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Bivalve suspension-feeding dynamics and benthic–pelagic coupling in an eutrophicated marine bay

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Abstract: The open exposed Laholm Bay in the Kattegat is eutrophicated through riverine input, mainly of N. The benthic macrofauna down to 10 m depth (60 km²) is dominated by the suspension-feeding bivalves *Cardium edule* and *Mya arenaria*. To estimate the seasonal and annual consumption of seston by the suspension-feeders in Laholm Bay, we carried out three sets of observations. (1) The abundance and biomass of the macrofauna in this depth interval were assessed along eight transects. (2) The secondary production of the two bivalves was estimated over a 10-month period in two sampling squares. (3) The filtration rate of *C. edule* was determined in natural seawater in laboratory experiments during different seasons. The bivalves can in theory filter all of the water volume down to 10 m in 3 days and, thus, make a significant impact on the phytoplankton concentration. In our study, however, they filtered only approximately half of their potential feeding capacity, perhaps because food availability was low due to low turnover close to the bottom or due to physical disturbance. The majority of the phytoplankton is exported from the bay. Bivalve abundance, biomass, production and growth rate were moderate and generally lower than in adjacent areas to the north. In autumn, the bivalves consumed >90% of the seston in comparison with net-zooplankton consumption. An energy-flow diagram for the bivalves is presented including estimates of bivalve N excretion and biodeposition.

Key words: Benthos; Energy flow; Filtration; Secondary production

INTRODUCTION

Marine eutrophication is the process when increasing amounts of nutrients are introduced into the sea causing enhanced primary production. In several sea areas with reduced water exchange and stratification, this has recently created severe biological effects, e.g., in the Baltic (Andersin et al., 1978; Weigelt & Rumohr, 1986), in the Kattegat on the Swedish west coast (Rosenberg, 1985; Rosenberg & Loo, 1988) and in the German Bight in the North Sea (Rachor, 1985). In well-flushed areas, the initial result can be enhanced secondary production as in the intertidal flats in The Netherlands (Beukema & Cadée, 1986). Marine eutrophication is a rapidly growing environmental problem in many coastal areas around the world and will probably increase in the near future due to increased input of nutrients by rivers from a growing human population close to the coast and from atmospheric deposition (Larsson et al., 1985; Rosenberg,

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1985; Nixon et al. 1986; Fleischer et al., 1987). We have recently observed a growing interest in a broader understanding of the ecosystem response to increased nutrient levels in the sea (e.g., Nixon et al., 1986).

Laholm Bay, one of the most important nursery grounds for fish in the Kattegat (Pihl, 1986), has an area of $\approx 300 \text{ km}^2$ and 20% of this is 0–10 m deep (Fig. 1A). It is exposed and has sandy sediments with an organic content of $< 1\%$ between 0 and 10 m. The tidal range is $\approx 10 \text{ cm}$. A strong horizontal halocline is found at $\approx 15 \text{ m}$. The salinity above the halocline varies between 12 and 25‰ and below the halocline between 32 and 34‰. Below the halocline, eutrophication-induced hypoxia has developed close to the muddy bottoms every late summer to autumn in 1980–87 (Rydberg, 1986; Rosenberg & Loo, 1989). Laholm Bay directly receives annually $\approx 5000 \text{ t}$ total N from five main rivers (Rydberg, 1986). N is the limiting nutrient in general (Granéli et al., 1986) and the mean annual primary production in 1981–85 was $136 \text{ g C} \cdot \text{m}^{-2}$ (Edler, 1986). The annual production of the benthic microflora at 5–20 m was estimated at $10\text{--}15 \text{ g C} \cdot \text{m}^{-2}$ (Granéli & Sundbäck, 1986). In the southern part of the bay, the formerly dominant macroalgae of the genus *Fucus* have disappeared and have been replaced by *Cladophora* spp. and *Enteromorpha* spp. (Wennberg, 1987).

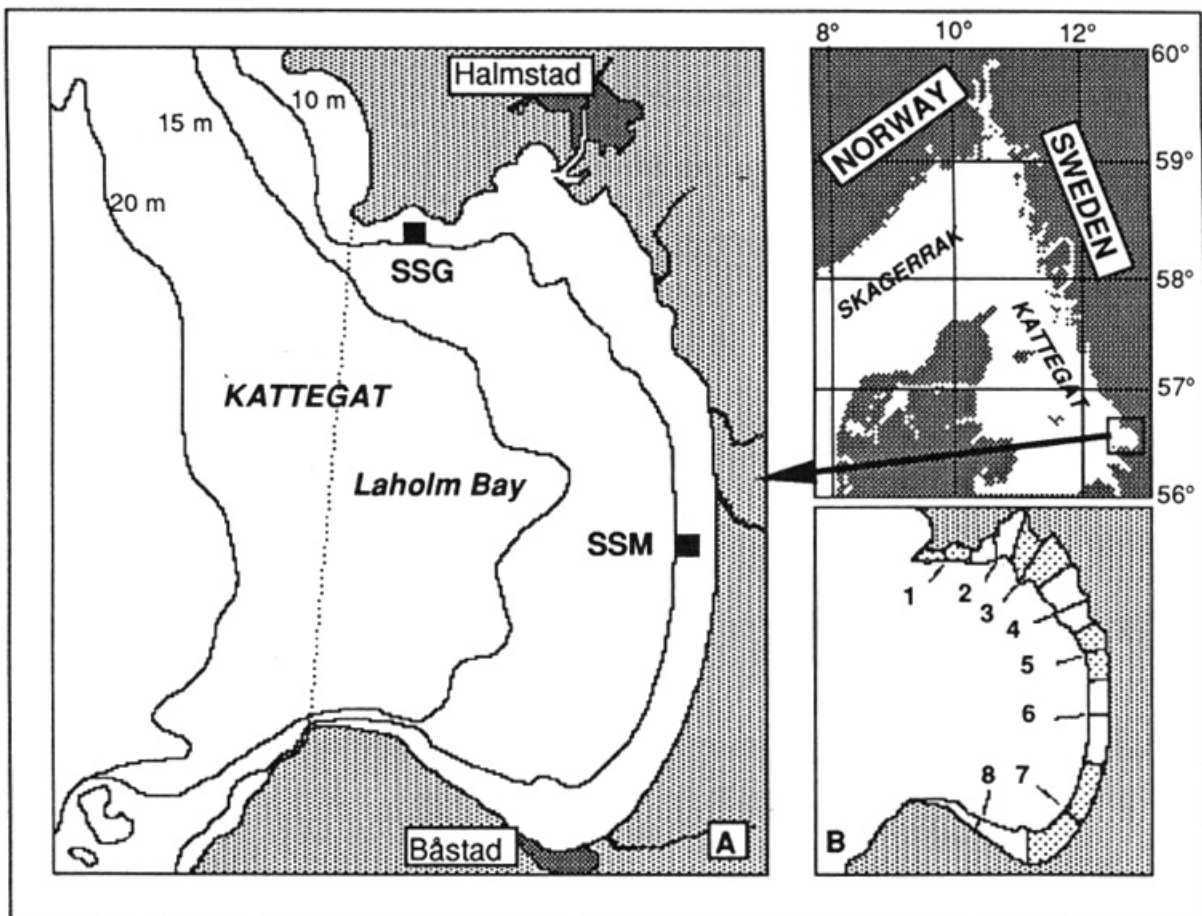


Fig. 1. (A) Map of Kattegat with Laholm Bay (east of dashed line) and benthic sampling squares SSG and SSM. (B) Benthic Sampling Transects 1–8, each with surrounding transect areas.

The macrozoobenthos in the shallow parts has earlier been studied by Möller (1986) and Rosenberg & Loo (1988). The latter authors and Rosenberg & Edler (1981) have reported mortality of, in particular, the dominant bivalves *Cardium* (= *Cerastoderma*) *edule* and *Mya arenaria* in the shallow (0–10 m) parts in 1980, 1981 and 1984–87. In some years, this was noted in patches, in others it had a wide distribution. The cause may be periodic hypoxia.

The present investigation deals with the coupling between plankton algae and benthic suspension-feeders in Laholm Bay. One objective was to estimate how much of the phytoplankton biomass the benthic suspension-feeders could consume down to 10 m water depth and if this could hold down the initial eutrophication effects in the bay such as reduced transparency. Such effects of suspension-feeding bivalves have been suggested for San Francisco Bay (Cloern, 1982; Nichols, 1985) and for estuaries in North Carolina, U.S.A. (Officer et al., 1982). This study is part of a larger multi-disciplinary research programme in the area (Rosenberg, 1985).

This investigation comprises three parts. (1) The production and elimination of the benthic animals were assessed during June 1985–April 1986 in two sampling squares at 5–8 m where maximal biomass had previously been reported (Möller, 1986). In this way, summer settling and subsequent growth of the dominant suspension-feeding bivalves were followed and their food demand estimated. (2) The benthic macrofaunal standing stock in Laholm Bay was assessed in April 1985 by taking samples along eight transects down to 10 m (Fig. 1B). (3) The filtration rate by the dominant suspension-feeder, the bivalve *C. edule*, was studied in experiments with natural surface seawater during different seasons. These results and published data made it possible to make a crude estimate of the consumption by the dominant suspension-feeders in the shallow parts of Laholm Bay in relation to phytoplankton biomass.

