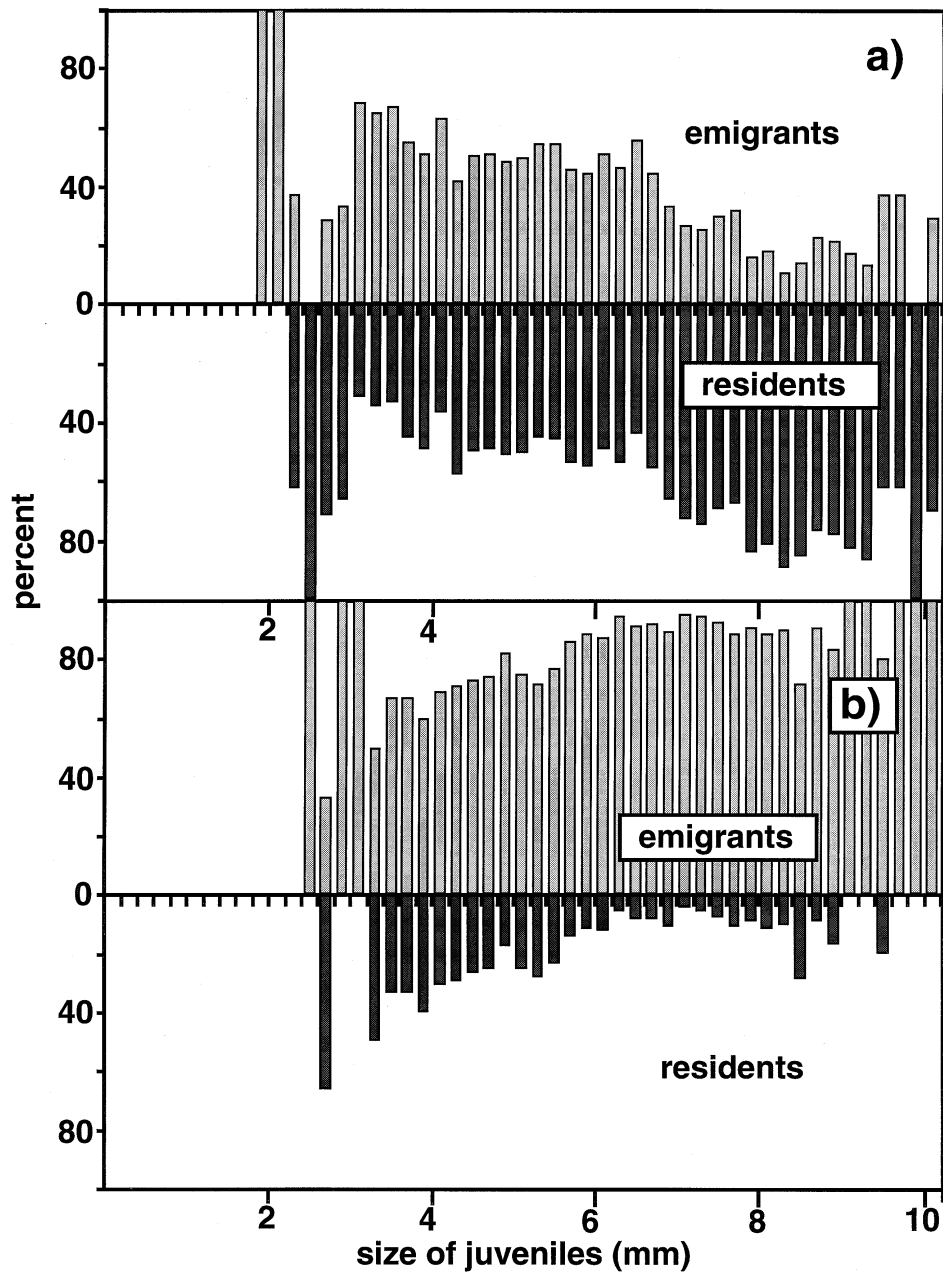


Figure 4. (a) Percentage of juveniles in each size class remaining as residents (dark shading) or emigrating (light shading) from experimental trays without predators; all juveniles recovered from $N=3$ controls were pooled. (b) Percentage of juveniles in each size class remaining as residents (dark shading) or emigrating (light shading) from experimental trays with predators; all juveniles recovered from $N=3$ predator treatments were pooled.

