Physical factors and biological interactions regulating infauna in shallow boreal areas

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ABSTRACT: Infauna, including all post-larval stages, were quantitatively sampled from 1977 to 1984 in a shallow (< 1 m) unvegetated, semi-exposed soft bottom area, situated on the Swedish west coast. Variations in the infaunal abundance, biomass and production are shown to be the result of temperature conditions and predator-prey interactions. Temperature is considered to be an important physical factor causing annual and seasonal variations in spat recruitment, biomass and survival over the winter. During the post-recruitment period, infaunal abundances are mainly controlled by intra- and interspecific competition, particularly the predation of mobile epibenthic animals. Intra- and interspecific interactions between adult bivalves and spat, as demonstrated in experimental studies, showed that high adult survival inhibited spat recruitment. In the absence of overwintered adults, spat survival increased. Interspecific interactions between adult bivalves showed that late-arriving species are able to eliminate older established species. The importance of physical factors, e.g. exposure, water depth and currents, in determining variations in the abundance, biomass and production of infauna, is also discussed. Results suggest that both abiotic factors and biological interactions are important regulating mechanisms for infaunal densities in shallow unvegetated boreal areas.

INTRODUCTION

For many years ecological studies on marine soft bottoms in general have emphasized the role of physical factors in determining infaunal variations (Petersen 1918, Thorson 1957, Hulings & Gray 1976). Many recent ecological studies, however, have paid more attention to the influence of biological interactions and these may include factors such as predation (Virnstein 1977, 1978, 1979, Peterson 1979, Ambrose 1984, Weinberg 1984, Pihl 1985), competition for space (Woodin 1974, Levinton 1977, Peterson 1979, Peterson & Andre 1980, Whitlatch 1980), competition for food (Fenchel & Kofoed 1976, Young & Young 1978) and adult interference with larval settlement (Segerstråle 1962, Woodin 1976, Williams 1980, Peterson 1982). Most of the investigations mentioned above were carried out in intertidal areas by manipulative field experiments. The present investigation was made in unmanipulated study areas having a tidal amplitude of only 0.1 m.

The abundance, biomass and production of the infaunal species *Corophium volutator* (Pallas), *Mya*

arenaria L., *Cardium* (= *Cerastoderma*) *edule* L. and *Nereis diversicolor* O. F. Müller in shallow Swedish waters have been described in previous publications (Möller & Rosenberg 1982, 1983, Möller 1985).

In this paper the role of physical and biological processes in structuring infaunal abundance, biomass and production will be analysed. The results discussed are derived from quantitative field investigations made over several years which included simultaneous studies of the infauna and the mobile epibenthic fauna. Thus it is possible to demonstrate the significance of predator-prey interactions in the natural habitat. All post-larval sizes of the 2 faunal categories were included in the sampling regime, thus adult-juvenile interactions were fully explored. Inclusion of the smallest post-larvae and individuals is essential to a detailed study of recruitment and survival in infaunal populations, since 96 to 97 % of all molluscs and about 70 % of polychaetes start their benthic life as members of the smaller (< 0.5 mm) meiofauna (Thorson 1966).

Most of the interannual data derive from the unvegetated semi-exposed Gullmarsvik (Area 6; Fig. 1) on the Swedish west coast studied between 1977 and 1984 and additional results are presented from other shallow water habitats, which reflect the influence on the

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infauna of such physical factors as exposure and sediment composition.

AREAS STUDIED

In this study 13 shallow unvegetated areas and 2 vegetated were investigated on the Swedish west coast (Fig. 1). According to exposure, organic content in the sediment and presence of vegetation, the areas were grouped into 4 habitat categories (Table 1). These

Fig. 1. Map showing location of areas investigated

were: (1) exposed, (2) semi-exposed and (3) sheltered areas situated between 0 and 1 m water depth with almost no vegetation, and (4) vegetated meadows dominated by *Zostera marina* (L.) from 1 to 3 m depth. Each habitat category was investigated in at least 2 different regions. Areas 1, 5, 6, 11 and 14 were intensively sampled (in some months every week) over a period of 2 to 8 yr between 1977 and 1984. Remaining areas were sampled during 'survey studies' in June and September 1981 and/or 1982.

Areas studied had a seasonal mean water temperature variation from below zero in most winters to about

18 °C in summer (Fig. 2). During the investigation period from 1977 to 1984, about half of Gullmarsvik was normally covered with ice from December to March and in sheltered parts of this area temperature maxima in summer could reach extremes of above 25 °C on sunny days. Salinity normally fluctuated around 20 ‰ with extremes of 1 and 30 ‰ in the areas along the Skagerrak coast, while salinity in the Kattegat was normally somewhat lower because of the influence of Baltic water. The tidal amplitude was about 0.1 m, but high air pressures could occasionally cause prolonged exposure of the study areas.

METHODS

In unvegetated areas of 1 to 4 hectares each, infauna was quantitatively sampled at random using cores of various sizes (16, 87 or 290 cm²). Sampling precision was maintained by taking 20 to 40 samples on each sampling occasion, which resulted in a standard error usually < 30 % of the mean. During the recruitment period, when the abundance was high and the animals were small, the 16 cm² corer was used. In autumn and spring, when the animals were usually fewer and larger, the 87 cm² corer was used. The 290 cm² corer was used to follow the development of large overwintering adults of *Mya arenaria* and *Cardium edule*. During the recruitment period all of the upper 5 cm of sediment was decanted and sieved through 0.2 mm meshes and animals were analysed and measured under a stereomicroscope. When investigating older animals with the larger corers, sieves of 0.5 or 1.0 mm were used. Biomass was calculated as unpreserved ash-free dry weight (ADW) from length-weight relations (Möller & Rosenberg 1982, 1983, Möller 1985). Samples from the *Zostera* meadows were taken by diving, using an 87 cm² core. Samples were sieved through 0.5 mm meshes.