METHODS

SAMPLING

To estimate growth and production of the dominant suspension-feeders, two sampling squares were selected, Sampling Square G (SSG) in the northern part of Laholm Bay and Sampling Square M (SSM) in the centre of the bay (Fig. 1A). SSG and SSM are both sandy and exposed to winds from south and west. Each square was 400 × 400 m, with a depth of 5–8 m. The “Latin square design” (Sokal & Rohlf, 1969) was followed whereby 16 random samples were taken, one from each row and in each column of a sample grid. The material was obtained by either of two bottom grabs a 0.05-m² Ponar or a 0.1-m² Van Veen. The samples were immediately sieved through a 0.5-mm screen and the residue preserved in 70% ethanol. During the settling period June–July 1985, a subsample of 28 cm² was taken from the main sample and immediately preserved in 70% ethanol. This was later sieved through a 160- μ m screen to obtain the bivalve spats. The material was sorted and bivalve shell length determined

at 12 × magnification. Samples were taken on five occasions in 1985–86 (see Table III for dates). Bivalves recruiting to the bottom in the summer of 1985 are referred to as 0-group (0-gr) and 1-yr-old bivalves as 1-group (1-gr). Open bivalves with both shells attached and containing some flesh were defined as recently dead, closed bivalves with flesh were defined as living.

All animals except bivalves were weighed after blotting on filter paper. Dry weight (DW) and wet weight of bivalves were determined as in Table I. The relationship between length and DW obtained on unpreserved animals for *Mytilus edulis* and *Macoma baltica* is given in Table I. These were dried to constant weight at 60 °C (Crisp, 1971). The correlation between length x (mm) and DW y (mg) was obtained from $\ln y = b \ln x + \ln a$ (Table I). The relationship between length and ash-free dry weight (AFDW) for *M. arenaria* and *C. edule* is given in Table II. The biomass was calculated from a regression between length and AFDW obtained on unpreserved animals with shells. These were dried to constant weight at 60 °C and combusted for 5 h at 550 °C (Crisp, 1971). The correlation between length x (mm) and AFDW y (mg) was obtained from $\ln y = b \ln x + \ln a$ (Table II).

On 24 April 1985, samples were taken along eight transects at 3,4,5,6,8 and 10 m in Laholm Bay (Fig. 1B, Table IV); two samples were taken at each station with a 0.1-m² Van Veen grab. To determine bivalve length frequency at each of the sampling depths, all transect samples from the same depth were pooled and converted to 1 m².

The number of specimens · transect area⁻¹ was calculated by integrating the numbers from 0 to 10 m along each transect. The relationship between *C. edule* length L (mm) and shell-free dry weight (SFDW) W (mg) was obtained from our own measurements in April 1985 on unpreserved animals: $W = 0.130 \cdot L^{2.798}$ with a range of 11.0–29.0 mm, $n = 24$ and $r = 0.95$. These were dried to constant weight at 60 °C (Crisp, 1971). The filtration rate F (l · h⁻¹) was a function of SFDW W (g): $F = 11.60 \cdot W^{0.70}$, according to Møhlenberg & Riisgård (1979).

CALCULATIONS

Production P was estimated according to Crisp (1971):

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

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 , N is the mean population density and Δw the individual mean weight increment between successive samplings.

Other equations used were: $A = P + R$, $I = (A/AE) \cdot 100$ and $F = I - A$ where A is absorption, R is respiration, I is ingestion, AE is absorption efficiency and F is faeces production.

Respiration of *C. edule* and *M. arenaria* was calculated according to Newell & Bayne (1980) (Table III), using the energy conversion: 1 ml O₂ = 19.88 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 *Scorbicularia plana* (Hughes, 1970); flesh DW = 1.6 flesh AFDW; 2 (shell AFDW) = total AFDW (own measurements).

FILTRATION AND EXCRETION EXPERIMENTS

In laboratory experiments, filtration rate and absorption efficiency were studied at different seasons with varying food concentrations and temperatures. Filtration was studied in June and October 1985 and April and May 1986 and absorption in June 1985. To estimate filtration rates of *C. edule*, samples of inhaled and exhaled water were siphoned through glass tubes placed above the inhalant and exhalant apertures of the bivalves according to Møhlenberg & Riisgård (1979). Instead of exposing the mussels to algal cultures, however, a flow of natural surface seawater was maintained. The particle counter was an Elzone 80 XY with 128 channels. Two orifice tubes were used of 190 and 48 µm. The minimum measured particle size was 1.5 µm and the maximum 71.7 µm. The total volume of particles in the water from inhalant and exhalant apertures was calculated and the difference between these was the clearance rate; the estimated plateau represents the filtration rate (Møhlenberg & Riisgård, 1979). The retention efficiency of *C. edule* was close to 100% at a particle size down to 2 µm (Møhlenberg & Riisgård, 1978).

To estimate absorption efficiency, faeces and seston in the seawater were collected on Whatman GF/C glass microfibre filters with a pore size of 1–2 µm. Three bivalves produced faeces together in the same aquarium and three samples were taken for the organic content analyses. Calculation was done according to the Conovers (1966) ratio, i.e., reduction of the organic content in the bivalve faeces in relation to the organic content in the seston. To determine seston concentration, 2 l seawater were used. Before filtration, the filters were washed with distilled water, heated to 500 °C and then weighed. Those containing the filtrate were washed with distilled water, dried at 70 °C and then weighed. They were then heated to 500 °C and weighed again to give the DW and AFDW of the filtrate.

The excretion of ammonium, urea and dissolved organic N were analysed on 19 June 1985 (F. Sörensson, pers. comm.). At this date, we also analysed absorption efficiency. Three bivalves with different weight were used in the experiment, and the correlation between SFDW x (g) and ammonium excretion y (µmol · h⁻¹) was obtained from $\ln y = 0.618 \ln x + 1.28$, $r^2 = 0.998$. The correlation between SFDW x (g) and urea

excretion y ($\mu\text{mol} \cdot \text{h}^{-1}$) was obtained from $\ln y = 0.589 \ln x - 0.814$, $r^2 = 0.841$. For estimates of C:N ratios, see Table XI.

RESULTS

ABUNDANCE, BIOMASS, PRODUCTION AND GROWTH IN SAMPLING SQUARES

The abundance, biomass and production of suspension-feeders in the inner part of Laholm Bay were assessed at SSG and at SSM (Fig. 1A) during June 1985–April 1986. The organic content of the sediment was $0.64 \pm 0.07\%$ ($\bar{x} \pm \text{SE}$) at SSG and $0.38 \pm 0.04\%$ at SSM.

Number of species, abundance and biomass

The number of species was highest at both sites during autumn 1985 when a total of 31 species was found at SSG and 26 at SSM. In general, more species were found at deeper sites.

The highest mean abundance was found in June, with $\approx 60\,000 \text{ ind} \cdot \text{m}^{-2}$ at SSM and $\approx 10\,000 \text{ ind} \cdot \text{m}^{-2}$ at SSG. *Spisula subtruncata* had the highest recruitment at this time. Bivalves dominated in abundance at both SSG and SSM during the settling period June–July 1985 and in biomass during the autumn (Table V). Species with high abundance were, for example, *Hydrobia* sp. and *Pygospio elegans*. The adult population of *C. edule* had the highest biomass (83% of total) at SSM in October 1985.

The seasonal variation in bivalve abundance is illustrated in Fig. 2. The highest number of 0-gr *C. edule* was found in July, with $2500 \text{ ind} \cdot \text{m}^{-2}$ at SSM and

TABLE I

Relationship between length x (mm) and DW y (mg) with shell for *A. islandica*, *C. edule*, *M. baltica*, *M. bidentata*, *M. edulis* and *S. subtruncata* according to $\ln y = b \ln x + \ln a$, with correlation coefficient (r) and numbers measured (n). DW with shell of *M. arenaria* was based on AFDW data from Table II in October 1985, then multiplied by a factor of 4. To transform DW with shell to wet weight with shell, all bivalves were multiplied by 2.6.

