

Benthic faunal energy flow and biological interaction in some shallow marine soft bottom habitats

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ABSTRACT: Infauna, including macrofauna and temporary meiofauna, and mobile epibenthic fauna have been quantitatively investigated in more than 15 shallow (0 to 1.5 m) soft bottom areas from 1977 to 1982 on the Swedish west coast. The areas are grouped into 3 types of habitats having little or no vegetation: (1) exposed, (2) semi-exposed, (3) sheltered, and 1 habitat (4) where vegetation dominates. Results are presented mainly from 4 intensively studied areas, representative of each of the habitats. *Infaunal annual production* varies between and within habitats depending on temperature, recruitment strength, available space and predation pressure. Comparisons with lower salinity areas in the Baltic show lower infaunal production and production/biomass ratios there than on the Swedish Skagerrak coast. *Epibenthic faunal annual production* is similar within habitats; highest in vegetated areas (about 6 g AFDW m⁻²) followed by semi-exposed areas (4 to 5 g AFDW m⁻²). It is suggested that each habitat has a carrying capacity for epibenthic faunal production. Epibenthic faunal production is 5 to 10 times higher in semi-exposed habitats on the Skagerrak coast than in similar habitats on the Baltic coast. As production of the epibenthic fauna is similar between years within habitats despite significant interannual variations of infaunal production, food is not likely to be a limiting factor for epibenthic faunal production in summer-autumn in Swedish Skagerrak shallow waters. In most years 51 to 75 % of *production of dominant infaunal prey organisms* is consumed by epibenthic carnivores in semi-exposed unvegetated habitats. However, in years with heavy infaunal settlement the percentages are much lower. In an exposed area consumption exceeds infaunal production and epibenthic carnivores also prey upon semi-pelagic mysids. In a sheltered area about 10 % of the infaunal production is eaten and the fate of the remainder is unknown. In a vegetated area the epibenthic faunal consumption is about 4 times that of infaunal production. Here about 75 % of the food consumed by the dominant carnivore *Palaemon adspersus* is non-carnivorous epifauna, mainly amphipods. Thus, infauna is the quantitatively most important food category for epibenthic carnivores in exposed, semi-exposed and sheltered habitats with little or no vegetation, while in vegetated habitats non-carnivorous epifauna is the dominant prey. *Energy flow* through the 4 different shallow habitats is discussed in general terms and presented diagrammatically for 2 of them. Exposed and semi-exposed shallow unvegetated habitats are largely fuelled by phytoplankton produced offshore, utilized by suspension feeders. In vegetated habitats the primary food is largely produced within the area and detritus and 'small' herbivores are important in this energy flow. Sheltered unvegetated habitats are largely based on detritus as food. In all these habitats a significant part of the animal production during summer and autumn is later transferred to deeper waters by migration and there constitutes a valuable food resource for coastal fish populations.

INTRODUCTION

Population biology and community structure in marine soft bottom habitats have been studied intensively for many years. Recently more attention has been paid to the functional aspects of these communities. This has, in particular, involved studies in shallow waters of animal production and interactions including predator-prey relations. Many of these

studies have concerned the macro-infauna and the population controls and structuring effects exerted on the infauna by predators, mainly mobile epibenthic animals. The results from several such studies are partly based on laboratory or field experiments, e.g. cages (Reise 1977, Virnstein 1977, Peterson 1979, Hulberg & Oliver 1980, Arntz 1981, Virnstein et al. 1983). Although such studies are useful they do not give conclusive information regarding predator-prey

interactions in a natural habitat. On the other hand, unmanipulated investigations performed in the field have concentrated either on infauna or on mobile epibenthic carnivores, and when the interactions between these categories are quantified the results from one or the other are at least partly extrapolated from literature data (e.g. Kuipers et al. 1981, Evans 1983).

The aim of this paper is to describe biological interactions and energy flows of the soft bottom benthic communities from some shallow water (< 1.5 m) habitats on the Swedish west coast, (Skagerrak-Kattegat) (Fig. 1), which have different exposures, sediment structures and vegetation cover. This is a compilation of results from field investigations, carried out between 1977 and 1982, of infauna (Möller & Rosenberg 1982, 1983, Möller 1985) and mobile epibenthic fauna (Pihl & Rosenberg 1982, 1984, Baden & Pihl 1984, Pihl 1985) and also partly including diurnal migrating fish (Pihl 1982). The studies of infauna and epibenthic fauna were undertaken at the same time in the respective research areas. The epibenthic fauna and the infauna comprises all post-larval size groups, i.e. both temporary meiofauna and macrofauna. The 2 latter categories are referred to in the

following as infauna. Permanent meiofauna was sampled only in 1978 in Gullmarsvik.

AREAS INVESTIGATED

The study areas are grouped in 4 habitat categories; 3 with almost no vegetation and with different exposures: exposed, semi-exposed, and sheltered; and the fourth dominated by vegetation (mainly *Zostera marina* [L.]). Each habitat was investigated in 3 to 7 different areas and 15 and 22 areas were investigated for infauna and epibenthic fauna, respectively. Most of the results presented here are from the 4 localities presented in Fig. 1. Exposure was calculated as effective fetch (Håkanson & Jansson 1983). Values for each locality were: Varberg (exposed) > 3 km, Gullmarsvik (semi-exposed) 1.4 km, Bassholm (sheltered) 0.4 km and Finnsbo (vegetated) 1.6 km.

