

PRODUCTION AND ENERGY BUDGET IN MARINE SUSPENSION FEEDING POPULATIONS: *MYTILUS EDULIS*, *CERASTODERMA EDULE*, *MYA ARENARIA* AND *AMPHIURA FILIFORMIS*

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ABSTRACT

The pelagic primary production and the secondary production of four species of benthic suspension feeders were frequently measured over a period of approximately one year in four different habitats. Simplified energy budgets over one-year periods are presented including ingestion, absorption, faeces production, respiration and secondary production. The production of a *Mytilus edulis* culture exceeded primary production by about 6.25 times, whereas semi-exposed shallow-water populations of *Cerastoderma edule* and *Mya arenaria* had a production roughly equal to primary production. In an exposed area, the latter species had a secondary production:primary production ratio of 0.15:1, whereas for a deeper-living (40 m) *Amphiura filiformis* population this relation was 0.0034:1. *M. edulis* followed by *C. edule* and *M. arenaria* in the semi-exposed habitat had the comparatively lowest Respiration:Absorption ratios and the highest Production:Absorption ratios. This study emphasizes the ecological importance of horizontal advective processes for energy transfer from the pelagic to the benthic system.

Key words: secondary production, primary production, benthic-pelagic coupling, assimilation, absorption, respiration, ingestion, physical oceanography

1. INTRODUCTION

Phytoplankton is the main basic food source for benthic invertebrates. The supply of food to the benthos is generally episodic and may be related to periods of great sedimentation subsequent to phytoplankton blooms (Smetacek, 1980; Berger *et al.*, 1989). In arctic (Grebmeier *et al.*, 1988) and boreal (Christiansen & Kanneworff, 1985) waters such tight benthic-pelagic couplings have been demonstrated, and the episodic food input is rapidly consumed (Graf, 1992; Graf *et al.*, 1983). In tidally induced frontal areas sedimentation of seston may be enhanced, which can have a significant impact on the species composition and the biomass of benthic communities (Creutzberg *et al.*, 1984; Jenness & Duineveld, 1985). In a classical paper, Hargrave (1973) demonstrated that the sedimentation of organic carbon may be proportional to the ratio: carbon input/mixed layer depth, which reflects increased mineralization with increased depth of mixing. Hargrave (l.c.) also suggests that when the primary production is low, a larger proportion will reach the sediment. Later, however, Wassmann (1990) showed that an increased

primary production may lead to an export from the photic zone that is even higher than expected from a linear relationship.

Suspension feeders may collect particles before they settle on the bottom (labile material) or as resuspended material (generally less labile). In shallow waters the near-bottom horizontal transport of seston has been shown to support a secondary production of infaunal suspension-feeding bivalves that may even exceed the primary production per m² (Möller & Rosenberg, 1983; Möller *et al.*, 1985). Suspension feeders can trap particles that are transported horizontally close to the bottom. Grizzle & Morin (1989) have suggested, based on studies with the suspension-feeding hard clam *Mercenaria mercenaria*, that horizontal seston fluxes may be a major factor affecting growth of suspension-feeding bivalves. However, too high current speeds may limit growth in suspension feeding-bivalves (Wildish & Kristmanson, 1985). The importance of habitat characteristics and degree of exposure for this kind of benthic-pelagic coupling and secondary production has been evaluated by Möller *et al.* (1985) and Graf (1992).

In the present paper we have chosen four habitats

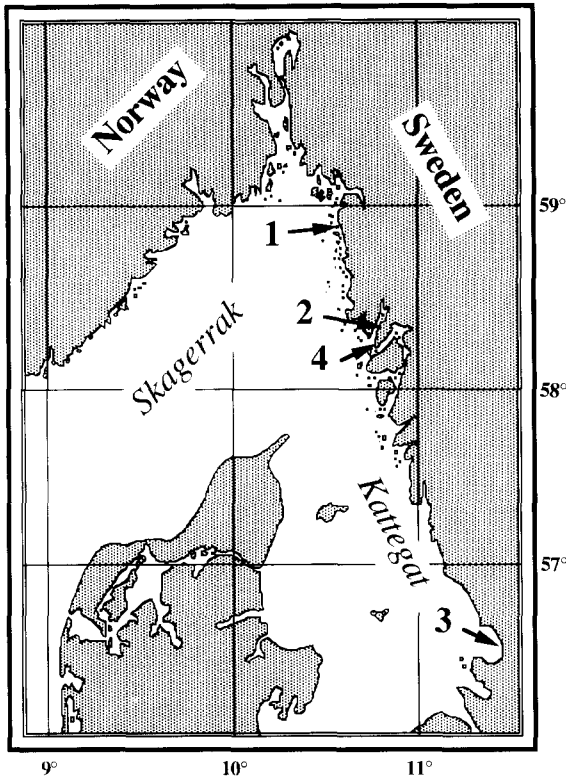


Fig. 1. The areas with sampling locations in the Skagerrak: (1) Strömstad archipelago, (2) Gullmarsfjord and (4) mouth of the Gullmarsfjord, and in the Kattegat: Laholm Bay (3).

dominated by suspension feeders and sampled frequently over about one year (Fig. 1). The objective is to compare the secondary production of the dominant suspension feeders with the primary production in the respective areas, and to compare energy budgets of the benthic populations. The primary production of the four habitats varied between 177 and 247 gC m⁻²·y⁻¹ (Fig. 2). Despite that rather small differences in primary production, we are able to demonstrate large differences in secondary production. This emphasizes the importance of the physical oceanography as a significant factor for growth of shallow-water suspension feeders.

The populations studied were the dominant macrofaunal species in their respective habitats, all suspension feeders. First, a population of cultured *Mytilus edulis*; second, shallow semi-exposed populations of *Cerastoderma edule* and *Mya arenaria*; third, shallow exposed populations of *C. edule* and *M. arenaria*; and fourth, a deeper (40 m) population of *Amphiura filiformis*.