Organic content in the sediment (0 to 5 cm) was obtained after drying to constant weight at 60 °C and then combusting for 5 h at 550 °C. Exposure was calculated as effective fetch (km) (Håkanson & Jansson 1983).

Abundance, biomass and production of dominant infauna are given in Möller & Rosenberg (1982, 1983) and Möller (1985); estimates of food selection and consumption of mobile epibenthic fauna and migratory fish are from Pihl (1982, 1985) and Pihl & Rosenberg (1984). Change in abundance and biomass of the infauna along a depth transect from 1 to 10 m were studied by divers, who took two 0 to 10 cm sediment samples using an 87 cm² core, at 1 m depth intervals. These were sieved through 0.5 mm meshes.

The movement of spat in and out of 2 sites at 1 m

Fig. 2. Monthly means of surface salinity (top) and water temperature (bottom) with maximum and minimum ranges from the Gullmarsfjord at Bornö Hydrographical Station. Periods of ice in Gullmarsvik are indicated

depth in Gullmarsvik was studied. Spat was caught in 125 μ m plankton nets set at 0 to 20 cm and 20 to 40 cm above the bottom. At each site 2 nets were set out; one with the open mouth facing inwards and the other facing outwards towards the mouth of the bay. The openings were 20 $\times$ 15 cm. These experiments lasted for 24 h.

Aluminium cages for predation enclosure experiments were 70 $\times$ 70 cm and 15 cm high covered with 1 mm nylon meshes. On each sampling occasion, 3 to 6 cores (16 cm² each) were taken to 5 cm depth and sieved through 0.2 or 0.5 mm meshes. In order not to cause excessive disturbance in the enclosure experiments where adult-juvenile bivalve interactions were studied, areas having natural abundances of 0, 10 and 100 adult *Mya arenaria* per 0.5 m² were used. Abundances were estimated by counting the siphons several times before the start of experiments.

RESULTS AND DISCUSSION

Seasonality in infaunal species caused by physical factors

Exposure

In the exposed, high wave energy sandy areas in the Kattegat, the number of species, abundance and biomass appeared to be lowest of all areas investigated (Fig. 3; Table 1). In all the exposed areas the species *Bathyporeia sarsi* Watkin, *Nereis diversicolor*, *Pygospio elegans* Claparède, *Cardium edule* and *Mya arenaria* together contributed about 70 to 90 % of the total infaunal biomass. All these species, with the

exception of *B. sarsi*, can act as filter feeders and this trophic group thus dominates the biomass in the sandy exposed areas. The omnivorous *N. diversicolor* and the versatile *P. elegans*, often considered as a surface deposit feeder, are also capable of filter feeding with the aid of mucous nets within their tubes (Fauchald & Jumars 1979).

In the exposed areas of the Skagerrak, the shallow infaunal assemblages were richer, both in terms of the number of species, number of individuals and biomass, than those of the Kattegat (Fig. 3; Table 1). This was most probably a consequence of the protection obtained from a surrounding archipelago, i.e. the areas in the Skagerrak were less exposed to wind than areas in the Kattegat.

In the unvegetated semi-exposed and sheltered habitats, the total infaunal biomass before bivalve recruitment at the end of June was made up in general by 5 dominants: *Nereis diversicolor*, *Corophium volutator*, *Pygospio elegans*, *Hydrobia* spp. and oligochaetes. Following the recruitment of the spat in the semi-exposed habitats, *N. diversicolor*, *C. volutator* and oligochaetes were of less importance, and *Mya arenaria* and *Cardium edule* assumed a much greater importance. However, the total biomass varied considerably between years, probably according to the relative success of spat recruitment and survival.

The highest infaunal diversity (including some epifaunal amphipods and polychaetes) was found in vegetated *Zostera marina* habitats (Table 1). Oligochaetes and chironomids, the amphipods *Ericthonius* spp. and *Microdeutopus gryllotalpa* (Costa), and to a certain extent the polychaete *Nereis diversicolor* were the numerically dominant species during the year. However, most of the species were abundant for only brief

Fig. 3. Infaunal sampling survey in September along the Swedish west coast showing numbers of individuals m^{-2} (top), biomass $g\ m^{-2}$ (middle) and feeding category as percent of biomass (bottom). Areas are ranked according to the organic content in the sediment. (○) exposed areas in the Kattegat; (●) exposed areas in the Skagerrak; (□) semi-exposed, and (★) sheltered areas in the Skagerrak; (☆) vegetated areas. Bars: shaded, filter feeders; stippled, deposit feeders; open, *Nereis diversicolor* and *Pygospio elegans*

Table 1. Exposure (effective fetch, km), organic content in sediment (%), total number of infauna species, mean number of total individuals m^{-2} (with SE), total mean biomass ($g\ ADW\ m^{-2}$) and annual production ($g\ ADW\ m^{-2}$) of the 0-groups or of all year classes of *Nereis diversicolor*, *Corophium volutator*, *Mya arenaria* and *Cardium edule* in exposed areas in the Kattegat and the Skagerrak, and in semi-exposed, sheltered and vegetated areas in the Skagerrak