The research areas have a temperature range from below zero, with ice during most winters, to above 18°C in summer, which gives a relatively short season for animal production. Salinity varies, normally between about 15 to 30‰, and a low tidal amplitude of 0.1 m means that feeding can continue at all states of

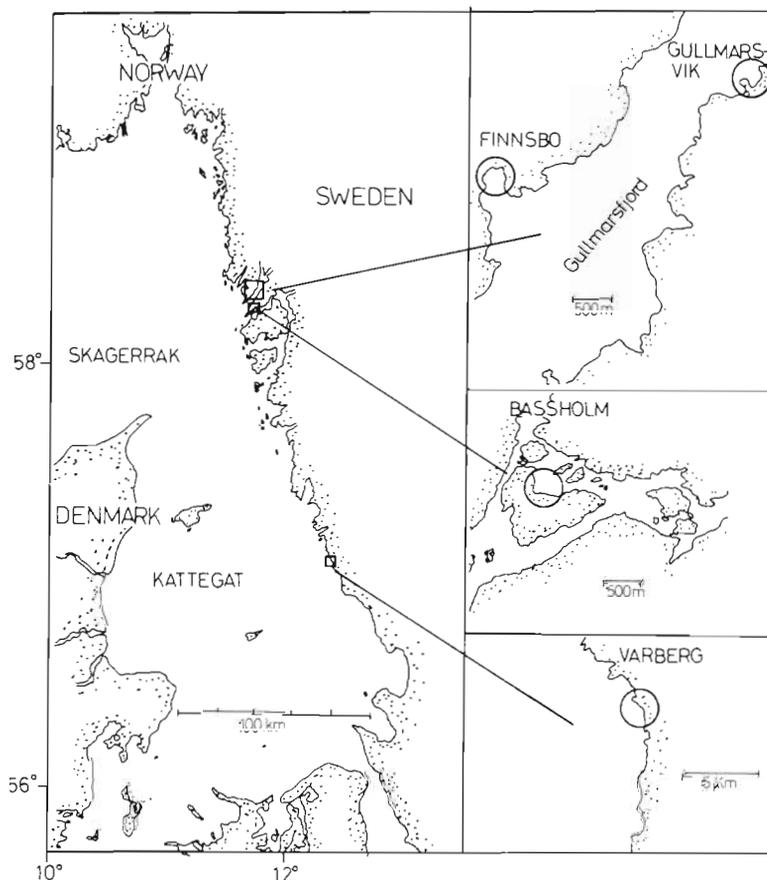


Fig. 1 Map of the 4 principal habitats studied. Habitats with no or scarce vegetation are Varberg (exposed), Gullmarsvik (semi-exposed) and Bassholm (sheltered). Habitat with vegetation is Finnsbo

the tide. Sea and shore birds are rarely seen in the research areas and their predation effects are therefore considered negligible. The areas investigated are not directly influenced by pollution.

METHODS

At each locality the investigated area was between about 1 and 4 ha (1 to 4×10^4 m²) and random samples in each area were taken for 1 to 6 yr from 1977 to 1982. Number of samples taken at each occasion was usually 20 to 40 and determined by the target of statistical precision: Standard Error (SE) < 25 to 30 % of mean abundance and biomass of dominant species.

In unvegetated areas infauna was collected by cores of various sizes; a small core (16 cm²) was used during the larval recruitment period, a medium core (87 cm²) from autumn to spring and a large core (290 cm²) was used when investigating the large overwintered bivalves. During the larval recruitment period all of the upper 5 cm of the sediment was decanted and sieved through 0.2 mm meshes. When the annual recruitment had ceased, a sieve of 0.5 mm was used and samples were taken down to 20 cm depth in the sediment. In vegetated areas samples were taken by diving. Here a core of 87 cm² and a 0.5 mm sieve were used.

Mobile epibenthic fauna was sampled by a portable drop-trap having a bottom area of 0.5 m². In unvegetated areas a 0.7 m high trap was used (Pihl & Rosenberg 1982). In *Zostera* meadows the trap was 1.5 m high and released from a small boat (Baden & Pihl 1984). The animals in the trap were collected with a 1 mm mesh net.

Seven areas, representing each of the habitats described earlier, were sampled 1 to 5 times mo⁻¹ during the ice-free period (Apr to Dec), while the remaining areas were visited twice a year (Jun and Sep) in 1981 and/or 1982.

Secondary Production (P) was estimated for each species from measurements of mean population density (\bar{N}) and the individual mean weight increment ($\Delta\bar{W}$) (ash free dry weight) between 2 successive sampling as:

$$P = \sum_{t=0}^{t=n} \frac{(\bar{N}_{t+1} + \bar{N}_t)}{2} \Delta\bar{W}, \quad (1)$$

and elimination as:

$$E = \sum_{t=0}^{t=n} (\bar{N}_t - \bar{N}_{t+1}) \frac{(\bar{W}_1 + \bar{W}_2)}{2} \quad (2)$$

For several species the estimates were made after separation into cohorts. Food selection and consumption by epibenthic predators were based on stomach

analysis. Complete details of methods are given in the papers cited above.

RESULTS

Dominants

The infauna and mobile epibenthic fauna are dominated in abundance and biomass by a limited number of species. Conspicuous infaunal species in most unvegetated habitats are the suspension feeding bivalves *Cardium edule* L. and *Mya arenaria* L., the deposit feeding amphipod *Corophium volutator* (Pallas), and the omnivorous polychaete *Nereis diversicolor* O. F. Müller. Exposed sandy areas are dominated by the amphipod *Bathyporeia sarsi* Watkin, and vegetated areas by non-suspension feeders such as oligochaetes and chironomids. These species make up a great part of the food of the mobile epibenthic carnivores in unvegetated areas. The commonest carnivores in unvegetated areas are the decapods *Crangon crangon* (L.) and *Carcinus maenas* (L.), and the fishes *Pomatoschistus microps* (Krøyer), *P. minutus* (Pallas) and *Pleuronectes platessa* (L.). In vegetation, *Palaemon adspersus* (Rathke) is a dominant together with *C. maenas*.

The great majority of the infaunal and epibenthic species mentioned are also dominants in other European shallow waters, e.g. in Denmark (Muus 1967), in the Wadden Sea (Reise 1977, Wolff & de Wolf 1977, Kuipers et al. 1981) and in England (Warwick & Price 1975).

Seasonality and recruitment

The marked seasonal variation between cold winters and warm summers makes temperature a critical ecological factor in Swedish shallow water environments. In autumn mobile animals migrate to deeper, warmer water where they overwinter, whereas sedentary forms burrow deep in the shallow water sediments. Thus no production is likely to take place in shallow areas during winter. During severe winters many sedentary animals are killed.

When water temperature rises in spring, mobile animals return to the shallow areas. Infauna and post-larval flatfish are mainly recruited in May and June, but cold winters and springs will delay this. The recruitment of post-larval *Crangon crangon*, *Carcinus maenas*, *Pomatoschistus microps* and *P. minutus* starts in July, 1 to 3 wk after the bivalve spat-fall. In semi-exposed areas the peak abundance of infauna and epibenthic fauna frequently exceeds 100 000 and 100 ind m⁻², respectively. Thus, the table is laid for predators and initial infauna mortality is considerable.