their mothers' burrows, the juveniles establish their own burrows in the adult habitat (see large juveniles of 6–10 mm size in Figure 4a). These juveniles are still too small to build burrows deep enough to be well protect-

ed from predator encounters. They escape from their shallow burrows in response to immediate predator contacts (see Figure 4b: a high proportion of large juveniles emigrates). This strategy is relatively effective in

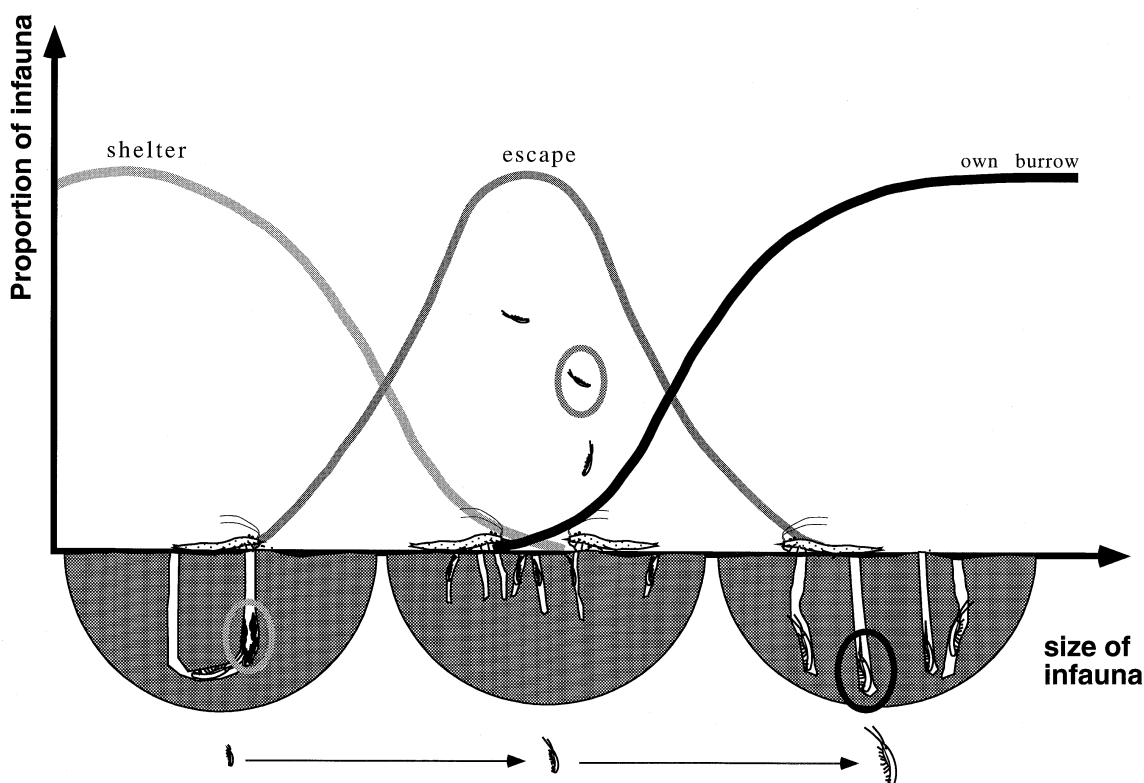


Figure 5. Predator avoidance strategies for small infauna of marine soft-bottoms in relation to their respective body sizes: high proportions of small infauna are expected to seek shelter in macrofauna burrows, medium-sized infauna is expected to avoid predators via escape reactions and large infauna is increasingly safe from epibenthic predation in their own burrows; all three predator avoidance strategies have been reported for respective infauna sizes (for references see text).

avoiding fatal predator encounters. The escape reaction in response to predators has been described for soft-bottom infauna (see e.g. Ambrose, 1984; Rönn et al., 1988; Thiel & Reise, 1993). Many escape reactions were observed in predator addition experiments and it can be assumed that they occur frequently in immediate response to predators. At least one study (Thiel & Reise, 1993) indicates that escaping amphipods only move short distances to get out of the immediate range of predators. Thus, these escape reactions can be considered as short-term as well as short-range response reactions to predators. Escapees seek a predator-free refuge within their general habitat. It has been discussed that high abundances of small benthic organisms in nocturnal plankton might be caused by escape reactions to benthic predators at night (e.g. Ambrose, 1984; Armonies, 1989, 1994). Thus, the escape reaction might be a very common predator avoidance strategy for soft-bottom fauna. This assumption, however, requires further experimental investigation.