The study areas have only small tidal amplitudes (5-10 cm), a summer surface water temperature of 15-20°C, and during extreme winters some weeks of ice. The temperature at 40 m is lowest in March,

≈5°C, and highest in October, ≈14°C. Salinity of the surface waters vary between 15 and 30 psu, and at 40 m depth it is about 34 psu.

2. MATERIAL AND METHODS

Equations used in energy flow measurements were: A=P+R, I=(A/Ae)·100 and F=I-A, where A is absorption, P is secondary production, R is respiration, I is ingestion, Ae is absorption efficiency and F is faeces production.

Production (P) was estimated according to Crisp (1984):

$$P = \sum_{t=0}^{t=n} \frac{\bar{N}_t + \bar{N}_{t+1}}{2} \Delta \bar{w}$$

and elimination (E) according to Winberg (1971):

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

where *n* is the number of sampling occasions at different sampling times *t*, \bar{N} is the mean population density, $\Delta \bar{w}$ the individual mean weight increment between successive samplings, and \bar{w} is individual mean weight.

Data on *M. edulis* production in the Skagerrak are from Loo & Rosenberg (1983) and energy-budget measurements from Rosenberg & Loo (1983). Data on *C. edule* and *M. arenaria* in a shallow semi-exposed habitat in the Skagerrak are from

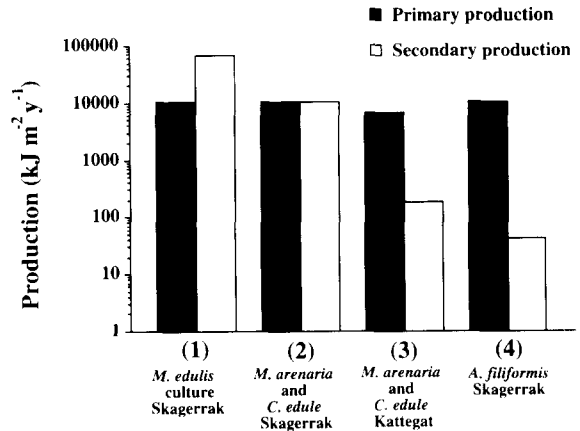


Fig. 2. (Black columns) Pelagic phytoplankton production (Edler, 1986; Lännergren, 1983; Lindahl & Herrroth, 1983; Lindahl *et al.*, 1991) and (white columns) secondary production (kJ·m⁻²·y⁻¹) of *Mytilus edulis* in a mussel culture (Rosenberg & Loo, 1983), *Cerastoderma edule* and *Mya arenaria* in the Gullmarsfjord (Möller & Rosenberg, 1983). *C. edule* and *M. arenaria* in the exposed Laholm Bay (Loo & Rosenberg, 1989) and *Amphiura filiformis* at 40 m in the Gullmarsfjord (Sköld *et al.*, 1994). Note the logarithmic scale.

TABLE 1

Relationship between shell-free dry weight (SFDW; g) and respiration rate ($\text{ml O}_2 \cdot \text{h}^{-1}$) for *Cerastoderma edule*, calculated from $V = a \times W^b$ (Newell & Bayne, 1980), where V is respiration rate and W is weight. * extrapolated values from rest of the year.

period of sampling (y/mo/day)	a	b
85/06/25-85/07/23	0.583	0.426
85/07/23-85/09/12	0.672	0.661
85/09/12-85/10/14	0.404	0.300
85/10/14-86/04/03	0.665	0.375
86/04/03-86/06/25	*	

Möller & Rosenberg, 1983). *C. edule* and *M. arenaria* production and energy budgets for the shallow exposed Laholm Bay, the Kattegat, are from Loo & Rosenberg (1989) for the period June 1985 to April 1986, and extrapolated for April to June 1986 based on the mean for these periods. Respiration of *C. edule* and *M. arenaria* was calculated according to Newell & Bayne (1980; Table 1) using the energy conversion: $1 \text{ cm}^3 \text{ O}_2 = 19.88 \text{ J}$ (Riisgård & Randløv, 1981). For transformation of *C. edule* biomass to energy content the following conversions were used: 1 mg flesh DW = 19.05 J, estimated for *C. edule* (Chambers & Milne, 1979), and 1 mg shell AFDW = 21.10 J, as obtained for *Scrobicularia plana* (Hughes, 1970); flesh DW=1.6 flesh AFDW; 2·(shell AFDW)=total AFDW (our own measurements).

To estimate the energy content of seston in Laholm Bay a conversion from chlorophyll a (Chl a) values (Edler, 1986) to energy was made as follows: energy (kJ) = Chl a (mg)/0.26 (Lännergren, 1983). For *C. edule* and *M. arenaria* an approximate average absorption efficiency of 60% was chosen for the energy budgets based on Newell & Bayne (1980).

For the *A. filiformis* population in the Skagerrak, production estimates are from Sköld *et al.* (1994). Absorption efficiency for *A. filiformis* was estimated from organic content in the stomach of freshly caught animals compared to organic content in faeces, which gave an absorption efficiency of 70% (range 70-96%) based on calculations according to Conover (1966). Respiration measurements from Ursin (1960) of $2.40 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ were used.

3. RESULTS

3.1. PELAGIC SUSPENSION FEEDING POPULATION *MYTILUS EDULIS* CULTURE

The mussels in the culture were attached to vertical ropes (0-6 m) and studied over a period of 1.5 years, subsequent to settlement in June, from August 1978 to March 1980. The study site was in the Strömstad archipelago close to the Norwegian border (Fig. 1). Our calculations are based on the period from August

1978 to August 1979. The biomass of other animals in the culture was about 1% of the total. Annual mean surface-water current speed in the area was 2 to $3 \text{ cm} \cdot \text{s}^{-1}$ (Larsson, 1984). Mean annual primary production outside the mussel culture was $222 \text{ g C m}^{-2} \cdot \text{y}^{-1}$ in 1979 (Lännergren, 1983). Energy content in seston, taken as an average over 1 to 5 m depth, was 6 kJ m^{-3} in winter and reached a peak of 45 kJ m^{-3} during autumn blooms. Available mean seston energy content per m^2 for the culturing period was 99 kJ d^{-1} .

