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ENERGY FLOW THROUGH THE SE KATTEGAT: A COMPARATIVE EXAMINATION OF THE EUTROPHICATION OF A COASTAL MARINE ECOSYSTEM

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ABSTRACT

Energy flow through the major compartments of the ecosystem of the south-east Kattegat has been assessed based on observations made between 1985-1989. In this increasingly eutrophic semi-estuarine coastal area, energy inputs are dominated by autochthonous production during the spring and autumn bloom periods (>90%), and by allochthonous fluvial sources during the winter (>50%).

An unbalanced annual carbon budget is presented, which demonstrates the predominance of infaunal benthic suspension feeders in the shallow areas (above 13 m), where their demand alone is 2.4 times the calculated carbon supply to the sediment. Benthic demand does not diminish below 13 m, but the proportion utilized by macrofaunal deposit feeders and meiofauna increases with lower suspension feeder demand, emphasizing the close coupling between pelagos and benthos at all depths in this system. Excess benthic demand over planktonic production is assumed to be met by lateral imports across the system boundaries.

Intermittent summer hypoxia below the halocline (mean depth 15 m) has a severe effect on the benthos of the area, leading to a reduction in epifaunal predation prior to the reduction of macrobenthic organisms. Such events lead to the temporary accumulation of sedimentary carbon before late autumnal mixing initiates the reoxygenation and eventual recolonization of the affected areas.

Comparisons with published carbon budgets for the Chesapeake Bay and the Baltic Sea suggest major differences between the relative roles of pelagos and benthos in these systems. In the Baltic, which is fuelled predominantly by autochthonous processes, pelagic carbon flows are about 4 times those of the benthos. Allochthonous inputs predominate throughout much of the year in the Chesapeake Bay, where pelagic flows are proportionately 1.5 x those of the benthos, whereas in the SE Kattegat benthic flows exceed those within the pelagos by about 25%.

The higher populations of epifaunal and nektonic predators found in the SE Kattegat system, as opposed to the other two systems, is a corollary of the greater energy flows through the benthic components. The demonstrable vulnerability to anoxia of these commercially important organisms emphasizes the sensitivity of such coastal systems to the consequences of increased nutrient inputs.

1. INTRODUCTION

The Kattegat is an enclosed shallow sea area (mean depth 23 m) bounded on the east by SW Sweden, on the north by the NE coast of Denmark and to the south by the Danish archipelago through which it is connected to the Baltic sea by the Öresund and the Belt channels (Fig. 1). The tidal range in the area is very low (<10 cm) and a strong halocline occurs between 10 and 20 m (mean depth 15 m) which separates brackish surface water of Baltic origin from oceanic bottom water originating from the Skagerrak and the North Sea. The area can be regarded, therefore, as the outer reaches of a large and complex estuarine system.

Over the past two decades, increasing concern has been expressed over growing signs of nutrient enrichment in various areas of the Kattegat. The first obvious evidence of the consequences of such enrichment was seen in Laholm Bay on the SE coast of Sweden, where large quantities of filamentous green algae washed ashore in the mid-1970s as a result of the increasing predominance of these algae over the previously dominant brown macroalgae (WENNBERG, 1987).

In 1980, fish kills attributed to low bottom-water oxygen concentrations were reported from the same area and subsequent years have seen a steady increase in observable and documented eutrophic effects in this and other areas of the Kattegat (ROSENBERG, 1985; BADEN *et al.*, 1990a).

The concern over these events prompted the Swedish Environmental Protection Agency to estab-