	Exposed					Semi-exposed				Sheltered				Vegetated	
	Kattegat		Skagerrak												
Areas	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Exposure (km)	>3	>3	1.4	2.1	1.7	1.4	1.5	1.3	1.1	0.4	0.4	1.0	0.8	1.6	1.4
Organic content (%)	0.3	0.5	0.7	0.8	0.9	1.1	1.3	1.3	1.4	3.3	3.5	4.5	5.2	4.6	6.7
Number of species	17		24			59				37				72	
Individuals m^{-2} (Jun)	1500 (500)		33600 (11800)			40300 ¹ (15700)				29600 (2400)				15900 (2200)	
Individuals m^{-2} (Sep)	5700 (2100)		16100 (4400)			31800 ¹ (11600)				35200 (6300)				30600 (18600)	
Biomass $g\ ADW\ m^{-2}$ (Jun)	0.7		4.3			10.8 ¹				8.4				3.2	
Biomass $g\ ADW\ m^{-2}$ (Sep)	3.4		10.5			13.0 ¹				17.2				17.4	
Annual production $g\ ADW\ m^{-2}$ (0-group)	5		15 – 40			10 – 270				25 – 40				1 – 10	
Annual production $g\ ADW\ m^{-2}$ (All year classes)	5		20 – 70			30 – 280				40 – 50				1 – 10	

¹ The exceptionally high bivalve recruitment in 1979 is not included

periods which usually occurred immediately following recruitment. Similar short-duration peaks were also found by Marsh (1973) when studying the epifauna in an eelgrass bed in Virginia, USA, where fluctuations were related to either reproductive or migratory activities. Predation from mobile epibenthic fauna must also be considered, as proposed by Young et al. (1976), Young & Young (1977) and Nelson (1980).

Infaunal communities in vegetated areas are usually found to exhibit higher densities and biomass values than nearby unvegetated areas (Santos & Simon 1974, Orth 1977, Reise 1978, Stoner 1980, Summerson & Peterson 1984). This was not the case in this study, as

number of individuals and biomass were highest in sheltered and semi-exposed areas in the summer and about the same in these 3 habitats (semi-exposed, sheltered, vegetated) in the autumn. One eelgrass meadow (Area 14), had an annual mean infaunal abundance of about 16 000 $ind\ m^{-2}$, with a range of about 3000 to 27 000 $ind\ m^{-2}$, i.e. abundances equal to those reported by Orth (1973) and Marsh (1973), but higher than found by Young et al. (1976), Stoner (1980) and Lewis & Stoner (1983). Orth (1973) and Young et al. (1976) used a 1 mm sieve, the others 0.5 mm sieves. Diversity and biomass values in vegetated areas were in general lower in this study than in those cited above.

However, variations of diversity and biomass values in different regions would be expected, as the importance of physical factors and biological interactions (see below) may vary with the particular habitat investigated. Diversity of amphipods has for instance been shown to increase significantly with decreasing latitude (Virnstein et al. 1984).

The infauna community of eelgrass beds in the Skagerrak was dominated by deposit and non-suspension species. These constituted 70 to 95 % of the total infauna.

Annual production of the dominant species (Fig. 4; Table 1) was about 5 g ADW m^{-2} in exposed sandy areas in the Kattegat and 20 to 70 g in exposed areas in the Skagerrak. In sheltered and semi-exposed areas in the Skagerrak production varied from 40 to 50 and 23 to 273 g ADW m^{-2} respectively, while vegetated areas had a production of 1 to 10 g ADW m^{-2} . In all areas an annual production above 50 g ADW m^{-2} was due to high recruitment or good survival of the bivalves *Mya arenaria* and/or *Cardium edule*. Production and production capacity of the dominant infauna in the areas investigated were in general found to be higher than in the Wadden Sea and in highly productive intertidal mud flats (Möller & Rosenberg 1982, 1983).

In conclusion, exposure is an important parameter in explaining the variation of production in shallow areas. Unvegetated semi-exposed areas on the west coast of Sweden, with a sediment organic content of 1.0 to 1.5 %, in general exhibit the highest biomass and production values of the areas examined. With increasing organic content in the sediment, the deposit feeder category increases at the expense of suspension feeders. Vegetated areas showed the highest infaunal diversity of all areas.

Fig. 4. Annual production (g ADW m^{-2}) of dominant infauna in a semi-exposed area (6), an exposed area in the Skagerrak (5), a sheltered area (11), an exposed area in the Kattegat (1) and a vegetated area (14). Production is calculated for all year classes and as a mean value for the whole area. Bars: shaded, *Nereis diversicolor*; with circles, *Corophium volutator*; stippled, *Cardium edule*; open, *Mya arenaria*; (★) *Bathyporeia pilosa* + *B. sarsi*; (☆) various species

Temperature

Seasonal variation between cold winters and warm summers makes temperature a critical ecological factor in boreal areas. During this investigation the winters of 1977/78, 1979/80, 1980/81 and 1981/82 could be referred to as normal along the west coast of Sweden (Fig. 2). Mean temperatures of surface water in the Gullmarsfjord for the period January to March in 1978, 1980, 1981 and 1982 were 0.9, 0.2, 0.4 and 0.2 °C, respectively. During these normal years the 0-group bivalves of *Mya arenaria* and *Cardium edule* did not survive the following winter (Fig. 5). Due to its ability to migrate to deeper sediment levels, however, *Nereis diversicolor* survived the winter and in spring the mean abundance was about 300 m^{-2} in Gullmarsvik. During ice-free periods, the amphipod *Corophium volutator* was mainly found in the inner parts of the areas with a water depth less than 0.5 m. During winters with ice the amphipods probably migrated to deeper water as only a few living specimens were found in sediments covered with ice. In Gullmarsvik the overwintering *C. volutator* population had a density of about 1900 ind m^{-2} (Möller & Rosenberg 1982) just after the break-up of the ice, thus indicating a migration from deeper water. Other abundant infauna species to be found in spring following a normal winter were *Hydrobia* spp. (1000 to 4000 ind m^{-2}), and oligochaetes (1000 to 2000 ind m^{-2}). Mean recruitment of dominant infauna species following the normal winters listed above is presented in Table 2. In 1980 the spat recruitment of *M. arenaria* and *C. edule* was low, probably due to biological interactions (discussed later), and is not included in the calculations.