Biomass increment of mean biomass was about 125% (AFDW with shell) in spring 1979 and 228% in autumn (Loo & Rosenberg, 1983). Phytoplankton biomass in spring and autumn made up >95% of the seston protein and carbohydrate content. However, in winter >90% of these substances were bound in detritus (Lännergren, 1983). Thus, food quality varied with season and as a consequence mussel energy content declined in the winter of 1978. The highest mussel production in 1978 was recorded in the autumn, coinciding with high phytoplankton biomass. Phytoplankton biomass was also high during the summer of 1979, but at that time a decrease in *Mytilus edulis* biomass was recorded as a result of gamete release.

Estimates of biomass, production, respiration, absorption, ingestion and faeces production were incorporated into an energy budget in Fig. 3. The absorption efficiency is likely to vary with season, temperature, food concentration and quality, and mussel size. Based on an absorption efficiency of 70% (Rosenberg & Loo, 1983), the amount of ingested food needed for one year was 239180 kJ m^{-2} , absorption was 167426 kJ m^{-2} and faeces production was 71754 kJ m^{-2} for the same period. Respiration was 58% and production 42% of absorption.

The production:mean biomass (P:B) was 2.2 (Table 2). The ratio between secondary production and primary production of *M. edulis* for the whole investigation period was 6.25:1. The growth efficiency, P:R, in this study was about 1:1.5.

3.2. SHALLOW SEMI-EXPOSED SUSPENSION FEEDING POPULATIONS *CERASTODERMA EDULE* AND *MYA ARENARIA*

From June 1979 to August 1982 the *Mya arenaria* and *Cerastoderma edule* populations were studied in the Gullmarsfjord (Fig. 1; Möller & Rosenberg, 1983). In the present study we have used the period June 1979 (recruitment period) to June 1980, the year with highest secondary production. *M. arenaria* and *C. edule* together made up 85-90% of total faunal biomass. Water depth in the studied area was between 0.5 and 1 m, where these populations had their highest densities. Organic content (ignition loss) within the top 5 cm of the sediments varied between 0.7 and 2.4%. Between 1978 and 1982 the mean annual pelagic primary production was 205 g C m^{-2} in that area (Lindahl & Hernroth, 1983).

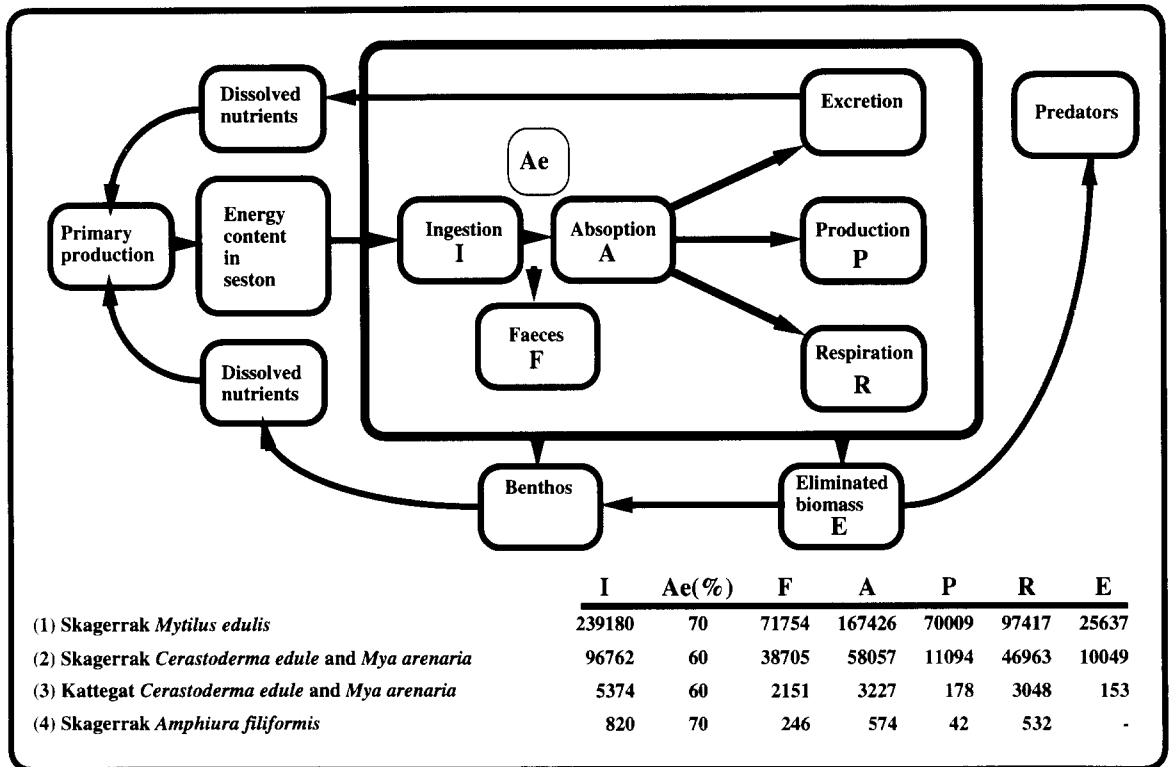


Fig. 3. Simplified energy-flow diagram in $\text{kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ of the (1) suspension feeding bivalve *Mytilus edulis* (Nyckelbyvik, Skagerrak; after Rosenberg & Loo, 1983), (2) the suspension feeding bivalves *Cerastoderma edule* and *Mya arenaria* in a semi-exposed habitat (Gullmarsfjord, Skagerrak; after Möller & Rosenberg, 1983), (3) the suspension-feeding bivalves *C. edule* and *M. arenaria* in an exposed habitat (Laholm Bay, Kattegat; after Loo & Rosenberg, 1989), and (4) the passive suspension feeding ophiurid *Amphiura filiformis* at 40 m depth (Gullmarsfjord, Skagerrak; after Sköld *et al.*, 1994). The larger boxed part refers to the energetic transfers within the animals.