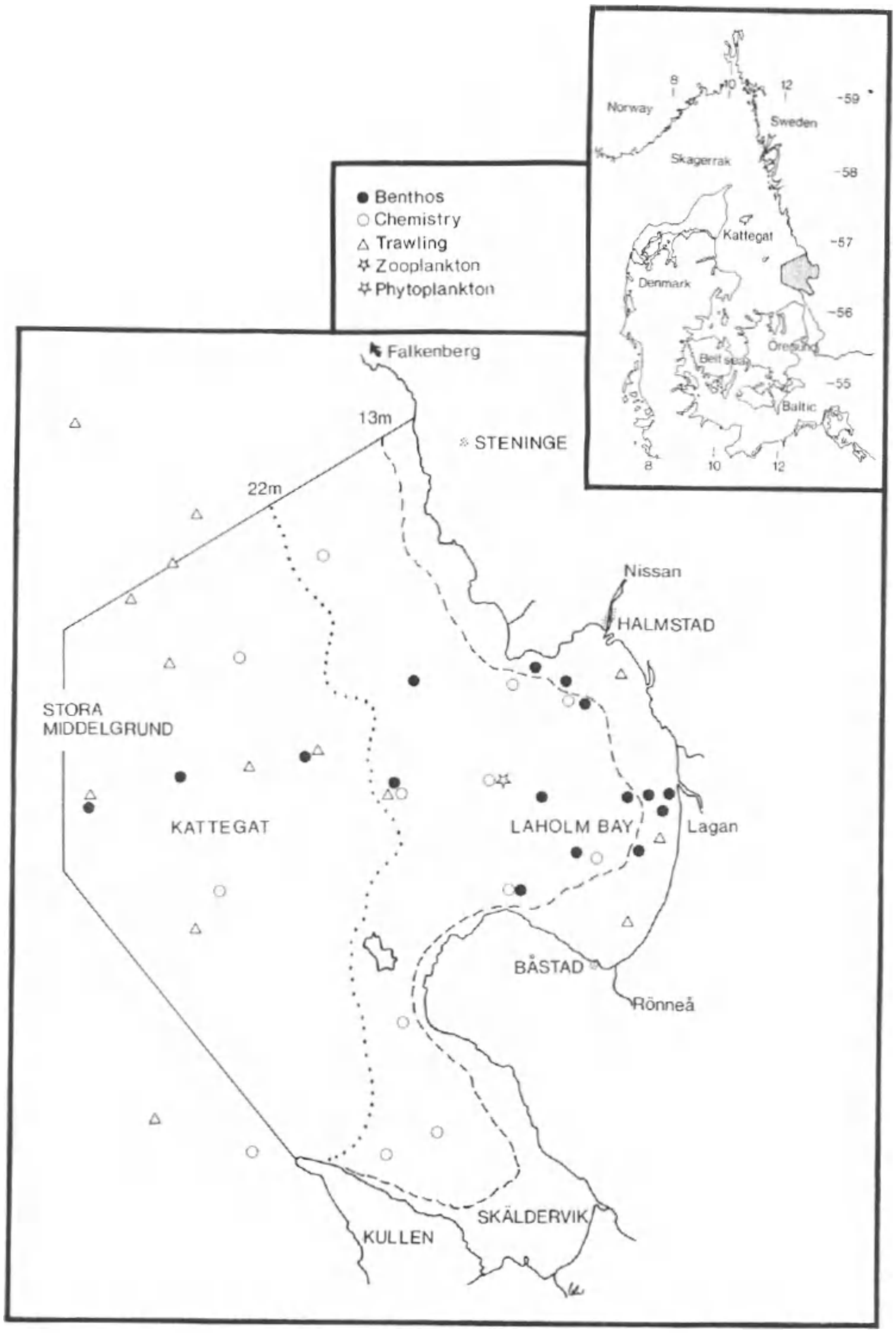


Fig. 1. Map of the study area showing the positions of the various stations occupied for differing sampling purposes and the geographical boundaries of the 'box' used as a basis for total input calculations.

or pools of energy inputs derived from a common and measurable source.

In this study sixteen compartments have been delineated based initially on those defined by WULFF & ULANOWICZ (1989) for their comparison of the Baltic and Chesapeake ecosystem, in order to allow direct subsequent comparison with flows through those systems. Some minor modifications were made to this model in order to adapt the pattern to fit the information available from the SE Kattegat system. The various compartments included in the SE Kattegat model are listed in Table 1, together with the data sources used to define the carbon data associated with each compartment. Wherever possible, the data used is derived from studies undertaken in the area during the 1983-89 studies (such sources are identified by an asterisk in Table 1). Inevitably, however, the local data coverage falls short of providing all the necessary information and, where necessary, relevant information from elsewhere or derived from composite general indices, has been used.

Three major input sources to the system have been identified, namely gross primary production, defined as the production of autotrophic pelagic bacteria, pelagic algae and that of benthic algae, inputs of dissolved organic carbon from rivers (DOC), and inputs of dissolved organic carbon from seawater flows across the boundaries of the defined area. Five heterotrophic compartments within the system have been allocated to groups of pelagic consumers, namely the nano-zooplankton (2 to 20 μm), micro-zooplankton (21 to 100 μm), meso-zooplankton (101 to 1000 μm), carnivorous pelagic invertebrates and pelagic fish. Benthic consumers occupy a further six compartments, defined as meiofauna, infaunal suspension feeders, infaunal deposit feeders, infaunal carnivores, other invertebrate epifaunal carnivores including *Nephrops*, and demersal fish. No direct measurements of benthic bacteria have been made in the area and in this analysis they have not been allocated a separate compartment. Because of their close relationship with sedimentary particulate organic carbon (POC) they are subsumed in that compartment. The quality of local information available for the computation of energy flows through each of these compartments is highly variable, as can be seen from a comparison of the available sources listed in Table 1. In some cases, detailed studies of individual species of major economic or ecological importance (*e.g.* JONSSON & TISELIUS, 1990; PIHL, 1989a; BADEN *et al.*, 1990a) or of production in particular communities (*e.g.* SUNDBÄCK & JÖNSSON, 1988; LOO & ROSENBERG, 1989; PIHL, 1989b) have allowed accurate estimates of flows through particular compartments based on contemporary local information. In other cases, lack of local knowledge of certain components or processes within a compart-

TABLE 1

The compartments and their principal constituents delineated for the energy flow network in the SE Kattegat (Compartments assessed in the SE Kattegat are indicated by an asterisk.)