Winter in 1978/79 was unusually cold and in some

Fig. 5. *Mya arenaria* (●) and *Cardium edule* (○). Mean abundance (ind m^{-2} with SE) of bivalves in the outer area (50 to 100 cm water depth) of Gullmarsvik from 1977 to 1984

parts of northern Europe considered the most severe of the past 15 yr (Beukema 1979, Arntz & Rumohr 1982, Möller & Rosenberg 1982). In the Gullmarsfjord the mean water temperature was $-0.2^{\circ}C$ from January to March and in Gullmarsvik ice appeared from December to March. Consequently, only a few large deep-dwelling *Nereis diversicolor* were found in the sediment in April 1979 and the returning overwintered population of *Corophium volutator* was also reduced compared to other years (Möller & Rosenberg 1982). Later, in June, an exceptionally heavy recruitment of *Mya arenaria* occurred on this sparsely populated bottom, with a mean of almost $500\,000\text{ ind }m^{-2}$ at 50 to 100 cm water depth (Fig. 5), i.e. an 8-fold increase compared to spat recruitment in years following a

normal winter (Table 2). This year class could still be followed in 1984. Recruitment of juvenile *N. diversicolor* was also higher, with a 10-fold increase compared to normal years. In contrast, development of the first *C. volutator* generation was poor, a consequence of either high predation from the mobile epibenthic fauna (see below) and/or the cold winter. Mortalities of infauna in shallow areas due to severe winters have also been reported from other areas, e.g. the Danish Wadden Sea (Smidt 1944) and the Dutch Wadden Sea (Kreger 1940, Beukema 1982). In these investigations the elimination of bivalves in winter was later followed by a high recruitment of bivalve spat.

Mean water temperature in the Gullmarsfjord from January to March in 1983 and 1984 was 2.3 and $1.2^{\circ}C$,

Table 2. Maximum mean abundance of juvenile recruitment per m^2 (with SE) of dominant infauna species following winters with mean temperature normal, mean temperature below average, and mean temperature above average during the period Jan to Mar in Gullmarsvik 1977–1984

Species	Mean temperature normal ($0.2 - 0.9^{\circ}C$)	Mean temperature below average ($-0.2^{\circ}C$)	Mean temperature above average ($1.2 - 2.3^{\circ}C$)
<i>Mya arenaria</i>	58 200 (9000)	457 500 (98 300)	7 200 (1900)
<i>Cardium edule</i>	34 900 (16 500)	37 100 (8200)	180 (80)
<i>Nereis diversicolor</i>	3200 (1300)	33 000 (9400)	2800 (1100)
<i>Corophium volutator</i>			
1st generation	13 500 (1800)	1100 (300)	8100 (2200)
2nd generation	9300 (1400)	8400 (2800)	9800 (1700)

respectively, i.e. these years were warmer than the other years and ice appeared for only a few weeks in the most shallow parts of the areas. Young *Cardium edule* survived in great numbers in January to March 1983 for the first time since the start of the investigation. As the next winter also was warm, the abundance of the 1982 year class was maintained (1500 ind m^{-2}) at 50 to 100 cm water depth from October 1982 until July 1984 (Fig. 5). Recruitment of juvenile *Nereis diversicolor* and *Corophium volutator* approached the same level as after normal winters, while the recruitment of the bivalves *Mya arenaria* and *C. edule* decreased dramatically due to biological competition (Fig. 5; Table 2) which will be discussed later.

In conclusion, temperature is an important physical factor causing annual and seasonal variations in e.g. spat recruitment and survival over the winter.

Infaunal changes along a depth transect

In order to study infaunal abundance and biomass changes with depth, samples were taken by divers every metre down to 10 m in 5 areas with different exposure. In general, abundance and biomass decreased with increasing depth in all areas investigated. In a semi-exposed area in the Skagerrak the biomass was about $3300 \text{ g wet weight m}^{-2}$ at 1 m and then gradually decreased to 5 m (Fig. 6). From 5 to 10 m the biomass was only about 1 % of that at 1 m. Of the biomass at 1 m, 99 % was *Mya arenaria* and *Cardium edule*.

In an exposed area in the Kattegat, however, the highest biomass and abundance were found at 4 to 6 m (Fig. 6) due to the high energy from wave action at shallower depths. At 6 m the biomass was about $1900 \text{ g wet weight m}^{-2}$; mainly large populations of *Mya arenaria* and *Cardium edule*, constituting 98 % of the total biomass. The maximum number of individuals was about $14\,000 \text{ m}^{-2}$ at 4 m in the exposed area com-

pared to the maximum of $45\,000 \text{ m}^{-2}$ at 1 m in the semi-exposed area. The organic content of the sediment was less than 1 % of the dry weight down to 10 m in the exposed area, while it increased with depth to about 4.5 % at 8 m in the semi-exposed area (Fig. 6).

In conclusion, the infaunal biomass is considerably higher in shallow waters (< 1 m) than in deeper waters (2 to 10 m); an exposed beach in Kattegat proved to be an exception, with maximal infaunal biomass at 4 to 6 m.

Currents

In shallow areas, wind-driven turbulence is likely to result in the translocation of animals living in the surface sediment. The effects of such displacements have rarely been considered in previous investigations evaluating production or abundance of infauna.

Beukema (1973) considered direct spatfall from settling larvae of *Macoma balthica* (L.) in the Wadden Sea to be small in comparison to a secondary spatfall occurring after the transport by tidal streams of spat which had settled and grown up elsewhere in sheltered coastal areas. When studying active or passive displacements of adult *Cardium edule*, however, Orton (1926), Thamdrup (1935) and Kreger (1940) could not find proof of any large displacements.