M. arenaria contributed 83% and *C. edule* 17% of the bivalve production. About 75% of the annual production of the 0-group bivalves occurred within a two-month period the first summer. The amount of ingested food needed for the two species was 96762 kJ, based on 60% absorption efficiency (Fig. 3). The absorption was 58057 kJ and the faeces production 38705 kJ. Annual P:B was 7.9. Growth efficiency, P:R, was 1:4.2. The ratio between secondary production and primary production was about 1:1 (Fig. 2).

3.3. SHALLOW EXPOSED SUSPENSION FEEDING POPULATIONS *C. EDULE* AND *M. ARENARIA*

Laholm Bay, in the southeast part of the Kattegat, covers an area of $\approx 300 \text{ km}^2$ and 20% is between 0 and 10 m deep (Fig. 1). The shallow bay is exposed and has sandy sediments with an organic content (ignition loss) of <1%. Biomass and production of *C. edule* and *M. arenaria* were assessed from the

TABLE 2

Ratios for *Mytilus edulis* culture (1), shallow semi-exposed *Cerastoderma edule* and *Mya arenaria* in the Skagerrak (2), shallow exposed *Cerastoderma edule* and *Mya arenaria* in the Kattegat (3) and deeper bottom *Amphiura filiformis* (4) populations. Ratio between secondary production (Sp) and pelagic primary production (Pp), production (P) and mean biomass (B), production (P) and absorption (A), respiration (R) and production (P), and respiration (R) and absorption (A).

	year	Sp:Pp	P:B	P:A	R:P	R:A
(1) <i>M. edulis</i>	1978-79	6.25	2.2	0.42	1.5	0.58
(2) <i>C. edule</i> and <i>M. arenaria</i>	1979-80	1	7.9	0.19	4.2	0.81
(3) <i>C. edule</i> and <i>M. arenaria</i>	1985-86	0.03	3.3	0.06	17	0.94
(4) <i>A. filiformis</i>	1990-91	0.0034	0.46	0.07	13	0.93

recruitment in April 1986 at 5 to 8 m water depth, where these populations had their highest densities (Loo & Rosenberg, 1989). The biomass of other animals in the infauna community was about 7% of the total.

Mean annual primary production in the outer Laholm Bay area during 1981 to 1985 was 136 gC m^{-2} (Edler, 1986). However, these measurements did not include the water column below the halocline, and later measurements have shown that $\approx 30\%$ of the production took place at that depth (Richardson & Christoffersen, 1991). Thus, we have added 30% to $136 \text{ gC}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ which equals $177 \text{ gC}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$.

Together, *M. arenaria* and *C. edule* ingested $5374 \text{ kJ m}^{-2}\cdot\text{y}^{-1}$ (Fig. 3). The share of *M. arenaria* of their added production was 73%, leaving 27% for *C. edule*. Theoretical maximal consumption of the suspension feeding bivalves in Laholm Bay resulted in $64 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, which was only half of their potential feeding capacity (Loo & Rosenberg, 1989).

Annual growth efficiency, P:R, was approximately 1:17 and the ratio between secondary production and primary production 0.03:1.

3.4. DEEPER BOTTOM SUSPENSION FEEDING POPULATION *AMPHIUURA FILIFORMIS*

This study site, investigated between 14 June 1990 and 4 November 1991, was located at the mouth of the Gullmarsfjord (Fig. 1) at a depth of 40 m. Energy budgets are based on studies performed between June 1990 and June 1991. The biomass of other animals in the community (excluding a few echinoderms) was 35-40% of the total and they were mainly deposit feeders. The top sediment (0 to 1 cm) had a mean organic carbon content of 3.5%. In 1990 the mean annual primary production in that area was $247 \text{ g C}\cdot\text{m}^{-2}$ (Lindahl *et al.*, 1991).

Secondary production and population dynamics of the suspension feeding (Buchanan, 1964) brittle star *Amphiura filiformis*, adults dominating, have been assessed by Sköld *et al.* (1994). Disc growth and gonad production accounted for ca. 69% ($1.8 \text{ g AFDW}\cdot\text{m}^{-2}\cdot\text{y}^{-1} \approx 37 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) of the total annual production within the population. About 13% ($0.34 \text{ g AFDW}\cdot\text{m}^{-2}\cdot\text{y}^{-1} \approx 6.8 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) of the total production was allocated to arm regeneration, probably a result of cropping by predators. Mean annual regenerated biomass in percent of total biomass for adult *A. filiformis* was between 12 and 30 (mean 22%), indicating the importance of *A. filiformis* arms as a food source.

Estimates of biomass, production, respiration, absorption, ingestion and faeces production for a mean abundance of 186 adult $\text{ind}\cdot\text{m}^{-2}$ gave an annual ingestion of about $820 \text{ kJ}\cdot\text{m}^{-2}$ based on an absorption efficiency of 70% (Fig. 3). Respiration was 93% and production 7% of absorption. Absorption efficiency

may vary with season, temperature, food concentration and quality, and brittle star size. Mucus is used to trap particles and these aggregates are transported to the mouth. Energy loss due to excretion of mucus is not known, but is probably of minor importance in an energy budget (Crisp, 1984).

Annual P:R was 1:13, and the ratio between secondary production and primary production was 0.0034:1.