compartment	*principal constituents*
1. Pelagic producers*	Planktonic algae; Autotrophic pelagic bacteria
2. Benthic producers*	Macroalgae; Benthic microalgae
3. Heterotrophic pelagic bacteria	
4. Micro- and nannozooplankton	Heteromicroflagellates; Ciliates
5. Meso-zooplankton*	Copepods; Rotifers; Cladocerans
6. Pelagic invertebrate carnivores	Medusae (*Aurelia*, *Cyanea*)
7. Meiofauna	
8. Benthic suspension feeders*	Bivalves (*Arctica*, *Cerastoderma*, *Mya* etc.) Ophiuroids (*Amphiura filiformis*)
9. Deposit feeders*	Bivalves (*Macoma*, *Abra nitida*, *Nuculana* etc.) Ophiuroids (*Amphiura chiajei*) Echinoids (*Brissopsis*) Polychaetes (*Polyphisia*, *Pygospio*, *Maldane*) Crustaceans (*Diastylis*)
10. Infaunal benthic carnivores*	Polychaetes (*Nephtys*, *Pholoe*, *Glycera*) Ophiuroids (*Ophiura*)
11. Invertebrate epifaunal carnivores*	Crustacea (*Crangon*, *Carcinus*, *Eupagurus*, *Nephrops*)
12. Planktivorous fish*	Clupeidae, Ammodytidae, *Gadus esmarkii*
13. Carnivorous fish*	*Pomatoschistus*, *Gasterosteus*, *Platichthys*, *Pleuronectes*, *Hippoglossoides*, *Gadus morhua*, *Merlangus*
14. Dissolved organic carbon (DOC)*	Fluvial inputs; exudates
15. Suspended particulate organic carbon (POC)*	Fluvial inputs; planktonic faecal aggregates
16. Sedimentary organic carbon*	Vertical sedimentation; horizontal transportation; benthic faecal aggregates

figures (RIEMANN *et al.*, 1990). The estimated annual and seasonal inputs to the area from these various sources are given in Table 2. Gross production figures have been estimated from primary production and exudate figures by assuming a 30% respiratory loss (WULFF & ULANOWICZ, 1989).

4.1.2. ALLOCHTHONOUS CARBON INPUTS (COMPARTMENTS 14, 15)

The amount of carbon reaching the area via the rivers which discharge along the coastline between Steninge and the Kullen peninsula (the Nissan, Lagan and Rönneån plus several smaller streams) has been estimated from official data provided by the Environmental Quality Laboratory, SNV, Uppsala. The estimated annual and seasonal inputs of dissolved organic carbon (DOC) and particulate organic carbon (POC) from these sources are detailed in Table 2. DOC inputs via marine inflows across the seaward boundaries of the area have not been included through lack of any reliable data on which to base estimates. This potential source thus constitutes one of the principal unknown elements in any attempt to balance a carbon budget for the area (see chap. 5).

4.2. PLANKTONIC INVERTEBRATE HETEROTROPHS

4.2.1. PELAGIC BACTERIAL AND MICRO-ZOOPLANKTON PRODUCTION (COMPARTMENTS 3, 4)

Few direct measurements of these elements in the network were undertaken in the course of the 1983-89 programme. Therefore, data provided by the detailed experimental carbon budget studies in Danish estuarine enclosures carried out by RIEMANN *et al.* (1990) has been used for their estimation, supplemented by information on bacterial and microplanktonic populations of the Skagerrak and Kattegat areas given by HAGSTRÖM *et al.* (1988), KIØRBOE *et al.* (1990) and ROSENBERG *et al.* (1990b). The Danish experimental studies provided a close approximation to the existing conditions in the SE Kattegat, however the authors emphasized a number of simplifications and assumptions which they needed to make in order to carry out their budgeting exercise. They used the model of AZAM *et al.* (1983) to divide organisms into arbitrary size groups assuming a predator/prey ratio of 10 and assumed a general value of 30% carbon conversion efficiency these assumptions, although necessary given the lack of understanding of these systems, are probably far too broad. Moreover, RIEMANN *et al.* (1990) warn against extrapolating their results to field situations. However, alternative calculations of bacterial biomass and production based on field measurements of bacterial numbers and productivity at a shallow station in the Skagerrak (ROSENBERG *et al.*, 1990b) result in very similar figures. Thus, in the absence of any better basis for estimating flows and sinks within these parts of the planktonic system, we consider this use of the data justified. The annual production and biomass of these components, calculated on this basis, are detailed in Table 3.

4.2.2. MESO-ZOOPLANKTON (COMPARTMENT 5)

Some field information is available from the area as to the standing stock, diets and growth rates of copepods (TISELIUS, 1988, 1989; JONSSON & TISELIUS, 1990; KIØRBOE & NIELSEN, 1990; NIELSEN & KIØRBOE, 1990). This has been supplemented by use of relationships detailed by KIØRBOE *et al.* (1985) to estimate respiration and consumption rates. The dominant copepods in the area are *Paracalanus parvus* and *Paracalanus elongatus* (TISELIUS, 1988). Little information on Rotifers and Cladocerans from the area is available, thus some general correction factors, based on relationships given in NIELSEN & KIØRBOE (1990), have been used to take these organisms into account. The results calculated on this basis are given in Table 3.

4.2.3. PELAGIC INVERTEBRATE CARNIVORES (COMPARTMENT 6)

Two species of predatory medusae, *Aurelia aurita* and *Cyanea capillata*, are common throughout the study area. No direct studies were undertaken on these organisms during the course of the project, thus estimates of their energy budgets have been based on information given by MÖLLER (1979, 1980) and SCHNEIDER (1989) for populations in Kiel Bight, an area of the outer Baltic system with similar geographical and hydrographical characteristics to the study area. This information has allowed an estimate of annual carbon flows to be made for these species which may be apportioned more or less equally between the summer and autumn periods. Thus, the adult medusae start appearing about the beginning of May, reach peak biomass levels by the beginning of July and thereafter decline precipitously. Their influence on the carbon flow, particularly in the impact of their predation on the meso-zooplanktonic component in the system, is thus strongly seasonal. The calculations of annual carbon flow for these organisms are shown in Table 3.