In order to evaluate the effects of wind-induced currents occurring during bivalve spat recruitment, an experiment with plankton nets was carried out in the semi-exposed Gullmarsvik. Plankton collections from nets with openings facing both into and out of the bay showed that the prevailing north and west winds gave a predominant transport inwards of juvenile bivalves, whereas winds from south and east reduced the transport inwards (Table 3). The highest inward transport of bivalve spat from water depths deeper than 1 m occurred on 22 June when winds from the north brought in about $82\,000$ individuals per m plankton net d^{-1} . In

Fig. 6. Infaunal abundance (ind m^{-2}), biomass (g WWT m^{-2}) and organic content in the sediment (0 to 5 cm) along a depth transect (0.5 to 10 m) in a semi-exposed area in the Skagerrak (○) and an exposed area in the Kattegat (●)

Table 3. The estimated in- and outward transport of bivalve spat obtained per m plankton net at 1 m water depth per 24 h in the western part of Gullmarsvik

Sampling date	Wind from	Force m s ⁻¹	In-transport of spat m ⁻²	Out-transport of spat m ⁻²
18 Jun 1982	NE	4	41 200	30 150
22 Jun	N	5	97 500	15 800
23 Jun	SE	4	4 200	5 100
29 Jun	W	3	20 600	6 100
6 Jul	NW	7	120 000	48 000
16 Jul	SE	6	4 800	3 400
5 Aug	S	3	400	500

general, the incoming bivalves were caught more than 95 % in nets 0 to 20 cm above bottom, and the rest in 20 to 40 cm. The maximum lengths of those *Mya arenaria* and *Cardium edule* which were translocated never exceeded 2 mm.

The highest densities of *Mya arenaria* and *Cardium edule* in Gullmarsvik were found within an area of about 4000 m² having a water depth of 50 to 100 cm. Within this area, 228×10^6 settled juvenile bivalves were found at the end of June 1982. Assuming a net inward transport of 6×10^6 spat d⁻¹ to this area, it would theoretically require 38 d to reach the same abundance as that obtained by random sampling 1 wk after the first recruits had arrived in the bay. Thus, direct larval settlement of *M. arenaria* and *C. edule* is the dominant factor controlling recruitment of bivalves in this bay. Secondary transport of bivalve spat is also significant, however. The translocation of bivalve spat by tidal currents ought to be more important in areas like the Wadden Sea (Beukema 1973) which have large areas of shallow waters compared to most inshore Swedish waters.

It may be concluded that shallow water currents cause displacement of spat during normal weather conditions, and consequently have a minor effect on estimates of production and abundance.

Seasonality of infaunal species caused by biological interactions

Predation

The assumption is often made that predation is important in structuring the infauna in marine unvegetated soft bottom communities in the lower intertidal zone (Blegvad 1928, Muus 1973, Reise 1977a, b, 1978, Virnstein 1977, 1979). This hypothesis derives mainly from experimental results involving the removal of predators using exclusion cages. After a period of time the density of the infauna, species diversity and biomass usually changed within the cages compared to

control areas. Such cages are known, however, to introduce many artifacts which are hard to control and the results are therefore often difficult to interpret (Arntz 1981).

In most years, high abundances of the dominant species (Fig. 5) during the main recruitment period were greatly reduced between July and the end of the year, when biomass approached zero. In order to evaluate the importance of predation by the epibenthic predators *Crangon crangon* (L.), *Carcinus maenas* (L.), *Pomatoschistus minutus* (Pallas), *P. microps* (Kröyer), *Pleuronectes platessa* L. and *Platichthys flesus* L., infaunal and epibenthic sampling were undertaken at the same time in the semi-exposed unvegetated Gullmarsvik from 1977 to 1979, and the stomach contents of the epifauna were analysed (Pihl & Rosenberg 1984, Pihl 1985).

In 1978, the biomass of juvenile *Corophium volutator*, *Mya arenaria* and *Cardium edule* was almost zero at the beginning of November, while there still remained about 4 g ADW of *Nereis diversicolor*. Altogether these species had a production that year (calculated for the whole area) of 23.0 g ADW m⁻² (Table 4). According to Pihl (1985) epibenthic fauna consumed 11.7 g of this production. If production of the deep-burrowing *N. diversicolor* is excluded, the epibenthic fauna consumed 86 % of the production of the 3 dominant infaunal species. The total consumption by epifauna of *C. edule* and *C. volutator* in 1978 was 92 and 98 % of infaunal production, respectively, and of the latter species *Crangon crangon* consumed 57 %, *Carcinus maenas* 19 %, *Pomatoschistus minutus* 10 %, *Pleuronectes platessa* 7 % and *P. microps* 5 % (Pihl 1985). During May and June the first generation of *C. volutator* usually constituted a food resource for the overwintered *C. crangon* and *C. maenas*. In 1981, the density of the first generation of *C. volutator* was low (Fig. 6) and at the same time the highest spring abundance of *C. crangon* and *C. maenas* of all the years investigated was found, with 10 and 5 ind m⁻², respectively. The following year the abundance of the first generation *C. volutator* was 100 times higher

while the epibenthic fauna consisted of only 1 or 2 ind m^{-2} (Möller et al. 1985a).