4. DISCUSSION

4.1. DIFFERENCES BETWEEN SUSPENSION-FEEDING POPULATIONS

This is the first time energy budgets of several suspension feeding populations have been compared within a region with similar environmental conditions, and their secondary production related to pelagic primary production of the areas. Animal abundance, biomass and secondary production and pelagic primary production were assessed several times a month during the spring, summer and autumn in three of the studied areas, but with a somewhat lower frequency in Laholm Bay during the winter. Thus, the annual means are thought to be fairly accurate.

Primary production indicates the food potential produced in each area, but does not give detailed information on how much is coming into close contact with the suspension-feeding bivalves and *Amphiura filiformis*. The algal food produced in the water column is, in addition to the species of this study, also consumed by planktonic herbivores and other suspension feeders and deposit feeders in the benthic communities. However, the species studied were highly dominant suspension-feeding components of each community (Möller & Rosenberg, 1983; Rosenberg & Loo, 1983; Loo & Rosenberg, 1989; Sköld *et al.*, 1994). Thus, intraspecific competition for suspended food particles is likely to have been greater than interspecific competition.

Energy budgets of the suspension feeding populations studied in the four habitats resulted in great differences. The sites differed in hydrodynamic regime, food availability and depth. The *Mytilus edulis* culture had a production 6.25 times higher than the primary production, which shows the high production capacity of such a system. This high secondary production was a result of spatial distribution of high densities among the mussels, and the fact that most mussels probably had continuous access to nutritious food supplied by the currents. The fact that the growth efficiency of the cultured mussels (P:R=1:1.5) was equal to their potential rate (Fenchel & Finlay, 1983) suggests that the hydrodynamic environment was indeed favourable.

In the semi-exposed habitat in the Skagerrak, *Cerastoderma edule* and *Mya arenaria* had a production equal to primary production. These bivalves, bur-

ied in the sediment, had access to food transported in and out of the bay. It is possible that, in addition to the phytoplankton produced in the pelagic system and the availability of other suspended seston, benthic microalgae may also have been consumed by the bivalves. If that was the case, secondary production could have been somewhat lower than primary production on an annual basis. Most of the production of *C. edule* and *M. arenaria* in this habitat, however, occurred during two months only (Möller & Rosenberg, 1983), and during that period secondary production per m^2 must have been higher than primary production. The short season for secondary production was caused by epibenthic crustaceans eating the vast majority of the fast-growing juvenile bivalves (Möller *et al.*, 1985; Pihl, 1985). Thus, even though predation pressure was high during summer, this does not seem to have had a negative effect on the growth of *C. edule* and *M. arenaria*.

The combined production of *M. arenaria* and *C. edule* in the Skagerrak was higher than in some intertidal macrofaunal communities. In California, the bivalves *Gemma gemma*, *Macoma balthica* and *M. arenaria* were dominant and the total annual production was between 54 and 111 $g\ AFDW \cdot m^{-2} \cdot y^{-1} \approx 1080$ and 2220 $kJ \cdot m^{-2} \cdot y^{-1}$ (Nichols, 1977). In the Bristol Channel, southwest England, the total annual infaunal production was 13 $g\ AFDW \cdot m^{-2} \cdot y^{-1} \approx 260$ $kJ \cdot m^{-2} \cdot y^{-1}$ (Warwick & Price, 1975). In a Canadian intertidal sand flat, annual production of *M. arenaria* was estimated at 4.6 $g\ SFDW \cdot m^{-2} \approx 184$ $kJ \cdot m^{-2}$ (Burke & Mann, 1974). The annual production within the inner Oslofjord area of a sub-tidal population of *M. arenaria* was 6 $g\ AFDW \cdot m^{-2} \approx 120$ $kJ \cdot m^{-2} \cdot y^{-1}$ (Winther & Gray, 1985). Intertidal infauna, however, does not have the possibility of continuous feeding, which is one explanation why secondary production in such systems may be lower. *M. edulis*, *C. edulis* and *M. arenaria* in the present study were all young individuals with a high growth rate potential.

According to the ratio between pelagic primary production and secondary production of 1:1 for *C. edule* and *M. arenaria* in the present study in the Skagerrak, the importance of currents to transport food are accentuated. Related to the growth efficiency value, P:R 1.4:2, the actual growth was lower than the potential growth. Grizzle & Morin (1989) and Wolff (1977) discussed the importance of currents for the food availability for benthic suspension feeders where, for example, tidal currents can cause a vertical component of turbulent diffusion implying that pelagic production becomes available to benthic filter feeders. According to Mann & Lazier (1991), benthic suspension feeders take up energy-rich particles more rapidly and increase their metabolic rate as the current flows faster due to increased turbulent diffusion. From the systems described above, it is obvious that horizontal advective transport of suspended food particles is of significant importance for rapid growth in

suspension-feeding bivalves. Current speed has also been shown to affect the growth rate of benthic suspension feeding barnacles and bivalves (Crisp, 1960; Richardson *et al.*, 1980; Wildish & Peer, 1983).

The *C. edule* and *M. arenaria* populations in the Laholm Bay had a lower secondary than primary production of the same area. The production was low, only 5 $g\ AFDW \cdot m^{-2} \cdot y^{-1} \approx 178$ $kJ \cdot m^{-2} \cdot y^{-1}$ (Loo & Rosenberg, 1989), which is probably a result of physical disturbance by wave activity. In the Laholm Bay the wave activity disturbs the exposed bottoms more or less continuously down to various depths, and at depths shallower than 4 m the macrofauna is poor (Rosenberg & Loo, 1988). Other disturbances have also been reported when, over a period of several years, large amounts of *C. edule* and *M. arenaria* were washed ashore, possibly as a result of localized oxygen deficiency (Rosenberg & Loo, 1988). Another factor reducing the secondary production of these bivalves is probably fish and benthic predation. Juvenile flatfish are abundant in Laholm Bay (Pihl, 1989) and they consume juvenile bivalves (Pihl, 1982, 1985). A significant disturbance in the Laholm Bay is also suggested by the respiration:absorption ratio of 0.97. Thus, a combination of insufficient food availability and environmental disturbance seems to be the reason for a lower secondary production and growth efficiency of these two bivalves in Laholm Bay compared to the semi-exposed habitat in the Skagerrak.