Recruitment of the epibenthic species continues from July through October and occurs in pulses, or brood waves, probably caused by different hatching times and differential distribution by currents.

Production

Pelagic primary production in one of the regions studied, the Gullmarsfjord, was 180 to 230 g C m⁻² yr⁻¹ in 1978–79 (Lindahl & Hernroth 1983). Food for suspension feeders is, however, produced not only in the adjacent water mass. Transport of pelagic algae by currents from far distances is of great significance. This is especially important in years when secondary production is particularly high, e.g. 0-group *Mya arenaria* alone may produce 345 g Ash-Free Dry Weight (AFDW) m⁻² yr⁻¹ in a shallow (50 to 100 cm) semi-exposed area in the Gullmarsfjord (Möller & Rosenberg 1983).

Infaunal and mobile epibenthic faunal biomass and production in these studies (op. cit.) are considerably higher in shallow (<1.5 m) than in deeper (3 to 10 m) waters. Exposed beaches are an exception with maximum infaunal biomass at 4 to 6 m. Production is low in spring and early summer and in most years about ¾ of the annual production occurs during 3 mo (Jul to Sep). The production is in general equal to or higher than that in southern European waters (Pihl & Rosenberg 1982, Möller & Rosenberg 1983). The short production season in Swedish waters also results in a high productive capacity, i.e. high production/biomass (P/B) ratios (Fig. 2). One reason for this is the heavy annual recruitment of juveniles with high growth potential. Space for the infaunal juveniles is, in most years, created by high mortality in the previous year, caused by predation and by cold winter temperatures. In some years, e.g. in 1979, recruitment of bivalves is so high and feeding conditions so favourable, that a large number soon outgrow the size range available to the majority of predators. Under these circumstances, if the subsequent winter is not too cold, a strong year class can survive and later have significant interspecific and intraspecific effects on the survival of new bivalve recruits (Möller & Rosenberg 1983).

It has been shown that annual mobile epibenthic faunal production in Gullmarsvik was between 4 and 5 g AFDW m⁻² in 1977–80 (Pihl & Rosenberg 1982) and similar levels were also recorded in 1981–82 (unpubl.). Thus, regardless of the dominants' infaunal annual production, which varied by a factor of 1 to 22 (mean 6) between 1977 and 1982, the epibenthic faunal production (and also abundance) reaches about the same level each year. Also, in each of the other habitats, the annual epibenthic production has a tendency to reach a certain level (Pihl unpubl.). For example in unpol-

luted vegetated habitats the annual epibenthic production approaches 6 g AFDW m⁻² (Baden & Pihl 1984). This is probably about the maximum such areas can produce of this faunal category in Swedish shallow waters. These results may suggest that these shallow habitats each have a carrying capacity for total mobile epibenthic faunal production, and that food does not seem to be the limiting factor during the productive season. More likely space could be a limiting factor, through e.g. territorial interactions, which together with sediment structure (habitat complexity) sets the limits of production at the various habitats.

Energy flow and biological interactions

Consumption by mobile epibenthic carnivores in the semi-exposed Gullmarsvik (Fig. 1) in 1978 is shown in Fig. 2. Values of mean biomass and annual production for predators and dominant prey are also given. Consumption by mobile epibenthic carnivores was assessed in detail in this area that year (Pihl & Rosenberg 1984, Pihl 1985). Of the total consumption of 25.8 g AFDW m⁻² about 70 % is infauna; permanent meiofauna, mobile epibenthic fauna and 'detritus' make up about 10 % each. Of the meiofauna, harpacticoids and ostracods are frequently eaten by smaller predators. Post-larvae of *Crangon crangon* and *Carcinus maenas* are mainly eaten by *C. crangon*. 'Detritus' is here unidentified organic matter found in the stomachs of *C. maenas*. Predators consumed 98 % of the annual production of *Corophium volutator*, 92 % of *Cardium edule* and 62 % of *Mya arenaria*. Thus, not only is most of the production of these species transferred into mobile carnivores, but also their numbers and biomass are reduced almost completely within a few months (Möller & Rosenberg 1982, 1983).

In Fig. 3 elimination of *Corophium volutator*, *Cardium edule*, *Mya arenaria* and *Nereis diversicolor* is compared with consumption by mobile epibenthic predators of these species in 1978 in Gullmarsvik. Elimination and consumption are based on independent results. Consumption of *C. volutator* is high in spring and autumn compared to elimination, but low in summer. Calculated over the whole season, however, consumption equals elimination. Consumption of the 2 bivalves *M. arenaria* and *C. edule* is close to elimination during July and August. By September *M. arenaria* is probably too large a prey for the investigated epibenthic fauna, but could be eaten by other large predators such as 2+ group *Carcinus maenas*, 1–2 group *Pleuronectes platessa* and 1–4 group *Platichthys flesus* L., which occasionally visit the bay (Pihl 1982). For *C. edule* elimination is probably underestimated during autumn. The biomass is close to zero in December and elimination should then equal