The high annual production of 0-group *Mya arenaria* (345 g ADW m^{-2}) and of *Cardium edule* (73 g m^{-2}) in 1979 was probably a consequence of high settlement on unoccupied sediments denuded of organisms by the effects of the severe winter (see above) perhaps magnified by reduced predation pressure due to the late

Table 4. Annual 0-group production (g ADW $m^{-2} yr^{-1}$) of dominant infauna species and annual consumption (g ADW $m^{-2} yr^{-1}$) by mobile epibenthic fauna from Gullmarsvik in 1978. In brackets: consumption as percent of production

	Production	Consumption ¹
<i>Corophium volutator</i>	6.3	6.2 (98)
<i>Nereis diversicolor</i>	11.2	1.5 (14)
<i>Mya arenaria</i>	3.6	2.2 (62)
<i>Cardium edule</i>	1.9	1.8 (92)
	23.0	11.7 (51)

¹ Consumption estimates from Pihl (1985)

arrival and the low densities of the mobile epibenthic predators. These were delayed 1 to 2 mo in 1979 compared to other years (Pihl & Rosenberg 1982), thus the first recruited bivalves had an opportunity to grow beyond the critical size for being captured by the main predators. According to stomach analyses, *Crangon crangon* could not eat bivalves larger than 2 to 3 mm, while the more rarely occurring flounders (1 to 4 group) ate 10 to 12 mm bivalves (Pihl 1982). Consequently, due to the high bivalve production during 1979, the consumption by the epibenthic fauna was of minor importance compared to that in other years and a high density of bivalves still remained in December 1979 (Fig. 5).

In 1982, the populations of *Mya arenaria* and *Cardium edule* were again not greatly reduced before the end of the year. This could probably be related to low densities of overwintering (1-group) *Crangon crangon* and *Carcinus maenas* and of a reduced 0-group of *C. maenas* (Möller et al. 1985a). The comparatively high survival of *C. edule* in 1982 could also be a result of its faster than usual growth rate which occurred from August to November (Möller & Rosenberg 1983).

In conclusion, high mortality of infauna immediately after recruitment is mainly caused by predation by epibenthic fauna. High mortality of juvenile infauna could usually be related to high abundances of the epibenthic fauna and vice versa. In Gullmarsvik 50 to 75 % of the 0- to 1-group infaunal annual production of 4 dominants was usually consumed by epibenthic predators (Möller et al. 1985b).

Removal of predators using exclusion cages

A small experimental program was designed to study the role of epibenthic animals as predators on the infauna. Organic content and particle size analysis of the sediment were measured before and after the experiments.

Two cages, 0.5 m^2 each, were set up at the end of June and all epibenthic predators were removed from them. Although the experiment was designed to exclude large predators, the net could not prevent planktonic crab larvae recruiting into the cages in August. This settlement was later shown to have a great impact particularly on *Corophium volutator* (Fig. 7; Table 5). In Cage I the crabs were allowed to remain, whereas in Cage II most of the crabs were removed on 10 August. Twenty d later Cages I and II contained 96 and 25 juvenile crabs, respectively, and by the end of the experiment there were 41 and 17. When predators were removed, the numbers of *C. volutator* increased due to newly hatched juveniles, while *C. volutator* decreased continuously in the uncaged ambient control area. Following the crab settlement, the numbers of *C. volutator* decreased at a rate approximately related to the abundance of crabs. The highest density of crabs caused a complete extinction of *C. volutator*, but about 1600 ind 0.5 m^{-2} remained in the cage with few *Carcinus maenas* and about 900 ind 0.5 m^{-2} in the control area.

The bivalves *Mya arenaria*, *Cardium edule* and *Spisula subtruncata* were found within the cages at abundances of between 4000 and 12 000 ind 0.5 m^{-2}

Fig. 7. *Corophium volutator*. Mean abundance (ind 0.5 m^{-2} with SE) in Cage I (○) and Cage II (●) and from an uncaged ambient control area (□). The cages excluded large predators, but not settling crab larvae

Table 5. Mean abundance of dominant infauna species (with SE) per 0.5 m² from 2 cages having different abundances of juvenile *Carcinus maenas* and from an uncaged ambient control area. Experimental time from 30 Jun to 10 Oct 1978. *C. maenas* abundance described in text

Infauna species	Start of experiment	End of experiment		
		High abundance of <i>C. maenas</i> (Cage I)	Low abundance of <i>C. maenas</i> (Cage II)	Control area
<i>Corophium volutator</i>	6997 (1265)	0	1626 (362)	917 (153)
<i>Capitella capitata</i>	1376 (348)	653 (95)	1015 (97)	584 (92)
<i>Hydrobia</i> spp.	695 (223)	1070 (709)	2641 (1251)	778 (167)
<i>Cardium edule</i>	8410 (1293)	514 (37)	598 (153)	139 (41)
<i>Mya arenaria</i>	12552 (2377)	0	42 (9)	167 (40)
<i>Spisula subtruncata</i>	4031 (737)	1195 (167)	417 (69)	0
<i>Oligochaeta</i>	1432 (128)	1154 (258)	1710 (136)	834 (78)
Total ind 0.5 m ⁻²	41259 (11789)	5467 (1567)	9406 (2072)	4059 (166)
Number of species	18	16	17	12

from start, but decreased successively (Table 5). In the control area, *S. subtruncata* disappeared before the experiment was finished, but *C. edule* was still found in October. In October the mean biomass of the bivalves was 540 g wet weight 0.5 m⁻² in the cages compared to 0.1 g in the control area. In October, the number of species had decreased in the control area compared to June, while they were about the same inside the cages. The highest density of animals was found in the cage having few crabs.

In conclusion, when using caging to achieve exclusion of epibenthic predators, most infaunal species achieved higher population densities inside the cages than in the control area. An invasion of predators in form of planktonic crab larvae, a problem earlier discussed by Young et al. (1976), Arntz (1977) and Virnstein (1978), indicated that the rate of juvenile infaunal population reduction was related to the number of juvenile crabs.

Thus, epibenthic predators must be considered as important regulators of the infaunal community, a conclusion supported by the data from the stomach analyses of the epibenthic fauna presented above.