The *Amphiura filiformis* population had the lowest production, a lower secondary to primary production ratio, and a lower growth efficiency than the other two stations in the Skagerrak. These differences are probably due to a lower availability of nutritious food. This site is located below a halocline, which is suggested to act as a boundary for sinking particles (Smetacek, 1984). At this station material may be deposited intermittently, but a near-bottom current has been observed transporting material close to the bottom (pers. obs.). According to Graf (1992), the benthic-pelagic coupling for benthic organisms is more a horizontal than a vertical event. Also resuspended material of lower nutritious value than fresh phytoplankton may be part of the food available to *A. filiformis*.

A large proportion (82%) of the *A. filiformis* biomass was made up of adults, and the annual secondary production was mainly gonad production, somatic growth and arm regeneration (Sköld *et al.*, 1994). Thus, the age structure of this population may be one explanation for low production. On the other hand, large individuals with long arms should be able to catch suspended particles at a higher rate than small ones. It is likely, however, that lack of food has limited the establishment of a larger population as well as of a higher secondary production. In adjacent areas in the northern Kattegat, where food availability probably is significantly greater, *A. filiformis* density and biomass are much higher (Rosenberg, 1995). O'Con-

nor *et al.* (1986) found annual P:B ratios for adult *A. filiformis* from Galway Bay of about 2, *i.e.* higher than the 0.46 of the study by Sköld *et al.* (1994). Glémarec & Menesguen (1980) estimated an annual P:B of 2.8 and a two-year life span, in marked contrast with a 10-year life span, estimated in Galway Bay (O'Connor *et al.*, 1983) and by Sköld *et al.* (1994). Thus, feeding conditions may have been better in Galway Bay than in the habitat we studied in the Skagerrak.

Absorption efficiency of the populations in the present study varies between 60 and 70% and apparently coincides with other findings (Bayne, 1976; Loo, 1992). Respiration results are of great importance in energy budgets. These figures are based on laboratory experiments and are considered crude estimates. Respiration in nature can be higher due to competition, feeding activity (Kjørboe *et al.*, 1985) and environmental stress. In experimental conditions, the animals may be stressed and this may enhance respiration. Thus, respiration assessment in energy budgets may be less accurate than for secondary production.

Over a life cycle, secondary production should be equal to eliminated biomass (Crisp, 1984). In the young *C. edule* and *M. arenaria* populations this is almost so, as they were eliminated (mainly consumed) during their first year (Loo & Rosenberg, 1989; Möller & Rosenberg, 1983). The *M. edulis* culture was harvested after 1.5 years and therefore the P:B ratio and eliminated biomass is low in the calculations covering one year. The *A. filiformis* adult population was stable and elimination was mainly due to gamete release, arm nipping and mortality among juveniles (Sköld *et al.*, 1994).

4.2. LIMITING FACTORS FOR SUSPENSION-FEEDING POPULATIONS

It has been shown in experiments that hydrodynamic factors may be critical in determining the food available to suspension-feeding bivalves (Butman *et al.*, 1994; Wildish & Kristmanson, 1984). Food quality and quantity have been shown to be a limiting factor for suspension-feeding bivalves (Loo & Rosenberg, 1989; Wallace, 1980). Thus, these results coincide with the findings in the present study.

According to Gerritsen *et al.* (1994), hydrodynamics in large estuaries may restrict the potential of benthic suspension feeders to crop phytoplankton because the width and depth of such estuaries limit transport of pelagic waters to the littoral flanks of the estuaries, where benthic suspension feeders may be abundant. They showed that benthic suspension feeders are dominant consumers in shallow areas of the Chesapeake Bay, but are less so in deeper areas.

Muschenheim (1987), in experimental studies with the polychaete *Spio setosa*, showed that in a boundary layer above a sediment surface, the differential settling velocities of particles of different densities

have a natural sorting effect. The maximum flux of organically rich particles occurs at a higher level above the sediment than the maximum flux of inorganic particles. This may explain why a number of organisms, especially polychaetes, build tubes that protrude above the sediment surface and even the fact that some ophiuroids, *e.g.* *A. filiformis*, stretch their arms up in the boundary layer to catch suspended particles. Frechette & Bourget (1985) showed that *M. edulis* at 1.0 m above the bottom had an improved food supply and hence an improved growth rate compared to mussels near the bottom. Thus, these findings coincide with the results from this study, showing that it is advantageous for mussels to be suspended in the water.

5. CONCLUSIONS

These studies show that different suspension-feeding populations have significant differences in their secondary production rates and that this is habitat related. Current-mediated transport of seston to suspension feeders is of significant importance and may result in secondary production which is higher than primary production per unit area.