4.3. BENTHIC INVERTEBRATE HETEROTROPHS

Calculations for these compartments of the network are all based on a separate consideration of each of

(>95% of the biomass of that group), whilst below 22 m the brittle star *Amphiura filiformis* comprises over 91% of the feeding biomass of this trophic group. Other species contributing the remaining amounts of biomass to this trophic group have been considered to utilize energy proportionate to the major organisms at each depth. Energy flow through the *Arctica* populations has been assumed to approximate the flow occurring in *Cerastoderma* and *Mya*, since consumption rates per unit weight in *Arctica*, reported by WINTER (1969, 1978), are roughly comparable to those estimated for the latter two species. Thus estimates have been based on the biomass figures for the suspension feeding populations between 13 and 22 m (62% of biomass above 13 m). The P:B ratio of *Amphiura filiformis* given by O'CONNOR *et al.* (1986) has been used to estimate the production of the *Amphiura* populations below 22 m. Respiration values have also been calculated from information given by these authors and consumption estimates were based on assimilation efficiencies given by WARWICK *et al.* (1979).

B. BENTHIC DEPOSIT FEEDERS (COMPARTMENT 9)

The dominant deposit feeding organisms in waters shallower than 13 m in the study area were the bivalve *Macoma balthica* (62% of biomass of all deposit feeders). This species is also a suspension feeder in conditions of high phytoplanktonic abundance (HUMMEL, 1985b) and could thus be considered to contribute at least equally to the preceding compartment. However, given the high incidence of obligate suspension feeding species in the community, it is considered that the *Macoma* in the area are more likely to deposit feed. Other deposit feeders of importance are the polychaetes *Pygospio elegans* (19%) and *Scoloplos armiger* (9%). Estimates of production in these populations have been based on measurements of local biomass levels and literature values of P:B ratios (*Macoma*, HUMMEL, 1985a; polychaetes, WARWICK *et al.*, 1979). Seasonal variability in *Macoma* production has been based on information in HUMMEL (1985a). Respiration was calculated using the equation of MCNEILL & LAWTON (1970) and consumption estimated using an assimilation efficiency of 60% (WARWICK *et al.*, 1979) for all the deposit feeding organisms at all depths.

The dominant deposit feeders at depths between 13 and 22 m were the bivalve *Abra nitida* (35% of deposit feeder biomass), the crustacean *Diastylis rathkei* (19%) and the polychaetes *Myriochele* spp. (9%) and *Maldane sarsi* (9%). Production estimates for these species have been based on local biomass values and literature values for P:B ratios (RAINER, 1985, for *Abra*; ROBERTSON, 1979, for other species). In areas below 22 m the brittle star *Amphiura chiajei* made up 35% of the total deposit feeding biomass, the polychaete *Polyphisia crassa* 25% and the echinoid *Brissopsis lyrifera* 13%. P:B ratios for the echinoderm species given by BUCHANAN & WARWICK (1974) were used to calculate their production and that of *Polyphisia* was estimated by analogy from data given by NICHOLS (1977) for *Pectinaria*.

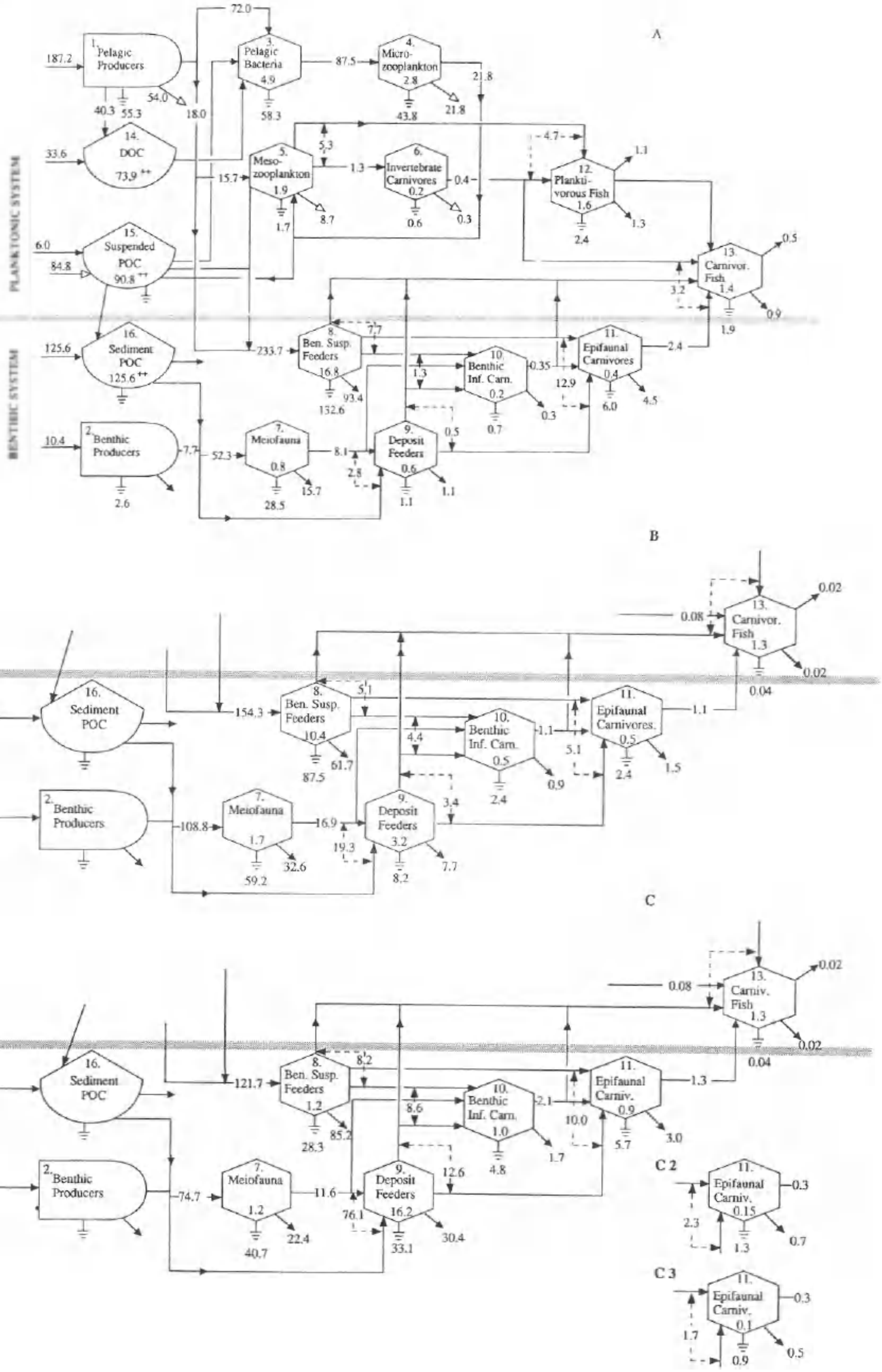
C. INFAUNAL BENTHIC CARNIVORES (COMPARTMENT 10)