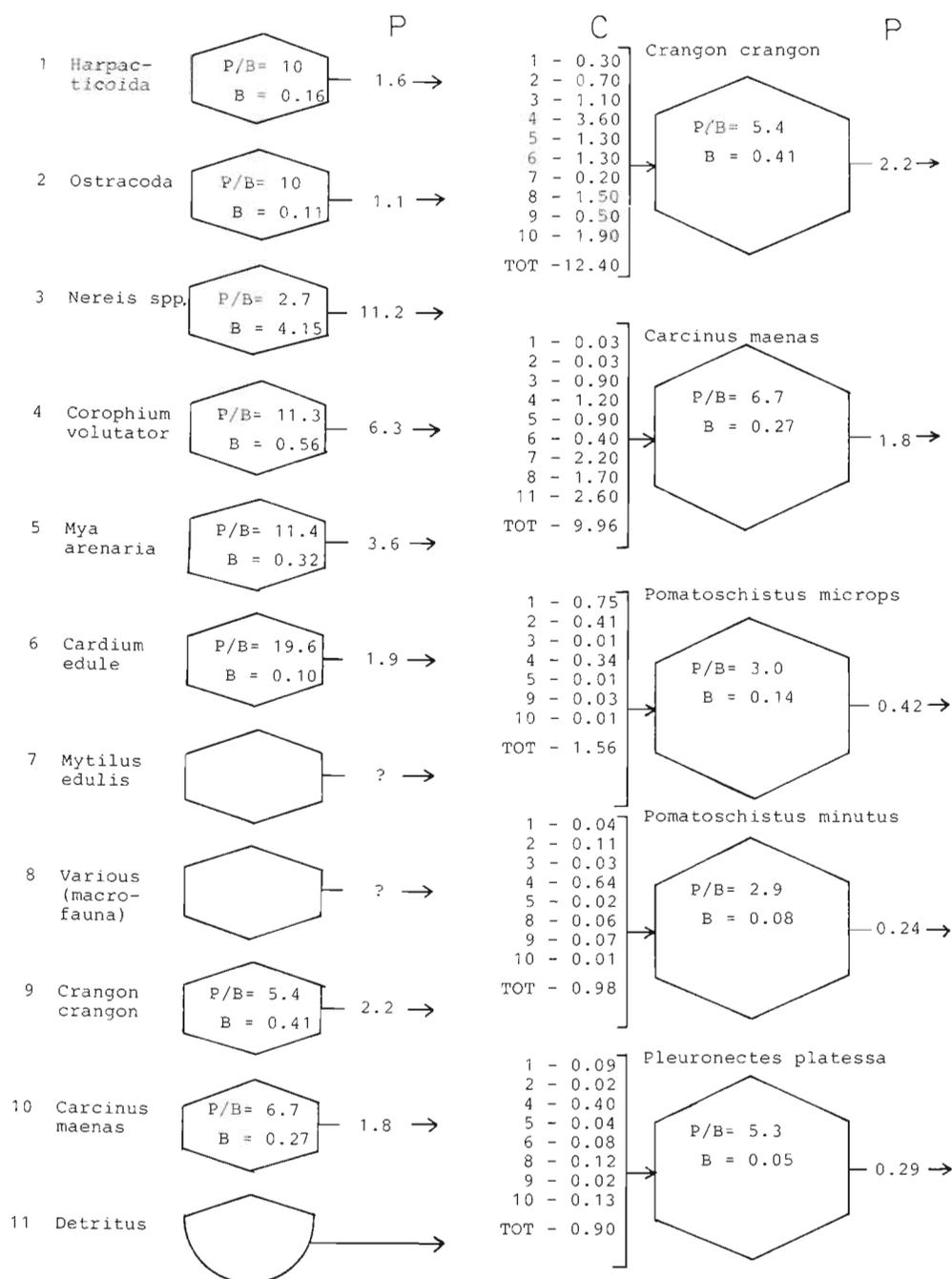


Fig. 2. Infaunal, permanent meiofaunal, and mobile epibenthic faunal mean biomass (B), annual production (P) and P/B ratios in Gullmarsvik in 1978. Annual consumption (C) is given for the epibenthic carnivores. All values are g AFDW m⁻²

the production of 1.9 g m⁻², but is actually lower (Fig. 3). Consumption of *N. diversicolor* is assessed at about 1/3 of elimination. Thus, the majority of the production of this polychaete is transferred to other parts of the food web.

From these results it could be concluded that, in Gullmarsvik in 1978, elimination of infauna is caused mainly by predation by epibenthic fauna. To examine if this is also the case in other years, annual consump-

tion by mobile epibenthic fauna, of the same dominant infaunal species, is compared to annual production of these infaunal species in Gullmarsvik for the years 1977 to 1982 (Table 1). Consumption estimates by the total epibenthic fauna in 1977 and 1978 and by *Crangon crangon* in 1979 are from Pihl & Rosenberg (1984) and Pihl (1985). For species other than *C. crangon* in 1979 and for all species in 1980 to 1982, consumption is estimated from production/consumption (P/C) ratios of

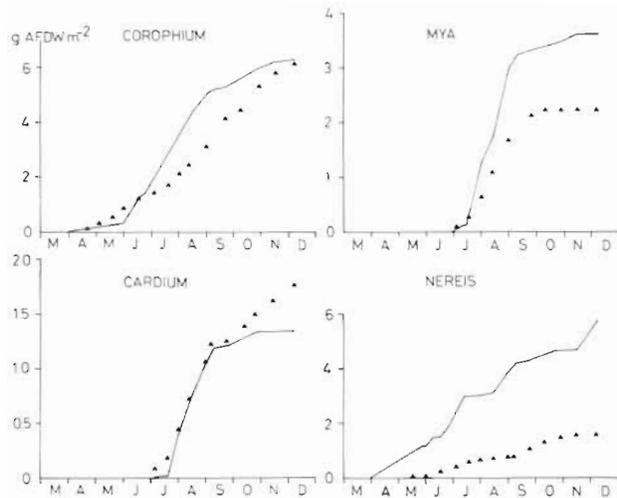


Fig. 3. Elimination (—) of 4 dominant infaunal species in relation to consumption (▲) (g AFDW m⁻²) of the same species by mobile epibenthic fauna in Gullmarsvik 1978. Infauna includes potential prey sizes for the epibenthos studied: 0-groups of *Mya arenaria* and *Cardium edule*, 0–1 group *Corophium volutator* and 0–2 group *Nereis diversicolor*. Note difference in scales on the ordinate

0.2 and 0.3 for crustaceans and fish, respectively (Pihl 1985). In 1977 and 1978 the above listed dominant infaunal species comprised about 50 % of the total food consumption and this figure is used to estimate the consumption of these species during 1979 to 1982.

In 1977, 1978, 1980 and 1981 epibenthic predator consumption was estimated at 51 to 75 % of the dominant infauna production. This shows that the epibenthic fauna had a great impact on the infauna community in those years. However, in 1979 and 1982, when infaunal production was high, the corresponding figures were 4 and 10 %, respectively. The high infaunal production in these years was probably caused by low predation by infaunal and epibenthic carnivores in spring and early summer, resulting in a high survival, particularly of bivalves, subsequent to settlement.