Parental protection for juveniles or early larval stages in marine soft-bottom fauna has been described for small bivalve species (Gallardo, 1993), some polychaete species (Bartels-Hardege & Zeek, 1990) and some amphipod species (this study; Thiel et al., 1997). The duration of extended parental care is most likely controlled by limited space and increasingly insufficient resource supply for the growing offspring. The size of juveniles when leaving their parents will determine their survival chances as recruits. Large recruits are expected to have better survival chances, but if not yet big enough to build deep burrows, they can avoid fatal predator encounters via the escape reaction.

Protection strategy in marine soft-bottoms

Marine soft-bottoms do not provide many shelters, and in shallow waters the surface sediments are frequently reworked by epibenthic predators. Small organisms are very susceptible to epibenthic predation, as they

often cannot achieve effective protection from predators. Cryptic habitats are relatively rare on marine soft-bottoms, and there are few reports of soft-bottom infauna containing untasty substances (Kem, 1985; Giray, pers. comm.). Small organisms (meiofauna and small macrofauna) can be found in high numbers in the burrows of larger macrofauna (e.g. Ockelmann & Muus, 1978; Ó Foighil & Gibson, 1984; Reise, 1985; Wetzel et al., 1995; Dittmann, 1996), seemingly undisturbed by the burrow founder (Figure 5). With increasing size of its guests, the burrow founder should pay more attention to them, as they might consume substantial amounts of oxygen, food or space in its burrow. Thus, with increasing size one should expect that shelter seeking organisms are kept out of the burrows of larger macrofauna. These organisms have to build their own burrows or tubes, but due to their relatively small size, their burrows will only reach a limited depths. The most effective strategy for these organisms is to stay in their burrows as long as they are undisturbed but to escape into the water column at predator encounters (Figure 5). With increasing size we expect to see fewer escape reactions, as larger organisms are able to build deep burrows safe from epibenthic predators (Figure 5).

It becomes evident that the protection strategy is not a risk-free undertaking for small infauna of marine soft-bottoms. However, it allows these organisms to inhabit areas with high predator abundance but otherwise optimal conditions (e.g. permanent water coverage and optimal food supply). Seeking shelter with larger organisms might be inhibited when resources for shelter-seekers or shelter-providers (food, oxygen) are limited. In general, small infauna engaged in the protection strategy are able to avoid risky migrations to predator-free areas, and they do not have to adjust their activity schedule to the presence or activity of predators.

Acknowledgments

Support for this study was received in form a graduate fellowship from the Center for Marine Studies at the University of Maine and grants from the Association of Graduate Students at the University of Maine. My participation at the 31st EMBS was supported by grants from the Association of Graduate Students, The Alumni Association and the School of Marine Sciences at the University of Maine. Ian Voparil and two anonymous reviewers provided important comments.

My very special thanks extends to Svetlana and Andrey for their hospitality during my stay in St. Petersburg.