The predominant infaunal invertebrate carnivores at all depths in the area were nephtid polychaetes, principally *Nephtys caeca*. This comprised over 81% of carnivore biomass at depths shallower than 13 m, 54% between 13 and 22 m and 15% at depths below 22 m. Thus, the variety of carnivores increases with depth, *e.g.* the polychaetes *Glycera alba, Goniada maculata, Pholoe minuta* (= *inornata*). Production estimates for this group have been based on local biomass data and an assumed P:B ratio of 2.0, a composite median figure arrived at by reference to data from studies on *Nephtys, Nereis* and *Glycera* (BAIRD & MILNE, 1981; BUCHANAN & WARWICK, 1974; MÖLLER *et al.*, 1985; WARWICK *et al.*, 1979) and general ratios given by GERLACH *et al.* (1985) and SCHWINGHAMER *et al.* (1986). Respiration estimates have been based on the relationships given by MCNEILL & LAWTON (1970) and consumption has been calculated using the assimilation efficiency given by KAY & BRADFIELD (1973).

4.4. LARGE MOBILE HETEROTROPHS

4.4.1. INVERTEBRATE EPIFAUNAL CARNIVORES (COMPARTMENT 11)

The dominant larger invertebrate carnivores in the area vary according to depth. In the shallower areas above 13 m, the shrimp *Crangon crangon* and the crab *Carcinus maenas* predominate. At depths between 13 and 22 m *Carcinus* is replaced by the hermit crab *Eupagurus*, although *Crangon* remains an important predator at these depths. Estimates of biomass, production and consumption in these populations have been based on detailed studies made in various embayments along the Swedish west coast to the north of the study area in the years immediately preceding the Kattegat project (MÖLLER *et al.*, 1985; PIHL, 1985; PIHL & ROSENBERG, 1982, 1984). Respiration estimates have been based on the formulae detailed by MCNEILL & LAWTON (1970). Production in these populations is minimal in winter when, between December and February, they migrate offshore to deeper waters.


A
PLANKTONIC SYSTEM
BENTHIC SYSTEM
1. Pelagic Producers
2. Benthic Producers
3. Pelagic Bacteria 4.9
4. Micro-zooplankton 2.8
5. Meso-zooplankton 1.9
6. Invertebrate Carnivores 0.2
7. Meiofauna 0.8
8. Ben. Susp. Feeders 16.8
9. Deposit Feeders 0.6
10. Benthic Inf. Carn. 0.2
11. Epifaunal Carnivores 0.4
12. Plankti-vorous Fish 1.6
13. Carnivor. Fish 1.4
14. DOC 73.9 ++
15. Suspended POC 90.8 ++
16. Sediment POC 125.6 ++
187.2
40.3
55.3
54.0
18.0
72.0
87.5
58.3
43.8
21.8
21.8
21.8
33.6
15.7
5.3
1.3
0.4
4.7
1.1
1.3
2.4
8.7
1.7
0.6
0.3
6.0
84.8
0.5
0.9
1.9
3.2
125.6
233.7
7.7
93.4
132.6
1.3
0.35
12.9
2.4
6.0
4.5
0.3
0.7
0.5
10.4
7.7
52.3
8.1
2.8
28.5
15.7
1.1
1.1
2.6
B
BENTHIC SYSTEM
13. Carnivor. Fish 1.3
0.02
0.08
0.02
0.04
16. Sediment POC
2. Benthic Producers
8. Ben. Susp. Feeders 10.4
154.3
5.1
61.7
87.5
4.4
10. Benthic Inf. Carn. 0.5
1.1
5.1
11. Epifaunal Carnivores 0.5
1.1
2.4
1.5
0.9
2.4
3.4
108.8
7. Meiofauna 1.7
16.9
9. Deposit Feeders 3.2
19.3
59.2
32.6
8.2
7.7
C
BENTHIC SYSTEM
13. Carniv. Fish 1.3
0.02
0.08
0.02
0.04
16. Sediment POC
2. Benthic Producers
8. Ben. Susp. Feeders 1.2
121.7
8.2
85.2
28.3
8.6
10. Benthic Inf. Carn. 1.0
2.1
10.0
11. Epifaunal Carniv. 0.9
1.3
5.7
3.0
1.7
4.8
12.6
74.7
7. Meiofauna 1.2
11.6
9. Deposit Feeders 16.2
76.1
40.7
22.4
33.1
30.4
C 2
11. Epifaunal Carniv. 0.15
0.3
2.3
1.3
0.7
C 3
11. Epifaunal Carniv. 0.1
0.3
1.7
0.9
0.5