So far we have concentrated on a semi-exposed

Table 1. Annual production (g AFDW m⁻²) of dominant infauna (0–1 group *Corophium volutator*, 0-group *Mya arenaria*, 0-group *Cardium edule* and 0–2 group *Nereis* spp.) compared with annual consumption of these species by the epibenthic fauna in Gullmarsvik in 1977–82

Year	1977	1978	1979	1980	1981	1982
Production of infauna	12.1	23.0	27.3	16.2	16.2	69.4
Consumption by epibenthic fauna	9.1	11.8	11.2	9.4	10.1	7.0
Consumption/Production (%)	75	51	4	58	62	10

sandy-silt area from which we have the longest sampling record. However, similar estimates of animal production are also available for some years from other shallow habitats in the region. The sheltered muddy Bassholm, the exposed sandy Varberg and the vegetated Finnsbo (Fig. 1) are examples of such different habitats. They are highly representative as to species, abundance, biomass and production for other similar habitats in the region. The epibenthic faunal consumption is partly derived from Pihl & Rosenberg (1984) but also estimated by using the P/C ratios given earlier and applying them to the production figures given by Pihl & Rosenberg (1982), Baden & Pihl (1984) and Pihl (unpubl.). Results are given in Fig. 4 together with infaunal production figures for the most important prey organisms (see above) from Möller & Rosenberg (1982, 1983) and Möller (1985). Consumption is also divided into different prey categories and their relative impor-

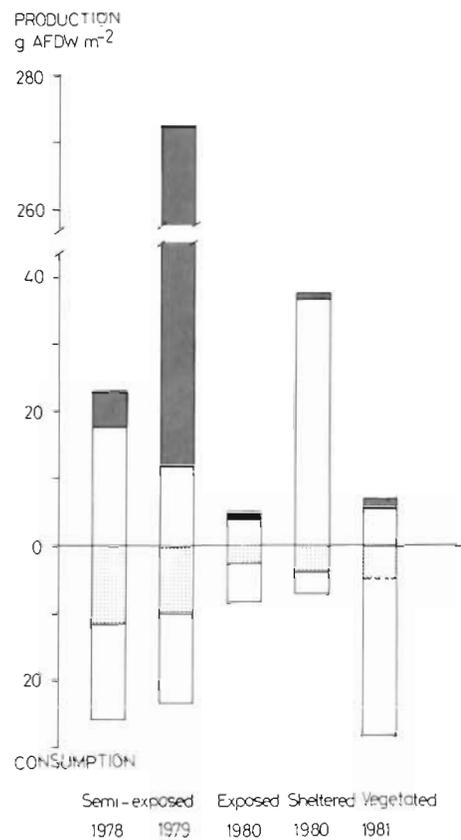


Fig. 4. Annual production (top) of infauna (0-group *Mya arenaria*, 0-group *Cardium edule*, 0–2 group *Nereis diversicolor* and 0–1 group *Corophium volutator*) at the 4 habitats shown in Fig. 1. These species make up a large proportion of infaunal prey for epibenthic carnivores. Proportion of the suspension feeders *M. arenaria* and *C. edule* is shaded. Total annual consumption (bottom) by mobile epibenthic carnivores is given for the same habitats and years. Estimated proportion consumed by carnivores of these 4 infaunal species' production is shown stippled

tance is assessed (Fig. 5). These separations are based on extrapolation from our published results (op. cit.) and unpublished information from our vegetated areas (Baden pers. comm.).

In the exposed and sheltered shallow areas epibenthic consumption (Fig. 4) and production are lower than in the other habitats. This is probably a result of unfavourable physical factors; i.e. in the exposed area wave action may normally be too strong and in the sheltered area the substrate may be too soft for some of the carnivores. Also, infaunal production is low in exposed areas (0 to 1 m), and the reason for consumption exceeding infaunal production is mainly feeding on mysids by *Crangon crangon* (see loop C in Fig. 5). In the sheltered habitat only about 10% of the infaunal production, dominated by *Corophium volutator* and *Nereis diversicolor*, is consumed and transfer loops for the rest of the energy are unknown.

In the vegetated habitat, infaunal production is about 7 g AFDW m⁻² yr⁻¹ and epibenthic consumption

is about 4 times higher. In this habitat the main predator in the 3 unvegetated habitats, *Crangon crangon*, is replaced by *Palaemon adspersus*. The majority of food (75%) for this species is taken from non-carnivorous 'small' epifauna, mainly amphipods. Although the production of prey organisms other than infauna is unknown, food does not seem to be a limiting factor for epibenthic production during summer and autumn.

Fig. 5 shows that infauna is the quantitatively most important food category for epibenthic carnivores in exposed, semi-exposed and sheltered shallow areas in western Sweden, and that small forms of epifauna dominate as prey in areas with vegetation. The most important larger predators are cod *Gadus morhua* L. and flounder *Platichthys flesus*, feeding in shallow (0 to 1 m) waters between dusk and dawn (Pihl 1982). In the semi-exposed Gullmarsvik, with an investigated area of 2 ha, the flounder consumes about 0.5% of the annual infaunal production. Cod, on the other hand eat epibenthic animals almost exclusively and their con-