Species	Length (mm)	a	b	r	n	Reference
<i>Arctica islandica</i>	5.0–12.0	$44.8 \cdot 10^{-3}$	3.66	0.95	34	Rumohr et al. (1987) (<i>Cardium glaucum</i>)
<i>Cardium edule</i>	5.0–12.0	$44.8 \cdot 10^{-3}$	3.66	0.95	34	Rumohr et al. (1987) (<i>Cardium glaucum</i>)
<i>Macoma baltica</i>	2.9–17.0	$37.4 \cdot 10^{-3}$	3.38	0.99	54	Olafsson (pers. comm.) (<i>Macoma baltica</i>)
<i>Mysella bidentata</i>	2.9–17.0	$37.4 \cdot 10^{-3}$	3.38	0.99	54	Olafsson (pers. comm.) (<i>Macoma baltica</i>)
<i>Mytilus edulis</i>	19.0–43.0	$135.4 \cdot 10^{-3}$	2.62	0.97	25	Own measurements
<i>Spisula subtruncata</i>	2.9–17.0	$37.4 \cdot 10^{-3}$	3.38	0.99	54	Olafsson (pers. comm.) (<i>Macoma baltica</i>)

8000 ind · m⁻² at SSG. The adult population at SSM was stable during the whole period, with an abundance of ≈ 45 ind · m⁻² and a length of ≈ 20 mm (Fig. 3). At SSG, a rapid decrease in the adult population of *C. edule* was observed in May 1985 by

TABLE II

Relationship between length x (mm) and AFDW y (mg) with shells for *M. arenaria* and *C. edule* according to $\ln y = b \ln x + \ln a$, with correlation coefficient (r) and numbers measured (n).

Species*	Length (mm)	a	b	r	n	Reference
<i>M. arenaria</i>						
0-gr	1-3	$42.29 \cdot 10^{-3}$	2.13	0.95	19	Möller & Rosenberg (1983)
1-gr Jun-Oct 1985	4-10	$22.29 \cdot 10^{-3}$	2.68	0.99	30	Möller & Rosenberg (1983)
1-gr Oct 1985-April 1986	4-25	$28.63 \cdot 10^{-3}$	2.75	0.99	42	Möller & Rosenberg (1983)
<i>C. edule</i>						
0-gr	4-9	$20.50 \cdot 10^{-3}$	2.66	0.95	30	Own measurements
Adults	4-21	$5.35 \cdot 10^{-3}$	3.40	0.99	38	Möller & Rosenberg (1983)

* 0-gr, bivalves recruiting to bottom; 1-gr, 1-yr-old bivalves.

TABLE III

Relationship between SFDW (g) and respiration rate (ml O₂ · h⁻¹) for *C. edule*, calculated from $V = a W^b$ (Newell & Bayne, 1980) where V is respiration rate and W is weight.

Period of sampling	a	b
25 Jun 1985-23 Jul 1985	0.583	0.426
23 Jul 1985-12 Sep 1985	0.672	0.661
12 Sep 1985-14 Oct 1985	0.404	0.300
14 Oct 1985-03 Apr 1986	0.665	0.375

TABLE IV

Sampling scheme for transects.

Depth (m)	Transect							
	1	2	3	4	5	6	7	8
3		+	+		+		+	
4	+		+	+	+	+	+	+
5		+	+		+	+	+	+
6	+	+		+	+	+	+	+
8	+	+			+	+	+	+
10		+	+	+		+	+	+

scuba diving (pers. obs.). Many dead bivalves were found with open valves and decaying flesh. Dead bivalves were also noted during trawling in Laholm Bay at the same period (L. Pihl, pers. comm.).

M. arenaria had a low recruitment at SSG in 1985. At SSM, it was higher, reaching $\approx 2000 \text{ ind} \cdot \text{m}^{-2}$ in July but decreasing later. The 1-gr *M. arenaria* had a density of 120 and 150 $\text{ind} \cdot \text{m}^{-2}$ during July 1985 at both sampling squares. Later, their density decreased and was as low as 2 $\text{ind} \cdot \text{m}^{-2}$ at SSM and 10 $\text{ind} \cdot \text{m}^{-2}$ at SSG in April 1986 (Fig. 2).

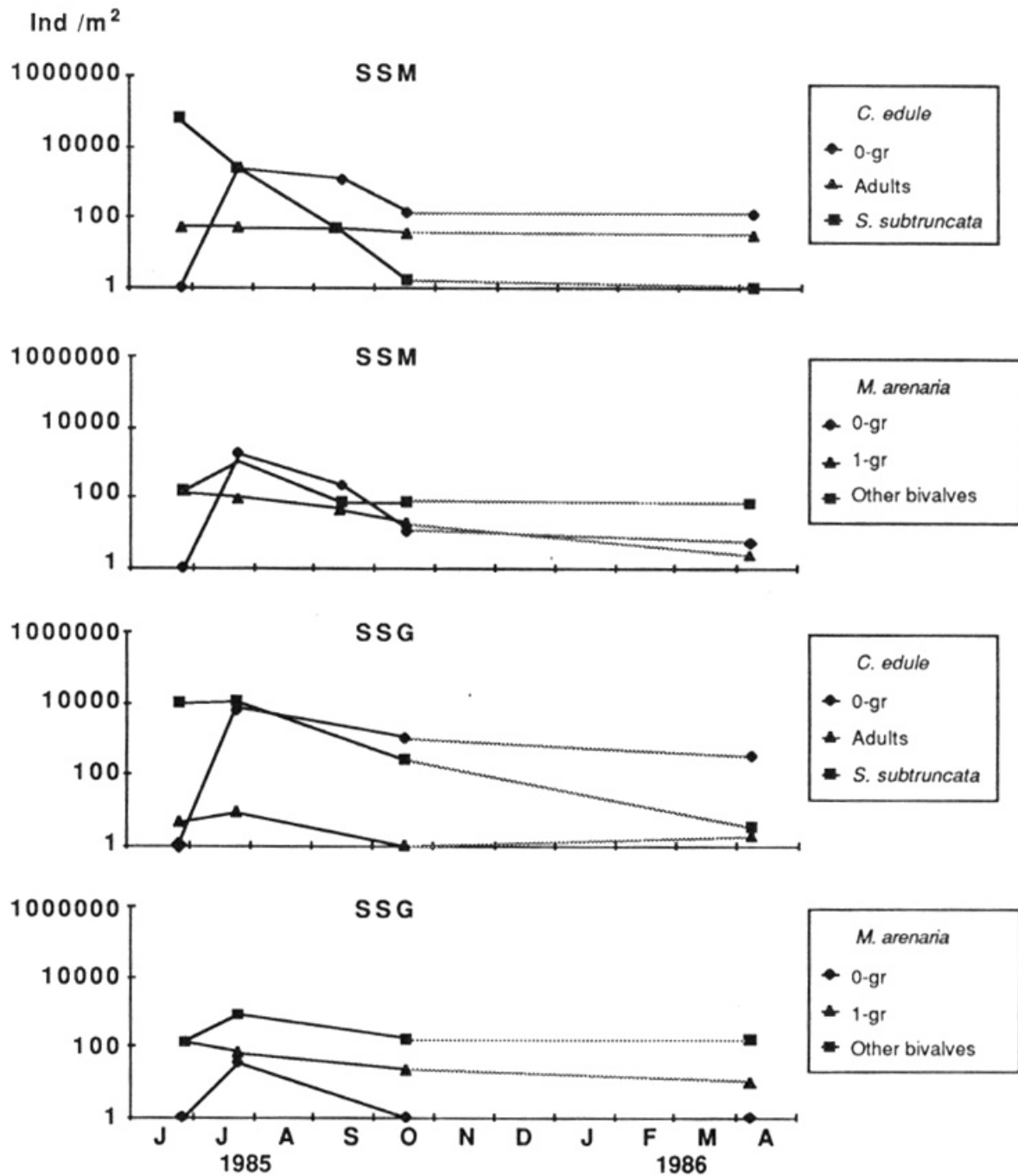


Fig. 2. Abundance of bivalves at SSG and SSM. "Other bivalves" include *M. baltica*, *M. edulis*, *M. bidentata* and *A. islandica*.

Production

M. arenaria and *C. edule* were the most abundant and had the highest biomass of the suspension-feeding animals in this study. Production of 0- and 1-gr *M. arenaria* at SSM

TABLE V

Biomass and abundance of dominant species and of total communities at SSM and SSG on 14 October 1985.

Species*	Biomass (wet wt)		Species	Abundance	
	$\text{g} \cdot \text{m}^{-2}$	%		$\text{ind} \cdot \text{m}^{-2}$	%
SSM					
<i>Cardium edule</i> , adults	277	83.2	<i>Pygospio elegans</i>	565	39.8
<i>Mya arenaria</i> , adults	30	9.0	<i>Scoloplos armiger</i>	239	16.9
<i>Macoma baltica</i> , 0-gr	16	4.8	<i>Hydrobia</i> sp.	156	11.0
<i>Mya arenaria</i> , 1-gr	4	1.3	<i>Cardium edule</i> , 0-gr	135	9.5
<i>Cardium edule</i> , 0-gr	1	0.7	<i>Eteone longa</i>	66	4.6
<i>Nephtys</i> sp.	1	0.3	<i>Macoma baltica</i> , 0-gr	45	3.2
Other species	2	0.7	Other species	213	15.0
Total	331	100.0	Total	1419	100.0
SSG					
<i>Mya arenaria</i> , adults	38	38.5	<i>Hydrobia</i> sp.	2716	50.1
<i>Macoma baltica</i> , 0-gr	29	29.4	<i>Cardium edule</i> , 0-gr	1069	19.7
<i>Hydrobia</i> sp.	9	8.6	<i>Pygospio elegans</i>	542	10.0
<i>Cardium edule</i> , 0-gr	6	5.9	<i>Spisula subtruncata</i>	256	4.7
<i>Mya arenaria</i> , 1-gr	6	5.9	<i>Diastylis rathkei</i>	172	3.2
<i>Nephtys</i> sp.	3	2.7	<i>Sphaerodoridium balticum</i>	155	2.8
Other species	9	9.1	Other species	515	9.5
Total	100	100.0	Total	5425	100.0

* 0-gr, bivalves recruiting to bottom; 1-gr, 1-yr-old bivalves.