effect on the secondary and tertiary producers in the system, however, sufficient information concerning seasonal population fluctuations in many of the consumer compartments is unavailable to allow a comparison of seasonal carbon flow networks in the area. It is worth emphasizing some major qualitative variations in the system between the different seasons which will have the effect of either switching emphasis in certain flow pathways in parts of the network, or indeed eliminating some pathways and/or compartments. Thus the pelagic invertebrate carnivores, overwhelmingly represented by the medusae *Aurelia* and *Cyanea*, are present only from June to September (SCHNEIDER, 1989), and have no influence on their meso-zooplanktonic prey at other times of the year. Predation on the shallow infaunal benthic populations is similarly reduced during the winter months through the offshore migration of epifaunal invertebrate and fish carnivores (MÖLLER *et al.*, 1985; PIHL, 1989a, 1989b). Secondary production levels in the system will be lower during the winter, but no reliable data is available to assess the magnitude of such seasonal changes.

5. DISCUSSION

5.1. AN UNBALANCED ANNUAL BUDGET

The simplified box model of the SE Kattegat system presented here suggests some major imbalances within the system, most notably between the supply of particulate carbon from the pelagos and the demand from the infaunal benthos. If the calculated results presented here are taken to be realistic then the total demand by benthic consumers exceeds the potential supply at all depths. The total respiratory demand for the system reaches an area-weighted average of 270 $gC \cdot m^{-2} \cdot y^{-1}$, whereas the total consumption shows an average of 410 $gC\, m^{-2} \cdot y^{-1}$. The latter figure is a linear summation of consumption across all compartments and thus conceals a contribution from recycled carbon. Therefore, it would not necessarily be expected to balance the carbon input (STRAYER, 1988; SCAVIA, 1988), but the respiratory demand, being equivalent to known carbon losses from the system, might be expected to be in overall equilibrium with inputs. In fact it exceeds calculated inputs by some 25%, suggesting either an underestimation in some of the calculated sources or the addition of carbon to the system from other unestimated sources.

It should be noted, however, that no estimates of the supply of particulate and dissolved carbon entering the area via the exchange of water through the marine boundaries have been made. Whether this is a potential source or sink for carbon in the area is unknown. FLODERUS (1989), FLODERUS & HÅKANSON (1989) and RYDBERG *et al.* (1990) have suggested that considerable quantities of organic material form ephemeral detritus-rich mud blankets and are transported as a whole by resuspension processes from shallower to deeper areas within the Kattegat. Such resuspension events occur commonly in response to wind-driven turbulence throughout the year, but are particularly frequent during the autumn. Moreover, FLODERUS & PIHL (1990) have suggested that in the deeper waters trawling activity can significantly affect the frequency of resuspension events, and thus materially influence the distribution of fine, organic-rich material. Such processes are presently unquantified, but must be considered as possible agents for importing organics originating beyond their boundaries to the area.

The possibility that the measured primary production rate may be an underestimation of the true production in the area must also be considered. RICHARDSON & CHRISTOFFERSEN (1990) have recently reported a primary production rate of 290 $gC \cdot m^{-2} \cdot y^{-1}$ in an area some 40 km south of the study area, with over 30% of the summer production being concentrated below the pycnocline. Such sub-pycnocline production may not have been fully recorded during the present study, leading to a possible underestimation of the total production in the area. However, the area sampled by RICHARDSON & CHRISTOFFERSEN (1990) lies close to the entrance to the Öresund and in the vicinity of a front associated with the Baltic outflow, and those authors report the highest production levels from waters on either side of the front. The enhanced nutrient availability in such areas will undoubtedly increase the primary production values above those of adjacent, more stable waters. It should be noted, however, that the presence of such shallow and highly productive areas immediately to the south of the study area increases the likelihood of the advection of carbon detritus into the study area by the processes described above, or via the surface Baltic outflow which passes through the area (SVANSSON, 1984; RYDBERG *et al.*, 1990). An important imbalance was noted within the pelagic system in the flows to and from the meso-zooplanktonic compartment. The potential supply from autotrophic and heterotrophic sources was found to be nearly three times the estimated consumption. Even if considerable energy is lost through recycling within the microbial loop, the combined supply from phytoplanktonic and microbial sources greatly exceeds the assimilatory capacity of the recorded meso-zooplanktonic populations. Assessment of these populations in the area was not comprehensive, however, and was concentrated on specific copepod species for relatively restricted periods of time during the study period (TISELIUS, 1988). The data used may therefore underestimate meso-zooplanktonic consumption. However, the very high