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6. REFERENCES

- Bayne, B.L., 1976. Marine mussels: their ecology and physiology. Cambridge University Press, Cambridge: 1-506.
- Berger, W.H., V.S. Smetacek & G. Wefer, 1989. Ocean productivity and paleoproductivity - an overview. In: W.H. Berger, V.S. Smetacek & G. Wefer. Productivity of the ocean: present and past. J. Wiley & Sons, Chichester: 1-34.
- Buchanan, J.B., 1964. A comparative study of some features of the biology of *Amphiura filiformis* and *Amphiura chiajei* (Ophiuroidea) considered in relation to their distribution.—J. mar. biol. Ass. U.K. **44**: 615-624.
- Burke, M.V. & K.H. Mann, 1974. Productivity and production: biomass ratios of bivalve and gastropod populations in an Eastern Canadian estuary.—J. Fish. Res. Bd Can. **31**: 167-177.
- Butman, C.A., M. Frécette, W.R. Geyer & V.R. Starczak, 1994. Flume experiments on food supply to the blue mussel *Mytilus edulis* L. as a function of boundary layer flow.—Limnol. Oceanogr. **39**: 1755-1768.
- Chambers, M.R. & H. Milne, 1979. Seasonal variation in the condition of some intertidal invertebrates of the Ythan estuary, Scotland.—Estuar. coast. mar. Sci. **8**: 411-419.
- Christiansen, H. & E. Kannevorf, 1985. Sedimenting phyto-

- plankton as major food source for suspension and deposit feeders in the Øresund.—*Ophelia* **24**: 223-244.
- Conover, R.J., 1966. Assimilation of organic matter by zooplankton.—*Limnol. Oceanogr.* **11**: 338-345.
- Creutzberg, F., P. Wapenaar, G. Duineveld & N. Lopez Lopez, 1984. Distribution and density of the benthic fauna in the southern North Sea in relation to bottom characteristics and hydrographic conditions.—*Rapp. P.-v. Réun. Cons. int. Explor. Mer* **183**: 101-110.
- Crisp, D.J., 1960. Factors influencing growth rate in *Balanus balanoides*.—*J. Anim. Ecol.* **29**: 95-116.
- , 1984. Energy flow measurements. In: N.A. Holme & A.D. McIntyre. *Methods for the study of marine benthos*. Blackwell Scientific Publications, Oxford: 284-372.
- Duineveld, G.C.A., A. Künitzer & R.P. Heyman, 1987. *Amphiura filiformis* (Ophiuroidea: Echinodermata) in the North Sea. Distribution, present and former abundance and size composition.—*Neth. J. Sea Res.* **21**: 317-329.
- Edler, L., 1986. Växplanktonproduktionen i Laholmsbukten. Swedish Environmental Protection Agency, Stockholm, Report 3272: 66-74.
- Fenchel, T. & B.J. Finlay, 1983. Respiration rates in heterotrophic, free-living protozoa.—*Microb. Ecol.* **9**: 99-122.
- Frechette, M. & E. Bourget, 1985. Food-limited growth of *Mytilus edulis* L. in relation to the benthic boundary layer.—*Can. J. Fish. Aquat. Sci.* **42**: 1166-1170.
- Gerritsen, J., A.F. Holland & D.E. Irvine, 1994. Suspension-feeding bivalves and the fate of primary production: An estuarine model applied to Chesapeake Bay.—*Estuaries* **17**: 403-416.
- Glémarec, M. & A. Mesguen, 1980. Functioning of a muddy sand ecosystem: seasonal fluctuations of different trophic levels and difficulties in estimating production of the dominant macrofauna species.—*Bell. Bar. Libr. Mar. Sci.* **11**: 46-68.
- Graf, G., 1992. Benthic-pelagic coupling: A benthic view.—*Oceanogr. Mar. Biol. Ann. Rev.* **30**: 149-190.
- Graf, G., R. Schultz, R. Peinert & L.A. Meyer-Reil, 1983. Benthic response to sedimentation events during to spring at a shallow-water station in the western Kiel Bight.—*Mar. Biol.* **77**: 235-246.
- Grebmeier, J.M., C.P. McRoy & H.M. Feder, 1988. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food supply source and benthic biomass.—*Mar. Ecol. Prog. Ser.* **48**: 57-67.
- Grizzle, R.E. & P.J. Morin, 1989. Effect of tidal currents, seston, and bottom sediments on growth of *Mercenaria mercenaria*: results of a field experiment.—*Mar. Biol.* **102**: 85-93.
- Hargrave, B.T., 1973. Coupling carbon flow through some pelagic and benthic communities.—*J. Fish. Res. Bd Can.* **30**: 1317-1326.
- Hughes, R.N., 1970. An energy budget for a tidal-flat population of the bivalve *Scrobicularia plana* (da Costa).—*J. Anim. Ecol.* **39**: 357-381.
- Jenness, M.I. & G.C.A. Duineveld, 1985. Effects of tidal currents on chlorophyll *a* content of sandy sediments in the southern North Sea.—*Mar. Ecol. Prog. Ser.* **21**: 283-287.
- Kjørboe, T., F. Møhlenberg & K. Hamburger, 1985. Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action.—*Mar. Ecol. Prog. Ser.* **26**: 85-97.
- Larsson, A.M., 1984. Hydrographical and chemical observations in a coastal area with mussel farming, western Sweden.—*Dept. Oceanogr., Univ. Gothenburg, Rep.* **46**: 1-29.
- Lindahl, O. & L. Hernroth, 1983. Phyto-zooplankton community in coastal waters of western Sweden - an ecosystem off balance.—*Mar. Ecol. Prog. Ser.* **10**: 119-126.
- Lindahl, O., B. Andersson & L. Davidsson, 1991. Pelagial monitoring i Gullmarsområdet 1990.—*Swedish Environmental Protection Agency, Stockholm, Rep.* **3948**: 1-15.
- Loo, L.O., 1992. Filtration, assimilation, respiration and growth of *Mytilus edulis* L. at low temperatures.—*Ophelia* **35**: 123-131.
- Loo, L.O. & R. Rosenberg, 1983. *Mytilus edulis* culture: growth and production in western Sweden.—*Aquaculture* **35**: 137-150.
- , 1989. Bivalve suspension-feeding dynamics and benthic-pelagic coupling in an eutrophicated marine bay.—*J. exp. mar. Biol. Ecol.* **130**: 253-276.
- Lännergren, C., 1983. Musslornas föda - planktonalger. In: R. Rosenberg. *Odling av blåmusslor*. Signum, Lund: 36-48.
- Mann, K.H. & J.R.N. Lazier, 1991. Dynamics of marine ecosystems. Biological-physical interactions in the oceans. Blackwell Scientific Publications, Inc., Cambridge: 1-466.
- Muschenheim, D.K., 1987. The role of hydrodynamic sorting of seston in the nutrition of a benthic suspension feeder, *Spio setosa* (Polychaeta: Spionidae).—*Biol. Oceanogr.* **4**: 265-288.
- Möller, P. & R. Rosenberg, 1983. Recruitment, abundance and production of *Mya arenaria* and *Cardium edule* in marine shallow waters, western Sweden.—*Ophelia* **22**: 33-55.
- Möller, P., L. Pihl & R. Rosenberg, 1985. Benthic faunal energy flow and biological interaction in some shallow marine soft bottom habitats.—*Mar. Ecol. Prog. Ser.* **27**: 109-121.
- Newell, R.I.E. & B.L. Bayne, 1980. Seasonal changes in the physiology, reproductive condition and carbohydrate content of the cockle *Cardium (=Cerastoderma) edule* (Bivalvia: Cardiidae).—*Mar. Biol.* **56**: 11-19.
- Nichols, F., 1977. Infaunal biomass and production on a mudflat, San Francisco Bay, California. In: B.C. Coull. *Ecology of marine benthos*. Univ. S. Carolina Press, Columbia: 339-357.
- O'Connor, B., T. Bowmer & A. Grehan, 1983. Long-term assessment of the population dynamics of *Amphiura filiformis* (Echinodermata: Ophiuroidea) in Galway Bay (west coast of Ireland).—*Mar. Biol.* **75**: 279-28.
- O'Connor, B., D. McGrath & B.F. Keegan, 1986. Demographic equilibrium: The case of an *Amphiura filiformis* assemblage on the west coast of Ireland.—*Hydrobiologia* **142**: 151-158.
- Pihl, L., 1982. Food intake of young cod and flounder in a shallow bay on the Swedish west coast.—*Neth. J. Sea Res.* **15**: 419-432.
- , 1985. Food selection and consumption of mobile epifauna in shallow marine areas.—*Mar. Ecol. Prog. Ser.* **22**: 169-179.
- , 1989. Abundance, biomass and production of juvenile flatfish in southeastern Kattegat.—*Neth. J. Sea Res.* **24**: 69-81.