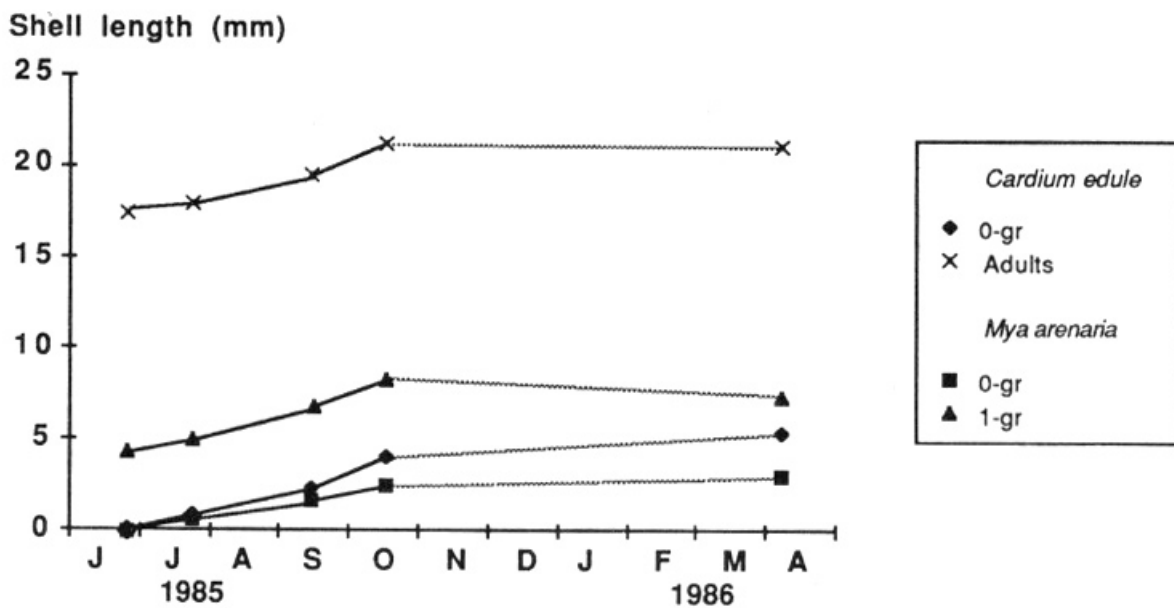


Fig. 3. Mean shell length growth of *C. edule* and *M. arenaria* at SSM.

TABLE VI

Estimates of production and elimination at SSM and SSG. *A*, abundance ($\text{ind} \cdot \text{m}^{-2}$); *B*, biomass ($\text{AFDW}, \text{mg} \cdot \text{m}^{-2}$) with shells; *P*, production ($\text{AFDW}, \text{mg} \cdot \text{m}^{-2}$); and *E*, eliminated biomass ($\text{AFDW}, \text{mg} \cdot \text{m}^{-2}$).

Date	<i>M. arenaria</i>										<i>C. edule</i>						
	0-gr			1-gr			0-gr				Adults						
	<i>A</i>	<i>B</i>	<i>P</i>	<i>E</i>	<i>A</i>	<i>B</i> *	<i>P</i>	<i>E</i>	<i>A</i>	<i>B</i>	<i>P</i>	<i>E</i>	<i>A</i>	<i>B</i>	<i>P</i>	<i>E</i>	
SSM																	
25 Jun 1985	0	0			150	126		13	0	0			52	4058			
23 Jul 1985	1940	29			100	177	66	66	2445	50			49	4517	227		288
12 Sep 1985	238	29	114	115	42	159	152	62	1228	308	318	124	51	7195	1700		-171
14 Oct 1985	12	4	20	18	18	169	172	143	135	135	440	559	38	6031	1861		2086
03 Apr 1986	5	3	1	<1	2	14	-26	-21	132	292	149	4	30	4510	-156		1311
	Sum	135	133			Sum	364	197		Sum	907	687		Sum	3632		3514
SSG																	
25 Jun 1985	0	0			126	328		160	0	0			4	940			
23 Jul 1985	35	3			63	216	-15	160	7910	101			9	980	-524		-571
14 Oct 1985	1	<1	1	3	21	226	338	267	1069	398	1644	1335					
03 Apr 1986	1	<1	<1		10	106	-28	108	338	206	214	388	2	485			
	Sum	1	1	3		Sum	295	535		Sum	1858	1723					

* ≥ 2 -gr *M. arenaria* are not included due to poor accuracy of estimates.

during June 1985–April 1986 was 0.14 and 0.36 g AFDW · m⁻², respectively (Table VI). The production of 0-gr *C. edule* during that time was 0.91 g AFDW · m⁻² at SSM and 1.86 g AFDW · m⁻² at SSG. The highest production of the adult *C. edule* was 3.63 g AFDW · m⁻² recorded at SSM.

Growth

C. edule settled in July 1985 had a length of 5 mm in April 1986 at SSM (Fig. 3). At SSG, the average size of *C. edule* was smaller at that time. At SSM, the growth of 0-gr *M. arenaria* during July 1985–April 1986 was ≈ 3 mm (Fig. 3); the 1-gr grew from 4 mm in June 1985 to 8 mm in October 1985 when the highest mean length was recorded.

In 1986, the spring phytoplankton bloom started in February and the beginning of March when the water temperature was between -0.5 to 3 °C. To assess if 0-gr *C. edule* could utilize this food resource, the growth rate was estimated near SSM at 3 m. Sampling started on 25 February when ice still covered the bay; the next sample was taken on 3 April and the last on 3 June. Daily specific growth rate during 25 February–3 April was 0.32% and during 3 April–3 June 0.25%.

BIVALVE ABUNDANCE, BIOMASS AND LENGTH FREQUENCY AT TRANSECTS

C. edule dominated in the biomass at the eight transects. Other species with high biomass were *M. arenaria*, *Macoma baltica*, *Hydrobia* sp. and *Nephtys* sp. The most abundant species were *C. edule*, *M. arenaria*, *Hydrobia* sp. and *P. elegans*. Overall, the species composition at the transects reflected that at the sampling squares.

In April 1985, adult *C. edule* were generally shorter at the deeper part of the transects (Fig. 5). The 0-gr showed no difference in length between 3 and 5 m. Only the 1984 year

TABLE VII

Total abundance, biomass and filtration rate of *C. edule* integrated from 0 to 10 m depth in northern part (22.5 km²) and southern part (25.4 km²) of Laholm Bay, respectively, in April 1985. Filtration rate *F* for each individual is calculated from $F = 11.60 \cdot W^{0.70}$ (Möhlenberg & Riisgård, 1979) where *F* is expressed in l · h⁻¹ and *W* = SFDW in g. Potential weight, based on length–weight equation, and filtration rate is also calculated for recently dead bivalves.

Transects, location	0-gr		Adults	
	Live	Dead	Live	Dead
1, 3 and 4, northern part of bay				
Total abundance (× 10 ⁶)	291.6	2713.6	127.2	138.4
Total biomass (g, × 10 ⁶)	0.3	3.3	14.0	9.0
Total filtration rate (l · h ⁻¹ , × 10 ⁶)	27.9	265.0	313.7	226.9
5–7, southern part of bay				
Total abundance (× 10 ⁶)	446.9	667.8	1639.9	238.1
Total biomass (g, × 10 ⁶)	0.4	0.7	112.8	12.6
Total filtration rate (l · h ⁻¹ , × 10 ⁶)	36.8	59.6	2861.5	339.0