References

- Ambrose, W. G., Jr., 1984. Increased emigration of the amphipod *Rhepoxynius abronius* (Barnard) and the polychaete *Nephtys caeca* (Fabricius) in the presence of invertebrate predators. *J. exp. mar. Biol. Ecol.* 80: 67–75.
- Armonies, W., 1989. Meiofaunal emergence from intertidal sediment measured in the field: significant contribution to nocturnal planktonic biomass in shallow waters. *Helgoländer Meeresunters* 43: 29–43.
- Armonies, W., 1994. Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. *Helgoländer Meeresunters* 48: 299–320.
- Bartels-Hardege, H. D. & E. Zeek, 1990. Reproductive behavior of *Nereis diversicolor* (Annelida: Polychaeta). *Mar. Biol.* 106: 409–412.
- Beukema, J. J. & J. de Vlas, 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. *Mar. Ecol. Prog. Ser.* 52: 193–200.
- Dittmann, S., 1996. Effects of macrobenthic burrows on infaunal communities in tropical tidal flats. *Mar. Ecol. Prog. Ser.* 134: 119–130.
- Gallardo, C. S., 1993. Reproductive habits and life cycle of the small clam *Kingiella chilensis* (Bivalvia: Cyamiidae) in an estuarine sand flat from the South of Chile. *Mar. Biol.* 115: 595–603.
- Günther, C.-P., 1990. Distribution patterns of juvenile macrofauna on an intertidal sandflat: an approach to the variability of predator/prey interactions. In Barnes, M. & R. N. Gibson (eds), *Trophic Relationships in the Marine Environment* (Proc. 24th Europ. Mar. Biol. Symp.). Aberdeen Univ. Press, Aberdeen, 77–88.
- Hay, M. E. & W. Fenical, 1996. Chemical ecology and marine biodiversity: insights and products from the sea. *Oceanogr.* 9: 10–20.
- Jormalainen, V. & J. Tuomi, 1989. Sexual differences in habitat selection and activity of the colour polymorphic isopod *Idotea baltica*. *Anim. Behav.* 38: 576–585.
- Kamermans, P. & H. J. Huitema, 1994. Shrimp (*Crangon crangon* L.) browsing upon siphon tips inhibits feeding and growth in the bivalve *Macoma balthica* (L.). *J. exp. mar. Biol. Ecol.* 175: 59–75.
- Kem, W. R., 1985. Structure and action of nemertine toxins. *Am. Zool.* 25: 99–111.
- Ockelmann, K. W. & K. Muus, 1978. The biology, ecology and behaviour of the bivalve *Mysella bidentata* (Montagu). *Ophelia* 17: 1–93.
- Ó Foighil, D. & A. Gibson, 1984. The morphology, reproduction and ecology of the commensal bivalve *Scintillina bellerophon* spec. nov. (Galeommatacea). *The Veliger* 27: 72–80.
- Ólafsson, E. B. & L.-E. Persson, 1986. The interaction between *Nereis diversicolor* O. F. Müller and *Corophium volutator* Pallas as a structuring force in a shallow brackish sediment. *J. exp. mar. Biol. Ecol.* 103: 103–117.
- Ólafsson, E. B., C. H. Peterson & W. G. Ambrose, Jr., 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanogr. Mar. Biol. Ann. Rev.* 32: 65–109.

- Reise, K., 1985. Tidal Flat Ecology. Springer, Berlin, 191 pp.
- Rönn, C., E. Bonsdorff & W. Nelson, 1988. Predation as a mechanism of interference within infauna in shallow water soft-bottoms; examples with an infauna predator, *Nereis diversicolor* O. F. Müller. J. exp. mar. Biol. Ecol. 116: 143–157.
- Shillaker, R. O. & P. G. Moore, 1987. The biology of brooding in the amphipods *Lembos websteri* Bate and *Corophium bonnellii* Milne Edwards. J. exp. mar. Biol. Ecol. 110: 113–132.
- Thiel, M. & K. Reise, 1993. Interaction of nemertines and their prey on tidal flats. Neth. J. Sea Res. 31: 163–172.
- Thiel, M., 1997. Extended parental care in a high food environment – ‘Babies don’t go in the mud’. In Hawkins, L. E., Hutchinson, S., Jensen, A. C., Willian, J. A. & M. Shearer (eds), Responses of Marine Organisms to their Environment: Proceedings of the 30th European Marine Biology Symposium, Southampton, September 1995. Southampton Oceanography Centre, Southampton, in press.
- Thiel, M., S. Sampson & L. Watling, 1997. Extended parental care in two endobenthic amphipods. J. Nat. Hist. 31: 713–725.
- Vlas, J. de, 1985. Secondary production by siphon regeneration in a tidal flat population of *Macoma balthica*. Neth. J. Sea Res. 19: 147–164.
- Wetzel, M. A., P. Jensen, O. Giere, 1995. Oxygen/sulfide regime and nematode fauna associated with *Arenicola marina* burrows: new insights in the thibios case. Mar. Biol. 124: 301–312.