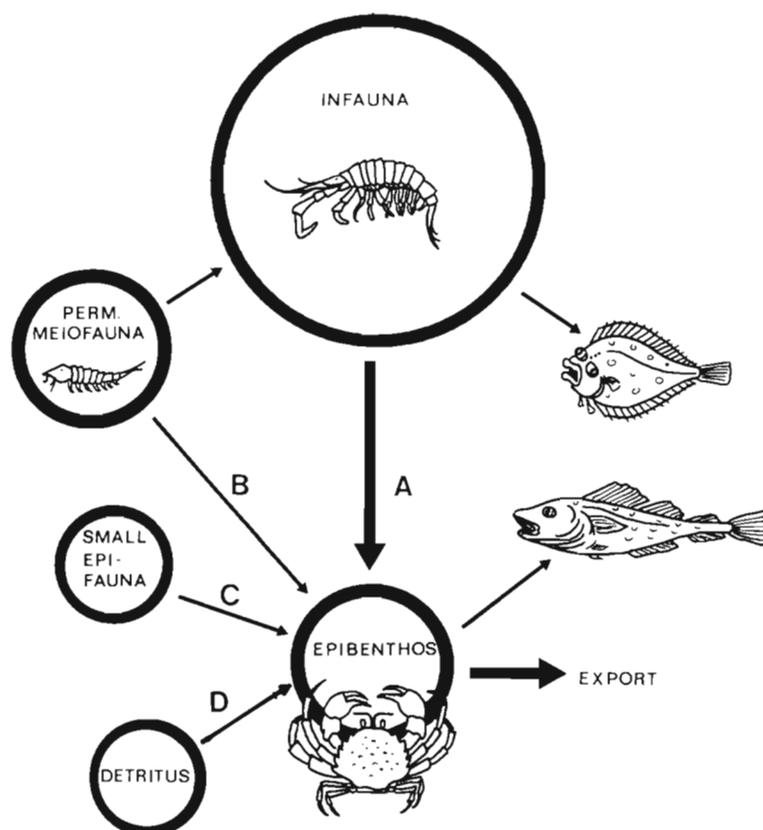


Fig. 5. Schematic presentation of the annual consumption by mobile epibenthic carnivores of infauna (including temporary meiofauna), permanent meiofauna, 'small' epifauna (including mysids) and 'detritus'. Total consumption and relative importance of the different loops in the 4 habitats are also given. Exposed, semi-exposed and sheltered habitats have little or no vegetation

Habitat	Epibenthic consumption				
	Total g AFDW m ⁻² yr ⁻¹	Different loops (%)			
		A	B	C	D
Exposed	9	55	10	35	0
Semi-exposed	26	70	10	10	10
Sheltered	7	60	30	0	10
Vegetated	30	15	10	60	15

sumption is estimated at about 7% of the annual production of these animals. Thus, a significant proportion of the epibenthic faunal production must be transferred to deeper waters through migration during the autumn and early winter. As cod is almost the only large predator of these organisms in shallow areas, an export to deeper waters of approximately 90% of the epibenthic production is a possible crude estimate. In some years, however, part of this production is consumed within the shallow area by large carnivores eating smaller ones.

From this section we can conclude that infaunal dominants, functional groups (guilds) and production vary between the 4 habitats. Variation between years can also be significant as observed for a semi-exposed locality. This variation is related to factors such as water temperature, recruitment strength, space available, growth conditions and predation pressure of the 2 dominant bivalves *Mya arenaria* and *Cardium edule*, which both have shown intra- and interspecific competition affecting survival (Möller & Rosenberg 1983).

DISCUSSION

A crude comparison of infaunal and epibenthic faunal community abundance, biomass, production and production capacity (P/B) in different salinity regions in shallow semi-exposed areas along the Swedish coast is presented in Table 2. Methods were the same or similar. The highest values are generally found in the Skagerrak and are lower in the reduced salinity regions on the southern and eastern Swedish coasts. Several of the infaunal dominants (see above) are the same in the Skagerrak, the Sound and the

Baltic, whereas chironomids are one of the dominants of the infauna and a preferred fish prey in the Bothnian Sea (Rosenberg et al. 1985).

Among the epibenthic fauna crustaceans are absent, or occur in low numbers, on the Swedish southern and eastern coasts, because of low salinity. This is the main reason for the comparatively lower abundance, biomass and production of mobile epibenthic fauna in those areas compared to areas on the Skagerrak coast. The major fish species are, however, the same in all these shallow waters and their biomass and production are rather similar.

In Fig. 5 we quantified the energy flow into epibenthic carnivores for different habitats. In the following we will expand this model into still simplified, but more elaborate, energy flow models of shallow benthic habitats, including some connections with offshore waters.

The most important energy flow pathways are emphasized in Fig. 6A for unvegetated semi-exposed habitats. The main energy inflow is in the form of phytoplankton biomass transported by current. Most of this is utilized directly by filter feeding bivalves and part of it is transferred directly, or indirectly as fecal pellets, on to the detritus pool. Benthic microalgae are also an important food resource for meio- and macrofaunal herbivores and detritivores. The role of microorganisms may be of significant importance as food for deposit feeders. Further down the food chain, important loops link filter feeders and deposit feeders to epibenthic carnivores. A small proportion (about 7%) of these are eaten by demersal fish migrating into shallow waters at night. Most of the energy bound in the epibenthic fauna is, however, exported to deeper waters through the autumn and early winter migra-

Table 2. Crude comparisons of the dominants of infaunal and epibenthic faunal communities. Abundance (ind m⁻²), biomass (g AFDW m⁻²), production (g AFDW m⁻²) and P/B ratios during the productive season (Jul to Sep) on semi-exposed soft bottoms at 0 to 1 m water depth along the Swedish coast (from Rosenberg et al. 1985)

	Skagerrak 15-30‰	Sound ~10 ‰	Baltic 6-7 ‰	Bothnian Sea 5-6 ‰
Infauna				
Abundance (× 10 ³)	5-500	8-20	-	3-30
Biomass	2-70	3-6	0.5-40	1-24*
Production	23-273	9-17	-	-
P/B	4-11	2.5-3.2	1-3	-
Epibenthic fauna				
Abundance	100	35	25	10
Biomass	1-3	0.5-0.9	0.5-1	0.1-0.5
Production	3-5	0.2-0.7	0.5-1	0.2-0.7
P/B	4-7	2-3	-	2-3