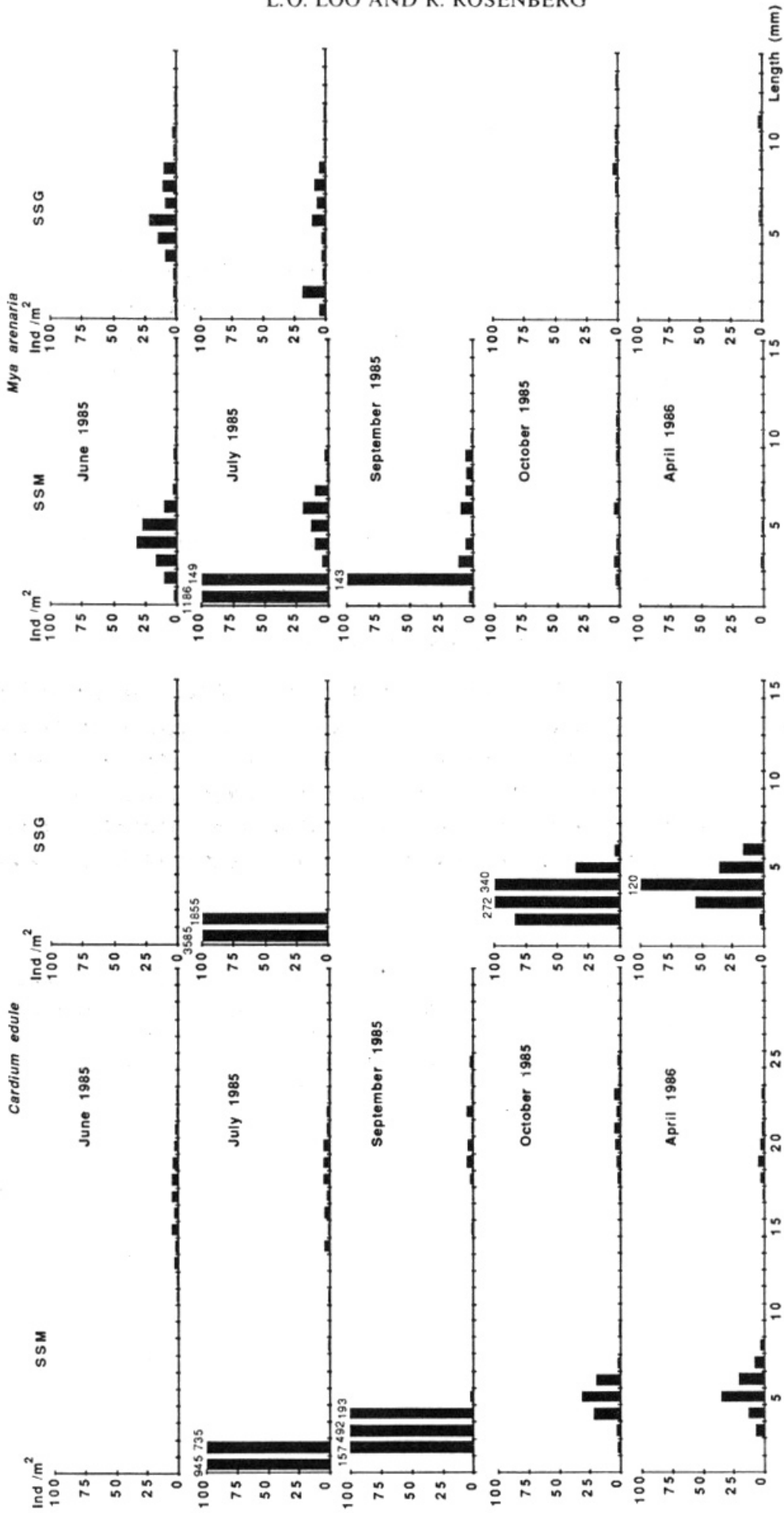


Fig. 4. Length-frequency diagrams for *C. edule* and *M. arenaria* at SSG and SSM. A few individuals of *C. edule* at SSG were >20 mm and are not shown.

class of *M. arenaria* was represented (Fig. 5); specimens from the shallow areas were more abundant and had a longer mean shell length than those from the deeper parts.

At Transects 1, 3 and 4, the frequency of recently dead 0-gr and adult *C. edule* was high (Fig. 6). At 3 and 5 m, the 0-gr dominated and at 6 and 10 m adults were most common among the recently dead. In general, few adults were found alive. At Transects 5-7, live adult *C. edule* dominated at most depths (Fig. 6). The highest density of live 0-gr *C. edule* was at 4 m. Dead specimens of both 0-gr and adults were found at 3 and 6 m depth.

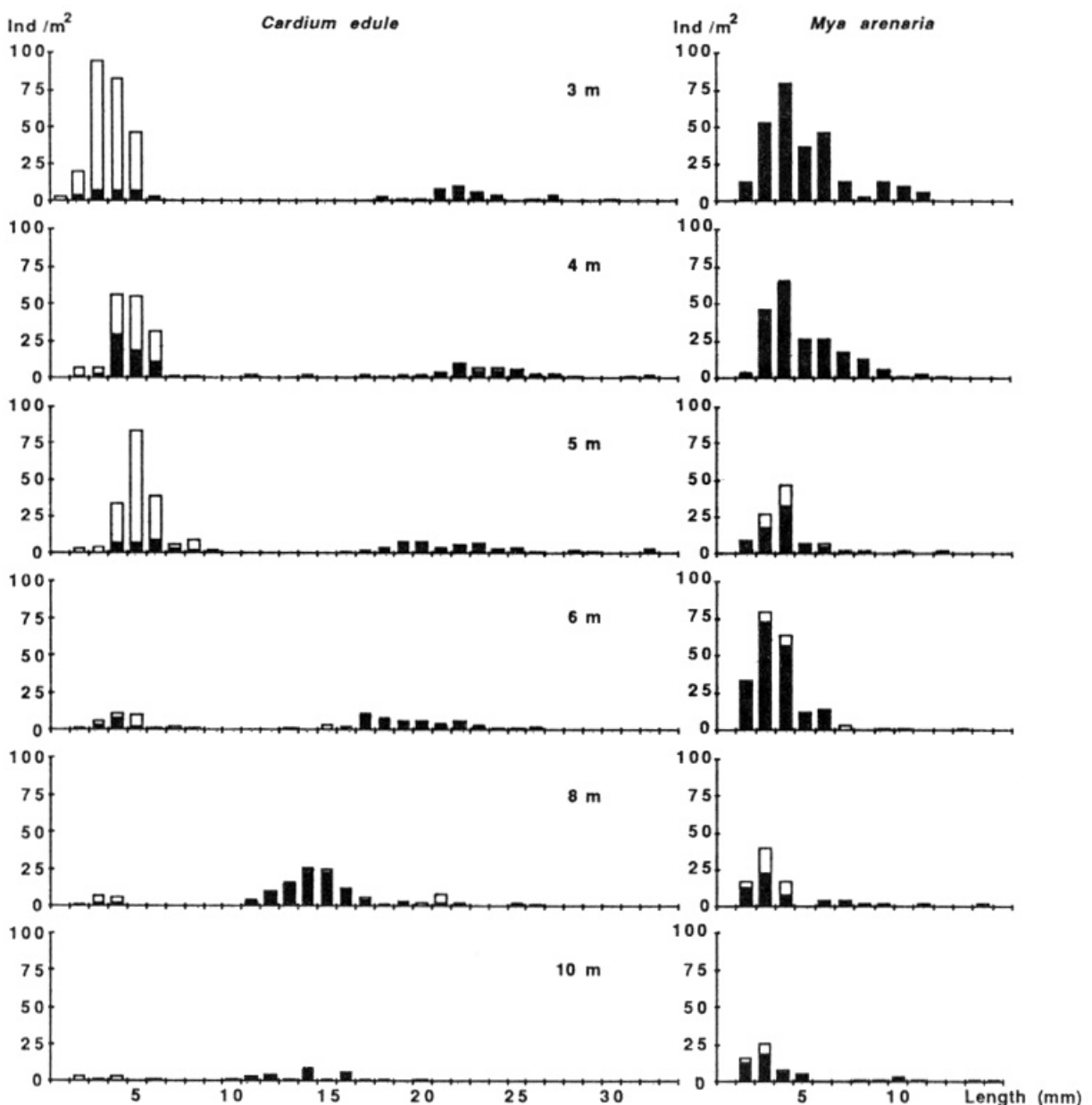


Fig. 5. Mean length-frequency at each depth from all transects of *C. edule* and *M. arenaria* in April 1985. Black bars are live bivalves and open bars dead bivalves.

In Table VII, total abundance and biomass for the northern and southern transect areas are presented separately because of the large differences seen in these parameters. Estimates for recently dead bivalves were also included. In the northern part of the bay, dead 0-gr *C. edule* were most abundant in the samples and in the southern part live adults were the dominant group.