TABLE 4

A comparison of the inputs to network compartments in the Chesapeake Bay and Baltic Sea systems (total carbon throughput, WULFF & ULANOWICZ, 1989) and the inputs to similar compartments in the SE Kattegat systems (mgC m^{-2} d^{-1}), separated into different water depth intervals for the benthos and carnivorous fish.

compartment	*Baltic*	*Chesapeake*	*Kattegat*		
Pelagic producers	570	1430	513		
Benthic producers	18	213	28		
DOC	77	499	202		
Suspended POC	300	1180	263		
Sediment POC	170	3380	344		
Plankton					
Pelagic bacteria	144	499	400		
Micro-zooplankton	168	490	240		
Meso-zooplankton	330	253	43		
Invertebrate carnivores	11	44	3		
Benthos					
			water depth (m)		
			< 13	13-22	> 22
Meiofauna	28	131	143	298	205
Suspension feeders	69	54	640	423	336
Deposit feeders	73	581	8	53	209
Infaunal and epifaunal carnivores	2	20	64	26	51
Nekton					
Planktivorous fish	10	7			13
Carnivorous fish	4	3	9	0.2	

Chesapeake is more stressed as a system than the Baltic proper. The analysis of the SE Kattegat presented here does not involve such computations, but some simple comparisons of the magnitude of flows between similar compartments in the various systems may suggest some conclusions as to its comparative status. The various compartments and flow paths defined for the Kattegat system were based on those defined by WULFF & ULANOWICZ (1989) in order to facilitate this further comparison. Table 4 lists the various total carbon throughputs to each compartment in the Baltic and Chesapeake systems with the inputs to each compartment in the SE Kattegat. These latter are not strictly comparable with the total throughputs of the other models, since they are derived directly from calculations based on observational data, whereas the throughputs include some computed recycling inputs to each compartment.

Nevertheless major differences between the inputs to comparable areas within each system are worth commenting on. Thus, the Chesapeake has considerably higher levels of both autochthonous and allochthonous inputs than either the Baltic proper or the SE Kattegat. The primary production in the Chesapeake is 2 to 3 times that in the other systems, the DOC is 7 times higher than in the Baltic and twice as high as in the Kattegat, and the POC in both the water column and the sediments is many times greater. Among the planktonic compartments the levels of bacteria and micro-zooplankton calculated for the Kattegat are roughly intermediate between those of the Chesapeake and the Baltic, but the meso-zooplankton and invertebrate carnivore levels are an order of magnitude below those of the other two systems. The predominance of the benthic suspension feeders in the Kattegat is very obvious when compared with the other systems, and benthic carnivores are also more important there than elsewhere. Deposit feeders in the Kattegat only approach the levels in the other systems in the deeper areas. Meiofauna appears to be somewhat more important, but these figures were crude estimates for the Kattegat. Both planktivorous and carnivorous fish appear to be a little less important in the Chesapeake than in the other two systems. In general, flow levels in the Kattegat system are intermediate between the low levels recorded for the Baltic and the very high levels in the Chesapeake.

In the Baltic the fish, mainly pelagic species, consume about 3.5% of the total available energy (ELMGREN, 1984). The same percentage is consumed by fish in the Kattegat, but an additional 4.3% is consumed by the invertebrate carnivores below a water depth of 22 m, where *Nephrops norvegicus* is a dominant species. Commercially important crustaceans are not available in the Baltic because of the hyposaline conditions.

Therefore, the most striking differences between the SE Kattegat and the other two systems is the

BRETT, J. R. & D.D. GROVES, 1979. Physiological Energetics. In: W.S. HOAR, D.S. RANDALL & J.R. BRETT. Fish Physiology, Vol. VIII. Bioenergetics and Growth. Academic Press, New York: 279-352.

BUCHANAN, J.B. & R.M. WARWICK, 1974. An estimate of benthic macrofaunal production in the offshore mud of the Northumberland coast.—J. Mar. Biol. Ass. U.K. **54:** 197-222.

CHAPMAN, C.J., 1980. Ecology of juvenile and adult *Nephrops*. In: J.S. COBB & B.F. PHILLIPS. Biology and management of lobsters. Academic Press, New York: 143-194.

CHRISTENSEN, H. & E. KANNEWORFF, 1985. Sedimenting phytoplankton as major food source for suspension and deposit feeders in the Öresund.—Ophelia **24:** 223-244.

CONAN, G.Y., 1978. *Life history, growth, production and biomass modelling of* *Emerita analoga, Nephrops norvegicus* and *Homarus vulgaris* (Crustacea, decapoda). Thesis, Ph.D., Univ. Calif. San Diego: 1-348.

CRISP, D.J., 1971. Energy flow measurements. In: N.A. HOLME & A.D. MCINTYRE. Methods for the study of marine benthos. Blackwell Scientific Publ., Oxford: 197-279.

EDLER, L., 1986. Produktion och näringsupplag av alger. Växtplanktonproduktionen i Laholmsbukten. In: R. ROSENBERG. Eutrofieringsläget i Kattegatt. Swedish Environmental Protection Agency, Stockholm. Rep. 3272: 66-77.

ELMGREN, R., 1984. Trophic dynamics in the enclosed, brackish Baltic Sea.—Réun. Cons. perm. int. Explor. Mer **183:** 152-169.

ENOKSSON, V., F. SORENSSON & W. GRANÉLI, 1990. Nitrogen transformations in the Kattegat.—Ambio **19:** 159-166.