* Calculated from dry weight

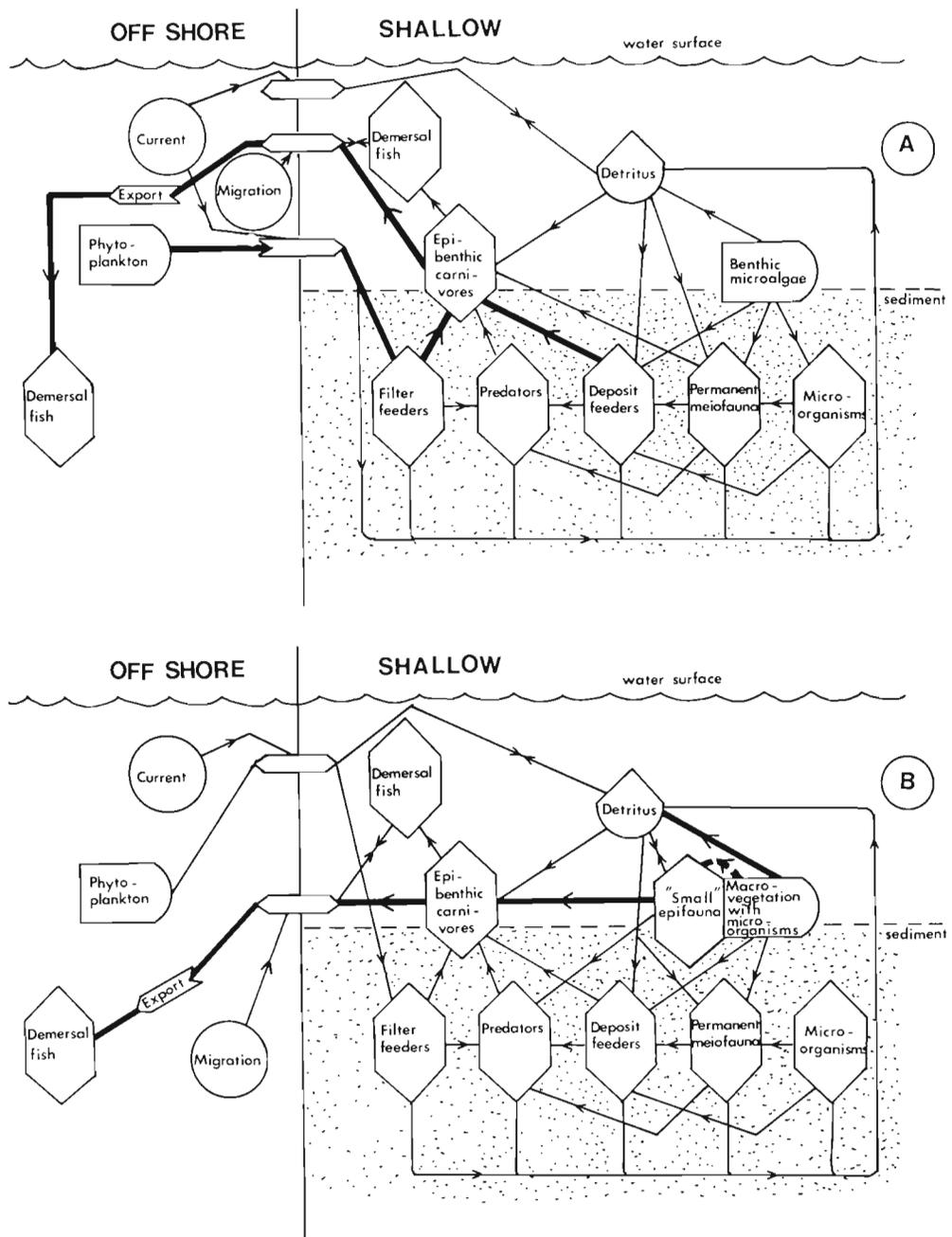


Fig. 6. Simplified energy flow diagrams of (A) un-vegetated semi-exposed shallow habitats, and (B) vegetated shallow habitats, with their main connection with offshore waters. Loops of special significance are emphasized. The role of microorganisms was not assessed

tions by these animals, which then comprise a potential food resource for demersal fish.

Energy flow in exposed areas is similar to that presented in Fig. 6A, but is modified with the degree of exposure. On open coasts with high exposure (as at Varberg, Fig. 1) the infaunal community is reduced in the upper meters close to the shore. In such environments the model seems appropriate for depths of about 4 to 7 m.

Thus, moderate to strong water exchange is characteristic for exposed and semi-exposed shallow habitats and the food for the dominant infaunal suspension

feeders is largely phytoplankton produced offshore and transported to these habitats by the currents. Part of the energy exported from these habitats is through seasonal epibenthic migration.

An energy flow model for habitats dominated by vegetation (mainly *Zostera marina*) is outlined in Fig. 6B. Here, the macrovegetation with epiphytes and associated microorganisms make up the basic pool of food. Part of this is eaten directly by 'small' epifaunal herbivores associated with vegetation and part of it is utilized by deposit feeders later, after decomposition. The energy transfer in the system is maintained by

shredding by isopods and amphipods (Robertson & Mann 1980). Deposit feeders constitute 70 to 95 % of the total infauna in the vegetated habitats studied, but the biomass is low compared to in semi-exposed and sheltered habitats. Epibenthic carnivores such as *Palaemon adspersus* feed mainly on the 'small' epifauna (mostly amphipods not assessed in this study). *Carcinus maenas* also eat 'detritus'. Infauna seems to be of less importance in this habitat compared to in unvegetated habitats. Foraging activity beyond the vegetated areas by these carnivores is probably of minor importance from spring through to autumn in the areas investigated (cf. Summerson & Peterson 1984). As for the semi-exposed habitats, the epibenthos in vegetated areas also leave the inshore areas in autumn and early winter.

Energy flow in sheltered habitats has similarities with that for vegetated areas presented in Fig. 6B. Vegetation is however of minor importance and the sheltered habitat is most likely fuelled to a major extent by detritus and benthic microalgae. These pools are utilized by the deposit feeders (e.g. *Corophium volutator*), which in turn are eaten by the epibenthic carnivores. An unknown proportion of the detritus in the sheltered habitats is likely to be supplied from outside and trapped inshore.

Thus, slow water exchange is characteristic for vegetated shallow habitats and the primary production is to a great extent produced within the habitat and is partly trapped as detritus. Infaunal detritivores and 'small' epifauna (herbivores) are dominant among the macrofauna. Part of the energy exported from such habitats is through seasonal epibenthic migration, but organic material can also be transported to deeper water during storms in autumn and winter. Characteristics for sheltered habitats are similar, with the exception that vegetation and associated 'small' epifauna are of less importance.