Adult-juvenile interactions

The influence of established infaunal populations on newly settled larvae has been discussed by many authors, e.g. Smidt (1951), Thorson (1957), Woodin (1976) and Peterson (1979). A principal conclusion of this literature is that larvae are in some way attracted to a sediment by the presence of adult animals. Some authors found that larvae could be directly attracted to settle by the presence of populations of their own species (Knight-Jones 1951, Thorson 1952) while others have suggested that larval settlement could be due to the presence of particular microorganisms (Wilson 1953, Woodin 1976).

A prerequisite condition when studying causal mechanisms for spat recruitment or survival is to have reliable sampling methods collecting all sizes of the spat. Theorizing on these mechanisms based on information obtained from samples retained in sieves of 1 mm or even larger will not of course give complete information concerning adult-juvenile interactions.

Adult-juvenile interactions of bivalves in natural habitat

Following the severe winter of 1978/79, all adult bivalves in Gullmarsvik were eliminated down to at least 1 m water depth. Without interactions from adult bivalves, the subsequent recruitment and settlement of the bivalve spat was extremely high with mean abundances of almost 500 000 ind m⁻² and a biomass value of 3.7 g ADW of *Mya arenaria*. During the spat recruitment in mid 1980, there still remained about 4000 overwintered 1-group *M. arenaria* m⁻². Probably due to competition for space a mean spat abundance of only 13 000 ind m⁻² were found this year, with a mean biomass of 0.03 g ADW (Fig. 5 & 8). The following year, however, the adult *M. arenaria* had decreased to about 100 ind m⁻² but because of growth the same biomass as in previous years was maintained (Fig. 8). Thus, the spat were offered more space for recruitment on the surface sediment than in the preceding year and consequently the spat density in 1981 was found to be of the same magnitude as for other normal years.

Thus, there seem to be some effective mechanisms preventing successful settlement and survival. Suspension feeders are known to filter particles out of the water column and, as suggested by Korrington (1941), Thorson (1950) and Hancock (1970), the mortality of settling spat might be due to such filtration. On the other hand, bivalve larvae have also been shown to pass alive through the mantle cavity and digestive

Fig. 8. *Mya arenaria* (●) and *Cardium edule* (○). Mean biomass (g ADW m⁻² with SE) in the outer area (50 to 100 cm water depth) of Gullmarsvik from 1977 to 1984

tract of adult bivalves (Mileikovsky 1974 and references therein). Once the spat are settled on the sediment surface they might be subjected to environmental stress from the siphons of adult bivalves. Kristensen (1957) found that *Cardium edule* larvae were inhaled by adults, wrapped in mucus and then discharged as pseudofeces, which, according to the author, could cause a significant mortality to juveniles less than 1 mm.

The reasons for the high recruitment of bivalve spat in 1979 compared to e.g. 1978 and 1981 are not to be explained by higher amounts of larvae in the water mass outside the bay. According to mesozooplankton samples (taken with vertical hauls by L. Hernroth, Kristineberg Marine Biological Station, from bottom to surface, with a standard UNESCO WP II 90 µm net) the mean maximum number of bivalves (> 125 µm) were about the same during the recruitment period these years, varying only between 27 000 and 30 000 ind m⁻².

A similar pattern of adult-juvenile interactions to that seen during 1980 seemed to appear after the relatively warm winter 1982/83 when a *Cardium edule* population of 1800 ind m⁻² survived, and the settlement of young *C. edule* and *Mya arenaria* was considerably less than in other years (Fig. 5). As in the years 1980 and 1981, the juveniles had a low survival and in September all *M. arenaria* had disappeared while a few juvenile *C. edule* m⁻² still remained.

Thus, the results imply a strong negative interaction between adult and juvenile *Mya arenaria* and *Cardium edule*. The reason for bivalve populations being dominated by specific age classes could be a result of the low survival of young bivalves caused by inter- and intraspecific competition. The dominance of specific

age classes within bivalve populations has also been reported by e.g. Fitch (1965) and Evans (1977).

Adult-juvenile interactions from experimental studies

As emphasized by Williams (1980), many authors unfortunately have theorized on causal mechanisms for settlement, recruitment and survival based on information gained from individuals retained on 1 mm or even larger sieve mesh sizes (Fitch 1965, Hancock 1973, Woodin 1976). A field experiment with controlled manipulation of different densities of adult *Mya arenaria* was performed in Gullmarsvik, with the intention of investigating whether the effectiveness of adult-juvenile interactions was dependent upon the abundance of adults. The clams used were 3 yr old with a mean length of 50 mm. The densities of adult *M. arenaria* were 0, 10 and 100 ind 0.5 m⁻². In order to include also the effect of predation from epibenthic mobile animals on juvenile bivalves, both uncaged and caged areas were manipulated.

Treatment with uncaged areas. The experiment was started just before the settlement of bivalves occurred in June and was continued for 49 d (Table 6). Generally, fewer juvenile clams settled in the areas having adult *Mya arenaria* than in the area without adults. Without adult bivalves interacting, the maximum abundance of settled bivalves was, at the beginning of the settlement, up to 8 times higher compared to areas having adults. The bivalve settlement was dominated in numbers by *M. arenaria* followed by *Cardium edule*. The tendency for having larger spat when few adults were present was not consistent for the sporadically occurring bivalve species (*Spisula subtruncata* and *Mytilus edulis*).