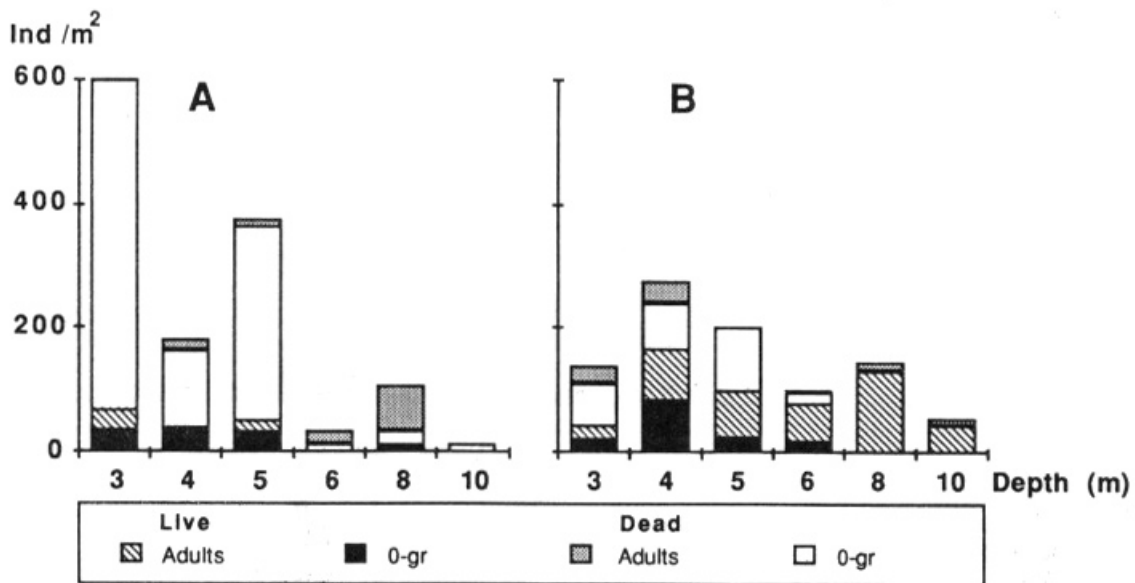


Fig. 6. Mean numbers of *C. edule* at different depths at Transects 1, 3 and 4 (A) and at Transects 5-7 (B) in April 1985.

TABLE VIII

Filtration at four dates and one measurement of absorption with three sizes of *C. edule*. Seston concentrations in inhalant water, temperature and salinity are also given.

Measurement	Filtration experiment				Absorption experiment
	04 Jun 1985	02 Oct 1985	07 Apr 1986	23 May 1986	19 Jun 1985
AFDW (g) shell	0.124	0.109	0.109	0.028	0.099
	0.309	0.327	0.230	0.082	0.204
	0.735	1.165	0.398	2.339	0.741
AFDW (g) flesh	0.094	0.066	0.077	0.108	0.069
	0.219	0.219	0.167	0.406	0.142
	0.559	0.815	0.214	0.658	0.536
Length (mm)	21	26	22	20	19
	30	33	26	29	26
	38	42	36	34	39
Absorption efficiency (%)	59	52	-	51	81
Seston DW (mg·l ⁻¹)	1.29	0.97	0.90	5.24	0.69
Seston AFDW (mg·l ⁻¹)	0.67	0.59	0.21	3.48	0.59
T (°C)	18	14	3	11	17
S(‰)	14	27	30	25	20

FILTRATION AND FILTRATION ESTIMATES

Experiments with *C. edule* indicated that the filtration rate increased with increasing size (Fig. 7). The seston concentration in the first experiment was moderate and the absorption efficiency was $\approx 59\%$ (Table VIII). The highest absorption efficiency measured during the experiment was 81% , in June 1985. The seston AFDW was high in relation to seston DW at that time.

In March 1986, when the water temperature was $\approx 0^\circ\text{C}$, no filtration occurred. At the next experiment in April 1986, the water temperature was 3°C and the bivalves were filtering actively, showing that bivalves can use the spring bloom if the temperature is close to 3°C . At the last date (23 May 1986), the filtration rate was below the "maximum", perhaps because the high seston concentration at that time reduced the filtration rate.

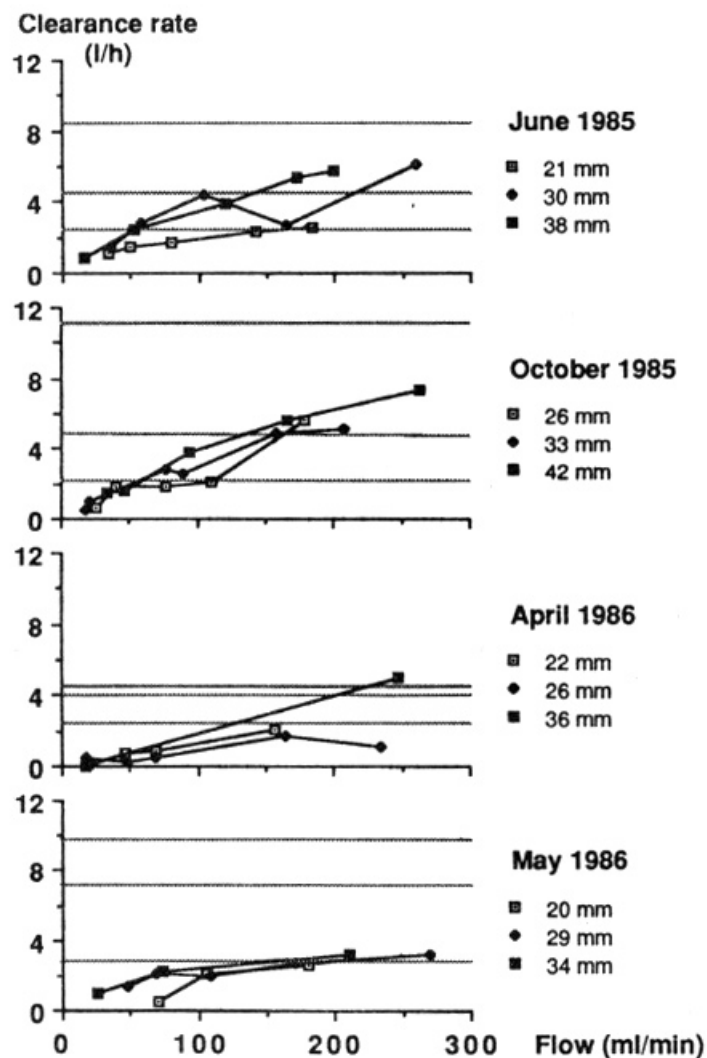


Fig. 7. *C. edule* clearance rates at four dates and temperatures and with three shell lengths (mm). Flow rate is flow through a glass tube placed above bivalve exhalant apertures. Three vertical lines in each diagram represent filtration rates of same sizes of *C. edule* at $10\text{--}13^\circ\text{C}$ according to Møhlenberg & Riisgård (1979).

The total filtration rate in the northern and southern Laholm Bay was estimated by integrating the biomass between 0 and 10 m and using the filtration rates obtained from Table VII. The dominant group by filtration was adult *C. edule* in the southern part.

DISCUSSION

Several factors can affect the amount of seston (including phytoplankton) in Laholm Bay: (1) the specific growth rate of phytoplankton; (2) the water residence time in the bay (including export); (3) the grazing of zooplankton; (4) the feeding activity of benthic animals; and (5) sedimentation–resuspension processes. The water residence time in Laholm Bay is ≈ 1 wk (Fleischer et al., 1985). In the first part of the discussion, we focus on the structure and function of, in particular, the suspension-feeding benthos. Then, we discuss benthic–pelagic coupling and present an energy flow diagram for the dominant suspension-feeders.

ABUNDANCE

In June 1985, at the time of the first sampling, the number of adult *C. edule* was very low in SSG but higher at SSM, indicating that the O_2 concentration near the bottom may have been low before the settling period June–July. Mortality of bivalves has been recorded many times in the 1980s at these shallow depths (Rosenberg & Loo, 1988). The only reasonable explanation presented so far is periodic O_2 deficiency (Rosenberg & Loo, 1988) although low O_2 concentrations in the water column have not been recorded in this part of the bay.

During July 1985–April 1986, the abundance of 0-gr *M. arenaria* decreased from 1940 to 5 ind $\cdot m^{-2}$ at SSM and that of the 1-gr from 150 to 2 ind $\cdot m^{-2}$. The difference between these two groups was due probably either to high settlement of *M. arenaria* in 1985 or high mortality during 1985–86. In 1985, the recruitment of 0-gr plaice in Laholm Bay was the highest of the 20th century and the main food resource of plaice was juvenile bivalves (L. Pihl, pers. comm.). This suggests that plaice, especially during 1985–86, could have had a great impact on the bivalve abundance in the area.

Thus, both periodic hypoxia and predation by plaice affect the numbers of bivalves in the shallow Laholm Bay. The bivalves eaten by plaice are crushed and, consequently, mortality due to this cause can be separated from that due to other causes. An additional mortality factor in winter, but of less importance, could be low water temperatures.

PRODUCTION AND GROWTH

Production of 0-gr *M. arenaria* at SSM during 1985–86 was 0.135 g AFDW $\cdot m^{-2}$ from 25 June 1985–3 April 1986 (Table VI). In two semi-exposed shallow (0–1 m) areas north of Laholm Bay, 0-gr production of *M. arenaria* during July–September has been between 1 and 20 g AFDW $\cdot m^{-2}$ but can be as high as 345 g AFDW $\cdot m^{-2} \cdot yr^{-1}$

(Möller & Rosenberg, 1983). Annual production in the inner eutrophic Oslofjord was estimated at $6 \text{ g AFDW} \cdot \text{m}^{-2}$ (Winther & Gray, 1985).