FLEISCHER, S., L. STIBE & T. WACHENFELDT, 1978. Inledande undersökningar 1976-78 av grönalgen *Cladophora glomerata* i Laholmsbukten. Länstyrelsen i Hallands län, Halmstad: Sammanfattande Rapp. 1 (Mimeo).

FLODERUS, S., 1986. En uppskattning av mängden kol och kväve i strandade makroalger i Laholmsbukten. Arbetsrapport, Naturgeogr. Inst, Uppsala Univ.: 1-8 (Mimeo).

——, 1989. Sediment sampling evaluated with a new weighing function and index of reliability.—Hydrobiologia **176/177:** 451-464.

FLODERUS, S. & L. HÅKANSON, 1989. Resuspension, ephemeral mud blankets and nitrogen cycling in Laholmsbukten, SE Kattegat.—Hydrobiologia **176/177:** 61-75.

FLODERUS, S. & L. PIHL, 1990. Resuspension in the Kattegat: Impact of variation in wind and climate.—Est. coast. Shelf Sci. **31:** 487-498.

GERLACH, S.A., 1971. On the importance of marine meiofauna for benthos communities.—Oecologia **6:** 176-190.

GERLACH, S.A., A.E. HAHN & M. SCHRAGE, 1985. Size spectra of benthic biomass and metabolism.—Mar. Ecol. Prog. Ser. **26:** 161-173.

GRANÉLI, E., K. WALLSTRÖM, U. LARSSON, W. GRANÉLI & R. ELMGREN, 1990. Nutrient limitation of primary production in the Baltic Sea area.—Ambio **19:** 142-151.

HAGERMAN, L. & S.P. BADEN, 1988. *Nephrops norvegicus*: field study of effects of oxygen deficiency on haemocyanin concentration.—J. exp. mar. Biol. Ecol. **116:** 135-142.

HAGSTRÖM, Å., F. AZAM, A. ANDERSSON, J. WIKNER & F. RASSOULZADEGAN, 1988. Microbial loop in an oligotrophic pelagic marine ecosystem: possible roles of cyanobacteria and nanoflagellates in the organic fluxes.—Mar. Ecol. Prog. Ser. **49:** 171-178.

HUMMEL, H., 1985a. An energy budget for a *Macoma balthica* (Mollusca) population living on a tidal flat in the Dutch Wadden Sea.—Neth. J. Sea Res. **19:** 84-92.

——, 1985b. Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea.—Neth. J. Sea Res. **19:** 52-76.

JANSSON, B., W. WILMOT & F. WULFF, 1984. Coupling the sub-systems - The Baltic Sea as a case study. In: M.J.R. FASHAM. Flows of energy and materials in marine eco-systems. Plenum Publ., New York: 549-595.

JONSSON, P. & P. TISELIUS, 1990. Feeding behaviour, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates with different swimming behaviour.—Mar. Ecol. Progr. Ser. **60:** 35-44.

KAY, D.G. & A.E. BRADFIELD, 1973. The energy relations of the polychaete *Neanthes* (= *Nereis*) *virens* (Sars).—J. Anim. Ecol. **42:** 673-692.

KIØRBOE, T. & T.G. NIELSEN, 1990. Effects of wind stress on vertical water column structure, phytoplankton growth, and productivity of planktonic copepods. In: M. BARNES & R.N. GIBSON. Proc. 24th Europ. Mar. Biol. Symp. Aberdeen Univ. Press, Aberdeen: 28-40.

KIØRBOE, 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.

KIØRBOE, T., H. KAAS, B. KRUSE, F. MØHLENBERG, P. TISELIUS & G. ÆRTEBERG, 1990. The structure of the pelagic food web in relation to water column structure in the Skagerrak.—Mar. Ecol. Progr. Ser. **59:** 19-32.

LOO, L.O. & R. ROSENBERG, 1989. Bivalve suspension feeding dynamics and benthic-pelagic coupling in an eutrophicated marine bay.—J. exp. mar. Biol. Ecol. **130:** 253-273.

MCNEILL, S. & J.H. LAWTON, 1970. Annual production and respiration in animal populations.—Nature **225:** 472-474.

MÖLLER, H., 1979. Significance of Coelenterates in relation to other plankton organisms.—Meeresforsch. **27:** 1-18.

——, 1980. Scyphomedusae as predators and food competitors of larval fish. ICES CM L:32: 1-17 (Mimeo).

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.

NICHOLS, F.H., 1977. Dynamics and production of *Pectinaria koreni* (Malmgren) in Kiel Bay, West Germany. In: B.F. KEEGAN, O. CEIDIGH & J.S. BOADEN. Biology of benthic organisms. Pergamon, New York: 453-463.

NIELSEN, T.G. & T. KIØRBOE, 1990. Effects of a storm event on the structure of the pelagic food web with special emphasis on planktonic ciliates.—J. Plankt. Res. **13:** 35-51.

WINTER, J.E., 1969. Über den Einfluss der Nahrungskonzentration und anderer Faktoren auf Filtrierleistung und Nahrungsausnutzung der Muscheln *Arctica islandica* und *Modiolus modiolus*.—Mar. Biol. **4:** 87-135.

——, 1978. A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems.—Aquaculture **13:** 1-33.

WULFF, F. & R.E. ULANOWICZ, 1989. A comparative anatomy of the Baltic Sea and Chesapeake Bay ecosystems. In: F. WULFF, J.G. FIELD & K.H. MANN. Network analysis in marine ecology. Methods and applications. Springer, New York: 232-256.

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