Table 6. Mean number of spat bivalves per 0.5 m² in uncaged areas having different abundances of adult *Mya arenaria*. (Number of spats are recalculated from an area of 16 cm² to 0.5 m²)

Species	10 Jun	15 Jun			28 Jun			28 Jul		
		100	10	0	100	10	0	100	10	0
		ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²
<i>Mya arenaria</i>	No	4688	6563	19531	938	2188	17656	2344	2031	6719
<i>Cardium edule</i>	recruitment	0	0	0	156	313	781	2188	1719	4063
<i>Spisula subtruncata</i>		0	0	0	0	0	313	0	0	0
<i>Mytilus edulis</i>		0	0	0	0	0	469	156	938	313
Total number of spat	0	4688	6563	19531	1094	2501	19219	4688	4688	11095

Treatment with caged areas. The general results of settlement in the cages (Table 7) were similar to uncaged areas with the difference that higher spat abundances were found in the cages. In the caged areas the numbers of settled bivalves on each of the 3 sampling occasions were higher when adult *Mya arenaria* was absent compared to when present. By the end of July the total number of bivalve juveniles was about 33 900 0.5 m⁻² in caged areas without adults compared to 11 100 0.5 m⁻² in uncaged areas, i.e. a difference mainly arising from predation by the epibenthic fauna.

The negative correlation found in this experiment between the number of settled spat and the density of adult suspension feeders was also observed by Williams (1980). He found that significantly more clam spat settled in areas with no, or moderate, adult clam abundances than in areas with high adult clam abundances. The reason for this was suggested to be related to the ingestion of larvae by adults and/or a preference of larvae to settle away from the adults. Peterson (1982) also demonstrated a reduction in successful recruitment at high adult densities in mud habitats of a suspension feeding bivalve. In a sand habitat, however, he was unable to demonstrate any significant

effect of adult density on the recruitment. The reason for this difference was assumed to be a consequence of differing levels of hydrodynamic energy and resultant differences in sediment mobility. New recruits in sand were supposed to be as mobile as the sandy sediments themselves, such that even a large impact of adults on larvae could be difficult to detect due to sand movements.

Thus, the results of the adult-juvenile field experiments indicate an effect of established *Mya arenaria* upon the settling bivalve spat. This suggests that the adult-juvenile interaction is an important factor influencing the densities of soft bottom communities in shallow areas. Woodin (1976) suggested a hypothesis that once a dense assemblage is established, few larvae will successfully settle and establish themselves in the assemblage. A high survival of adults, however, does not seem to completely prevent settlement, as thousands of juveniles per m² are usually found between the established adults during the recruitment period in Gullmarsvik (Table 2; Fig. 5). During years when bivalve survival was high, as in 1980 for *M. arenaria* and 1983 for *Cardium edule*, spat recruitment was significantly lower than other years, with mean biomasses of less than 0.1 g ADW m⁻² (Fig. 8). Indi-

Table 7. Mean number of spat bivalves per 0.5 m² in caged areas having different abundances of adult *Mya arenaria*. (Number of spats are recalculated from an area of 16 cm² to 0.5 m²)

Species	10 Jun	15 Jun			28 Jun			28 Jul		
		100	10	0	100	10	0	100	10	0
		ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²	ind 0.5 m ⁻²
<i>Mya arenaria</i>	No	6406	11563	23438	2188	12813	29219	6094	13125	19998
<i>Cardium edule</i>	recruitment	0	0	0	469	1719	1250	5625	6563	11094
<i>Spisula subtruncata</i>		0	0	0	0	938	1719	0	313	625
<i>Mytilus edulis</i>		0	0	0	469	313	2344	1250	781	2188
Total number of spat	0	6406	11563	23438	3126	15783	34532	12969	20782	33905

viduals of these spat never even reached a size larger than 2 mm and when juvenile recruitment ceased in August, the 0-group population decreased and was soon eliminated. This elimination could be due to competition for space and food as well as predation. When comparing numbers of spat in caged and uncaged areas, the significance of predation from the mobile epibenthic predators was suggested by the higher number of individuals within the caged areas.

Interactions between adult bivalves

From 1977 to 1983 the spat recruitment of *Mya arenaria* and *Cardium edule* was studied. During all the years investigated the number of recruits was higher for *M. arenaria* than for *C. edule* (Fig. 5). A corresponding tendency was also found in the biomass, except in 1982 when the biomass of *C. edule* exceeded that of *M. arenaria* from mid August (Fig. 8). August 1982 was found to be the warmest month of all during the period 1977–1984, with a mean temperature of 19.8 °C (Fig. 2). This combined with other favourable environmental factors such as food availability probably resulted in a faster growth rate. Thus, *C. edule* rapidly became too large for several predators (Möller & Rosenberg 1983). During 1983 the upper 5 cm of the sediment was completely covered by *C. edule* belonging to the 1982 year class and the increasing biomass of *C. edule* resulted in a continuous decrease in both abundance and biomass of *M. arenaria*. From an average biomass for this clam of about 80 g ADW m⁻² during the period 1979–1982, only a few g m⁻² was found in July 1984 corresponding to a mean abundance of 0.2 m⁻². Probably the siphons of *M. arenaria* had difficulty in reaching the sediment surface due to the thick carpet of *C. edule*, thus producing high mortality amongst the *M. arenaria*.

Peterson (1979) questioned some beliefs about the role and modes of interspecific competition in soft sediment systems. Although both the distributional and experimental evidence suggested that interspecific competition played a significant role in the organization of many shallow-water infaunal communities, there were no studies, according to Peterson (1979), demonstrating the active process of competitive exclusion in which one species actually eliminated another.

The study of interspecific competition in a natural habitat between *Mya arenaria* and *Cardium edule* in Gullmarsvik, however, has demonstrated a significant impact, where one species almost completely eliminated another species for some time. Although the initially established adult *M. arenaria* seemed to be able to prevent large bivalve settlements for many years, they could not impede the rapidly growing *C.*

edule population in 1982 resulting in the elimination mentioned above.

Thus, interspecific competition played an important role in influencing dominance between 2 species, which in this case ended with the elimination of the initially dominant species.

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