Production of 0-gr *C. edule* was $0.91\text{--}1.86 \text{ g AFDW} \cdot \text{m}^{-2}$ in our survey whereas further north higher production values were often seen between 1 and $10 \text{ g AFDW} \cdot \text{m}^{-2}$, ranging between < 1 to $100 \text{ g AFDW} \cdot \text{m}^{-2}$ (Möller & Rosenberg, 1983). Adult *C. edule* had the highest production and biomass in Laholm Bay during June 1985–April 1986, with a value of $3.632 \text{ g AFDW} \cdot \text{m}^{-2}$. Other production estimates of *C. edule* and *M. arenaria* from regions with similar habitats are rare but the few comparisons made here suggest that the secondary production in Laholm Bay was low. Causes may be low food concentrations close to the bottom or that this area is regularly affected by strong wave movements which resuspend the bottom substratum and disturb the growth especially of small individuals, or finally, that periodic hypoxia and predation affected the production.

The growth of *M. arenaria* at SSM was similar to that found in 1980–82 on the Swedish west coast (Möller & Rosenberg, 1983). A similar comparison for *C. edule* gave lower growth rates in Laholm Bay. Smaal et al. (1986) reported higher values of both biomass and growth rate in The Netherlands. The growth conditions in Laholm Bay, which seem to have been below normal rather than exceptional, may be due to low and fluctuating salinities.

The production : biomass ratios at SSM for the whole period for *C. edule* were 0.7 for adults and 4.6 for 0-gr and those for *M. arenaria* 2.8 for the 1-gr and 8.3 for the 0-gr. These estimates are of a same order as those obtained by Möller & Rosenberg (1983) for 0-gr *M. arenaria* but generally somewhat lower for 1-gr *M. arenaria* and 0-gr *C. edule*.

The specific daily growth rate for 25 February 1986–3 April 1986, including the spring bloom, was 0.32%. According to diagrams in Möller & Rosenberg (1983), the specific daily growth rate for the same period could be calculated to $\approx 0.61\%$. The results from the present study indicate that the bivalves can utilize the spring bloom only to some extent. The lower specific growth rate in Laholm Bay once more suggests that conditions were not optimal. Either the food concentration reaching the benthos in this eutrophicated area was lower than further north along the Swedish coast (see below) or the stress factors mentioned above also were reducing the growth rate. In an adjacent area at 30 m, the sedimentation subsequent to the spring bloom gave the highest annual supply of food for benthic animals (Christensen & Kanneworff, 1985).

BENTHIC-PELAGIC COUPLINGS AND ENERGY FLOW

The mean annual primary production in the outer Laholm Bay during 1981–85 was $136 \text{ g C} \cdot \text{m}^{-2}$ (Edler, 1986) which is not very high for a eutrophicated area. On the Swedish northwest coast, close to the Norwegian border, primary production in 1979 was $222 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Lännergren, 1983, pers. comm.) and in the Gullmar Fjord, south of that area, an annual mean of $205 \text{ g C} \cdot \text{m}^{-2}$ was obtained during 1978–82 (Lindahl, 1987).

The energy content of seston in the Laholm Bay during the autumn blooms of 1981–85 was between 9 and 18 $\text{kJ} \cdot \text{m}^{-3}$ with a mean of 13 $\text{kJ} \cdot \text{m}^{-3}$. These estimates were obtained by converting Chl *a* values from Edler (1986) to energy as: energy (kJ) = Chl *a* (mg) $\cdot 0.26^{-1}$ (Lännergren, 1983, pers. comm.).

Filtration rate and amount of food ingested by benthic suspension-feeders in Laholm Bay were calculated in three ways: (1) from data based on instantaneous measurements in low algal concentrations (Møhlenberg & Riisgård, 1979); (2) on the basis of our own filtration experiments with instantaneous measurements in natural surface water during different seasons (Fig. 7); (3) on the basis of production (data from sampling squares) + respiration (Table III) = absorbed food; and absorbed food/absorption efficiency (Table IX) = ingested food (a function of filtration rate and food concentration). Ingested food is a finite measurement during the whole season of production. The "maximum" filtration rates found in experiments by Møhlenberg & Riisgård (1979) are similar to ours, except in May 1986 when we obtained lower filtration rates.

TABLE IX

Energy parameters for *C. edule* and *M. arenaria* during 12 September–14 October 1985 at SSM. All numbers are in $\text{kJ} \cdot \text{m}^{-2}$. As a comparison, daily ingested food by net-zooplankton for same period is given (P. Tiselius, pers. comm.).

Species	Ingested food	Faeces	Absorbed food	Respiration	Production	Eliminated biomass food	Daily ingested food	Percent of daily ingestion
<i>C. edule</i>								
Adults	272	109	163	121	42	47	8.50	23
0-gr	683	273	410	400	10	13	21.34	59
<i>M. arenaria</i>								
1-gr	84	34	50	37	13	11	2.63	7
0-gr	94	38	56	55	2	1	2.94	8
Total	1133	454	679	613	67	72	35.41	97
Net-zooplankton						0.85	3	
Total							36.26	100

Calculations according to the first method, which represents the "maximum" total ingested amount of food for these suspension-feeders, gave a consumption of $64 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ with a mean seston concentration of $13 \text{ kJ} \cdot \text{m}^{-3}$. On the basis of production data (third method) from SSM, the total mean amount of food ingested daily by 0-gr and adult *C. edule* and 1- and 0-gr *M. arenaria* was $35 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ during autumn 1985 (Table IX). This period was used because production estimates are available for September–October and it is the time of the autumn bloom (Edler, 1986). Moreover, a comparison with the phytoplankton consumption by net-zooplankton can be made for that period.

Thus, the bivalves ingested only half of their "maximum" potential feeding capacity. A similar result was obtained if production in SSG was used. This indicates that the

bivalves did not feed at a maximal rate or that the filtration rates used in the calculations were too high. One cause for a low feeding rate may be that the bottom water has a low turnover rate and that part of the food does not come into close contact with the bivalves; another is that physical disturbance by wave activity on bivalve growth and production was significant. The suggestion that food availability was low seems to be the primary reason because both growth and production were lower than in other investigations, as discussed above. It has been shown in experiments with suspension-feeding bivalves that hydrodynamic factors may be critical in determining the food supply available (Wildish & Kristianson, 1984). Food quality and quantity have been shown earlier to be a limiting factor for suspension-feeding bivalves by Wallace (1980) and Rosenberg & Loo (1983).

On the basis of production estimates at SSM (from Table VI) in kJ, together with respiration data from Table III for September–October 1985, absorption was calculated. With an approximate average absorption efficiency of 60% (Table VIII; see also Newell & Bayne, 1980: June 1974–October 1975, $\bar{x} = 67.6 \pm 12.7\%$, $n = 11$, range = 47–83%), the amount of food ingested daily was obtained. The total of $35 \text{ kJ} \cdot \text{m}^{-2}$ for the bivalves can be compared with the daily ingestion by net-zooplankton of $0.85 \text{ kJ} \cdot \text{m}^{-2}$ (Tiselius, 1988). The zooplankton was collected by taking vertical tows with a 200- μm net in October. Dominant species were *Pseudocalanus elongatus* and *Paracalanus parvus* and consumption was estimated by gut fluorescence of Chl *a*. Thus, during September–October 1985, $\approx 97\%$ of the total seston consumed was ingested by benthic organisms and only $\approx 3\%$ by zooplankton, if the zooplankton activity was the same in 1985–86. *C. edule* and *M. arenaria* ingested 84 and 16%, respectively. The benthos–zooplankton comparison is indeed very crude but suggests that a great proportion of the phytoplankton are consumed by benthic suspension-feeders in shallow areas rather than by this size group of zooplankton.

The total food ingested daily by the bivalves during 25 June 1985–3 April 1986 was $14.8 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ (Table X). An energy flow diagram for June 1985–June 1986,

TABLE X
Energy parameters ($\text{kJ} \cdot \text{m}^{-2}$) for *C. edule* and *M. arenaria* in SSM during June 1985–April 1986.

Species	Ingested food	Faeces	Absorbed food	Respiration	Production	Eliminated biomass food	Daily ingested food	Percent of daily ingestion
<i>C. edule</i>								
Adults	1940	776	1164	1083	81	78	6.88	47
0-gr	1682	673	1010	990	20	16	5.96	40
<i>M. arenaria</i>								
1-gr	359	144	216	188	27	15	1.27	9
0-gr	186	75	112	102	10	10	0.66	4
Total	4167	1668	2502	2363	138	119	14.78	100

with extrapolations for April–June 1986, is presented in Fig. 8. *C. edule* and *M. arenaria* ingested 87 and 13% of the food, respectively. The annual total amount ingested was $5374 \text{ kJ} \cdot \text{m}^{-2}$.