Energy budgets for shallow water benthic communities have been calculated by Evans (1984) for a semi-exposed bay in the Gullmarsfjord, western Sweden. He estimated the loss to the benthic community from predation at a maximum of 24 to 34 % of annual production in 2 successive years. This is low compared with this study where, in years with normal recruitment, 51 to 75 % of the production of the dominant infauna was consumed by epibenthic predators. In 1977, when the work by Evans (1984) and that of this study were carried out simultaneously, epibenthic consumption of infaunal production was found to be twice as high in our study compared with that found by Evans. The main reason for the low consumption estimates in the latter study is that infauna samples were taken only 3 times each year and much lower abundances were recorded than those found in our study

(Evans 1983). Thus the annual spat recruitment of *Mya arenaria* and *Cardium edule* was either not recorded immediately following settlement, thus underestimating initial predation rates, or not recorded through loss in sieving the samples. Also, consumption by carnivores was comparatively lower in Evans' (1984) study, as a food conversion factor of 39 % for *Crangon crangon* was used whereas in the present study a factor of 19 % was calculated.

In an energy flow model for a tidal flat ecosystem, Kuipers et al. (1981) suggest that the 'small food web' (meio- and microfauna) is important as food for juvenile carnivores in the Wadden Sea and one reason for this is the low estimate of macrobenthic production (about 20 g AFDW m⁻² yr⁻¹). This estimate is based on an assumed P/B ratio of 1, which is low compared to our results. However, the different age structure, with a significant proportion of old individuals in the Wadden Sea (Beukema 1976), could result in low P/B ratios for the size groups >1 mm, which were investigated. Suppression of spat by the presence of adult bivalves, as was demonstrated in the present studies (Möller & Rosenberg 1983), could also occur in the Wadden Sea. Another possibility is that the carnivores eat the majority of spat and other juveniles, and that only a minor proportion reach sizes large enough to be collected as macrofauna.

An energy flow diagram was presented by Thayer et al. (1975) for a *Zostera marina* community in North Carolina, USA. They found an infaunal community of only 328 ind m⁻² and 6.6 g dry wt m⁻² (sieve: 1.2 mm meshes) dominated by deposit feeders. These figures are much lower than ours. The fish community in North Carolina has, on the other hand, a high mean biomass, 1.3 g dry wt m⁻². A comparison with the whole epibenthic fauna cannot be made, because the numbers of carnivorous crustaceans are added to those of the infaunal community.

Summerson & Peterson (1984) conclude from cage experiments made in the same region that epibenthic predators found in the seagrass bed during daytime restrict their predation on sandflat infauna to the nighttime, and that large predators take more infauna there than in the seagrass bed. From other investigations it is suggested that within the seagrass bed mobile epibenthic carnivores take epifaunal prey, i.e. amphipods, before infauna (Orth 1977, Virnstein 1977, Nelson 1979), which is in agreement with our study. The low infaunal biomass in vegetated areas recorded in our studies, could, in addition to epibenthic predation, be due to predation by predatory infauna as described by Ambrose (1984).

Indirect evidence of predation by mobile epibenthic carnivores on infauna have been provided in several cage experiments (e.g. Reise 1977, Young & Young

1977, Peterson 1979, Hulberg & Oliver 1980, Virnstein et al. 1983). Other investigations have concentrated on the food intake by members of the epibenthic community (e.g. Kuipers & Dapper 1981, Zander & Hartwig 1982, Thorman & Wiederholm 1983), and conclusions from these experiments, together with the results reported here, emphasize the importance of epifaunal predation in controlling infaunal populations.

Direct studies of food selection and consumption in relation to the production of prey animals, i.e. a functional analysis of the benthic system, are so far scarce. This work covers parts of the temporary meiofauna, macrofauna, mobile epibenthic fauna and migratory fish, with some notes about permanent meiofauna. Information needed for a more complete analysis would include e.g. production estimates for meio- and microfauna and the predator-prey relations between these and macrofauna. Only a few studies have as yet attempted such detailed analyses (e.g. Gerlach 1971, Ankar & Elmgren 1977, Warwick et al. 1979).

Because of the few energy flow measurements in shallow waters reported from other regions, it is difficult to evaluate how representative the models presented in Fig. 6A & B are for such habitats outside the Swedish west coast. However, based on such quantitative and qualitative results as are available from other regions in the northern hemisphere (e.g. Muus 1967, Peterson 1979, Kuipers et al. 1981, Virnstein et al. 1983, and references therein and in Table 3), it seems probable that the models could be generally applicable for comparable shallow waters in other northern boreal areas.

The importance of coastal waters as nursery and

feeding grounds for fish, and the need for their preservation, have been appreciated by some authors (e.g. Muus 1967, Zijlstra 1972, Boddeke 1978, Tiews 1978). It seems that western Swedish, and probably many Scandinavian, shallow waters are especially important in this respect, but that this importance has not been fully recognized in coastal zone management. The role of these areas in exporting epibenthos, both as fish food and as juvenile fish, to deeper waters in autumn and early winter, is probably of significant importance for demersal fish populations in many similar coastal areas.

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Table 3. Annual production (P), mean biomass (B) and production capacity (P/B) for dominants in infauna communities at some different depths and sediments. Values are in g AFDW m⁻² unless otherwise stated. The last 4 areas are western Sweden

Area	Depth m	Sediment (organic content, %)	P	B	P/B	Source
North Sea	80	Fine sandy silt	1.7	4.0	0.4	Buchanan & Warwick 1974
Baltic	46	Mud (4 %)	6.8*	4.3*	1.6	Cederwall 1977
Bristol Channel, U. K.	10-18	Sandy-mud	14.2*	11.1*	1.3	Warwick & George 1980
Wales	~13	Very fine sand (3 %)	25.8	45.8	0.6	Warwick et al. 1978
Netherlands	~7	Fine to very fine sand	50-57	-	1.6	Wolff & de Wolf 1977
San Francisco	0, MF	Mud	53-100**	13-24	4.5**	Nichols 1977
South England	0, MF	Fine silt and clay (13 %)	13.3	13.2	1	Warwick & Price 1975
Gullmarsfjord	0-1	Fine to very fine sand	21-27*	3.8-4.5*	4.6-7.0	Evans 1983
Gullmarsvik	0-1	Fine to very fine sand (~1 %)	23-273	2-70	4-11	} Möller & Rosenberg 1982 } Möller & Rosenberg 1983 } Möller 1985
Sandvik	0-1	Fine to very fine sand (~1 %)	19-58	2-7	4-9	
Bassholm	0-1	Sand-silt-clay (3.5 %)	41-53	4.5	4-7	
MF	Mudflat					
*	Dry weight					
**	Estimated from biomass					

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