- Richardson, C.A., D.J. Crisp & N.W. Runham, 1980. Factors influencing shell growth in *Cerastoderma edule*.—Proc. R. Soc. Lond. B. **210**: 513-531.
- Richardson, K. & A. Christoffersen, 1991. Seasonal distribution and production of phytoplankton in the southern Kattegat.—Mar. Ecol. Prog. Ser. **78**: 217-227.
- Riisgård, H.U. & A. Rindløv, 1981. Energy budgets, growth and filtration rates in *Mytilus edulis* at different algal concentrations.—Mar. Biol. **61**: 227-234.
- Rosenberg, R., 1995. Benthic marine fauna structured by hydrodynamic processes and food availability.—Neth. J. Sea Res. **34**: 303-317.
- Rosenberg, R. & L.O. Loo, 1983. Energy-flow in a *Mytilus edulis* culture in western Sweden.—Aquaculture **35**: 151-161.
- , 1988. Marine eutrophication induced oxygen deficiency: effects on soft bottom fauna, western Sweden.—Ophelia **29**: 213-225.
- Sköld, M., L.O. Loo & R. Rosenberg, 1994. Production, dynamics and demography of an *Amphiura filiformis* population.—Mar. Ecol. Prog. Ser. **103**: 81-90.
- Smetacek, V., 1980. Annual cycle of sedimentation in relation to plankton ecology in western Kiel Bight.—Ophelia, Suppl. **1**: 65-76.
- , 1984. The supply of food to the benthos. In: M.J. Fasham. Flows of energy and nutrients in marine ecosystems: theory and practice. Plenum Press, New York: 517-547.
- Ursin, E., 1960. A quantitative investigation of the echinoderm fauna of the central North Sea.—Meddr. Danm. Fisk.- Havunders. **2**: 1-204.
- Wallace, J.C., 1980. Growth rates of different populations of the edible mussel, *Mytilus edulis*, in north Norway.—Aquaculture **19**: 303-311.
- Warwick, R.M. & R. Price, 1975. Macrofauna production in an estuarine mud-flat.—J. mar. biol. Ass. U.K. **55**: 1-18.
- Wassmann, P., 1990. Relationship between primary and export production in the boreal coastal zone of the North Atlantic.—Limnol. Oceanogr. **35**: 464-471.
- Wildish, D.J. & D. Kristmanson, 1984. Importance to mussels of the benthic boundary layer.—Can. J. Fish. Aquat. Sci. **41**: 1618-1625.
- , 1985. Control of suspension feeding bivalve production by current speed.—Helgoländer Meeresunters. **39**: 237-243.
- Wildish, D.J. & D.L. Peer, 1983. Tidal current speed and production of benthic macrofauna in the lower Bay of Fundy.—Can. J. Fish. Aquat. Sci. **40**: 309-321.
- Winberg, G.G., 1971. Methods for the estimation of production of aquatic animals. Academic Press, London: 1-175.
- Winther, U. & J.S. Gray, 1985. The biology of *Mya arenaria* (Bivalvia) in the eutrophic inner Oslofjord.—Sarsia **70**: 1-9.
- Wolff, W.J., 1977. A benthic food budget for the Grevelingen Estuary, the Netherlands, and a consideration of the mechanisms causing high benthic secondary production in estuaries. In: B.C. Coull. Ecology of marine benthos. Belle W. Baruch Library in Marine Science **6**. University of South Carolina Press: 267-280.