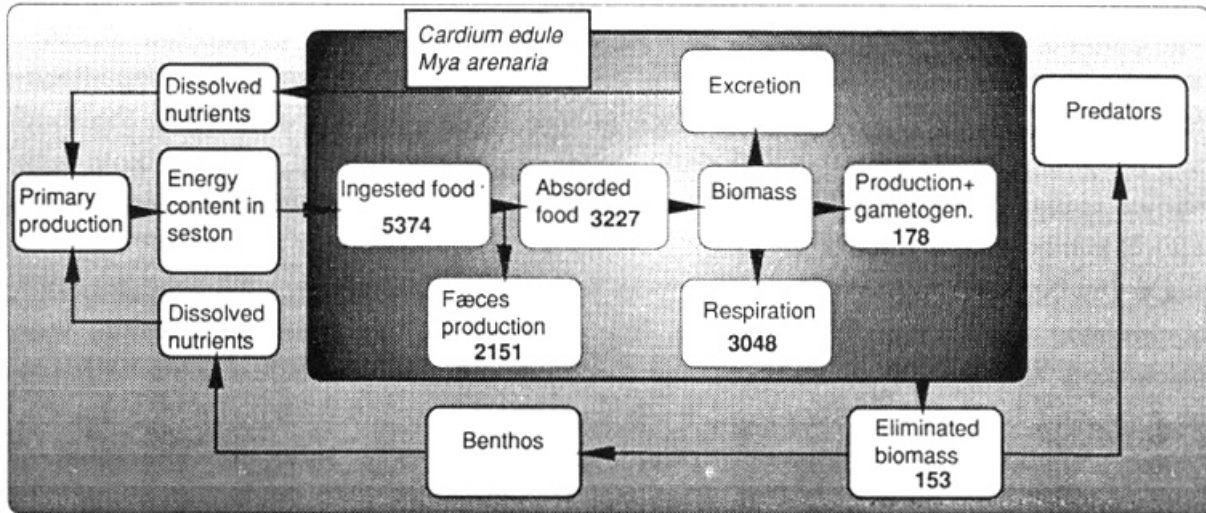


Fig. 8. Simplified energy-flow diagram for the suspension-feeding bivalves *C. edule* and *M. arenaria* at SSM during June 1985–June 1986 in $\text{kJ} \cdot \text{h}^{-2}$. Based on data from Table X and extrapolated for April–June 1986. Energy uptake as dissolved compounds (e.g., amino acids) is not included.

EXCRETION AND BIODEPOSITION

On 19 June 1985, total N and C were measured in phytoplankton and biodeposits (faeces) and ammonium, urea and dissolved organic N were measured in the exhaled water (excretion) from different size classes of *C. edule* (Table XI) as part of the filtration experiment. The estimates of N and C for the total area at 0 to 10 m (60 km^2)

TABLE XI

Ingestion (total N and C), excretion (ammonium and urea) and biodeposition (total N and C) for *C. edule* given as t N and $\text{C} \cdot \text{yr}^{-1}$ for 0–10 m depth in Laholm Bay (60 km^2). Calculations are based on mean individual weights obtained from transect studies. Values for *M. arenaria* were estimated from its percentage of ingested food (15%) given in Table IX. C was calculated from N figures by using atomic ratios C:N = 7.9 for ingestion and C:N = 8.5 for biodeposits (F. Sörensson, pers. comm.).

	Ingestion		Excretion	Biodeposition	
	N	C	N	N	C
<i>C. edule</i>					
Live	419	2841	100	156	1137
Potential of dead	115	781	34	43	312
Sum live and potential	534	3622	134	199	1449
<i>M. arenaria</i>	98	663	134	36	262
Sum	632	4285	268	235	1711

in Laholm Bay were based on the abundance and biomass of *C. edule* at the transects and on 50% of the "maximal" potential filtration rate (as discussed above). As many *C. edule* were recently dead, their potential contribution is also included in Table XI. On the basis of the daily percentage ingestion of *M. arenaria* (15%) at SSM (Table IX) and the assumption that this relationship is approximately the same in the whole bay, a crude estimate could also be made for this species.

In 0-gr *C. edule*, excretion of ammonia and urea was 93–96% of N biodeposition, i.e., of the same order of magnitude. For adult *C. edule*, N excretion was 60–64% of the N biodeposition. The ammonium:urea excretion ratio was $\approx 5:1$. Excretion of dissolved organic N was less than that of urea and negligible during that period. The C:N atomic ratio in the ingested particles was 7.9 and that in the biodeposits 8.5, i.e., the ratio changed to only a minor degree during passage through the animals. The relationship between excretion and biodeposition of N agrees rather well with findings for other bivalves (e.g., Jordan & Valiela, 1982).

Of the total annual riverine input of ≈ 5000 t total N, ≈ 2000 t are nitrate, ≈ 500 t are ammonium and the rest is organically bound N. The atmospheric deposition is ≈ 300 t inorganic N (IN) and the deep-water supply ≈ 1500 t IN (Rydberg, 1986). Rydberg also found that IN uptake is practically total in Laholm Bay and that no IN is transported out of the bay except during winter months. We have estimated that 20% of the atmospheric and deep-water supply will appear in the shallow Laholm Bay and all of the riverine supply.

Assuming that 80% is incorporated into phytoplankton as "new production", resulting in ≈ 2300 t N and ≈ 570 t (20%) into benthic macro- and microalgae, then, the two bivalves in Table XI ingest $\approx 27\%$ of the "new production" produced in Laholm Bay at 0–10 m. The excretion will in addition regenerate more production. In spring, phytoplankton take up $\approx 60\%$ of the IN as nitrate in central Laholm Bay whereas ammonia dominates the uptake in summer (Sahlsten & Sörensson, 1986; Sahlsten et al., 1988). Thus, the majority of the phytoplankton are neither consumed by suspension-feeding bivalves nor by net-zooplankton. A higher suspension-feeding standing stock than that in 1985 could have consumed more. Most of the phytoplankton are probably exported to Kattegat and some of that energy will later be deposited on the deeper bottoms.

C. edule and *M. arenaria* will annually produce ≈ 235 t N as biodeposits (Table XI). Part of this material will temporarily aggregate in ephemeral mud blankets, to be resuspended and exported by means of wave action and bottom currents. Such blankets have been mapped on bottoms > 10 m in Laholm Bay and the amount of N associated with them has been estimated to be ≈ 2000 t (Floderus & Håkanson, 1988). Thus, most of the biodeposits in Laholm Bay are likely to be transported to accumulation bottoms in the outer parts of the bay and to southeast Kattegat, like the surplus phytoplankton biomass. There, they contribute to O_2 consumption in the near bottom water. Part of the biodeposits are also likely to be mineralized in the water column and in the shallow parts. The contribution of the two suspension-feeders, with a potential annual biodepo-

sition of $\approx 29 \text{ g C} \cdot \text{m}^{-2}$ (Table XI), will be in the order of $591 \text{ O}_2 \cdot \text{m}^{-2}$ (1 g C corresponds to 2.05 O_2 , $RQ = 0.9$). Assuming that respiration of the bivalves is 50% of ingestion, i.e., $36 \text{ g C} \cdot \text{m}^{-2}$, this will result in a total respiration of $29 + 36 = 65 \text{ g C} \cdot \text{m}^{-2}$. This is approximately equal to $1351 \text{ O}_2 \cdot \text{m}^{-2}$. As a comparison, the annual benthic O_2 consumption at 20 m in 1985 in outer central Laholm Bay was estimated to be $431 \text{ O}_2 \cdot \text{m}^{-2}$ which is about half of that at similar depths in other areas (Enoksson & Granéli, 1986).

CONCLUDING REMARKS

Biological effects have been observed in shallow Laholm Bay, probably linked to eutrophication; these include mass mortality of bivalves and changes in composition of macroalgae. In addition, during several summers in the 1970s and 1980s filamentous macroalgae drifted close to the beaches and were washed ashore, causing problems for pleasure boats, swimmers and fishermen. Away from the coast, however, the general impression is that the water surface looks quite normal and the phytoplankton production of $136 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Edler, 1986) is not exceptional. The seston concentration in shallow Laholm Bay is reduced by benthic suspension-feeders. We have argued that this reduction would have been even greater if the water were more thoroughly mixed and if the suspension-feeding bivalves had survived for longer periods and in larger numbers.

The water volume at 0 and 10 m in Laholm Bay could theoretically be filtered by the suspension-feeding bivalves during 3 days. In northern San Francisco Bay, with a depth of 2 m, *M. arenaria* can filter all particles from the water volume $\approx 1 \text{ time} \cdot \text{day}^{-1}$ (Nichols, 1985). In southern San Francisco Bay, with a mean depth of 6 m, the bivalves can filter the water volume 1.2–1.8 times $\cdot \text{day}^{-1}$ (Cloern, 1982). There, the removal of seston by benthos was estimated to be a magnitude greater than that calculated for zooplankton, i.e., a similar relationship as in Laholm Bay. Cloern (1982), Officer et al. (1982), Nichols (1985) and ourselves have found that benthic suspension-feeders can reduce, and in some areas control, phytoplankton. Such control increases: (1) if the water body is shallow; (2) if the residence time is long; (3) if the water mixes at the bottom and allows a continuous supply of new food; and (4) if the suspension-feeding biomass is high.

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