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A Benthic Food Budget for the Grevelingen Estuary, The Netherlands, and a Consideration of the Mechanisms Causing High Benthic Secondary Production in Estuaries

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ABSTRACT

An annual food budget for the zoobenthos of a tidal estuary of 140 km^2 in The Netherlands is constructed. Although this budget is partly based on several questionable assumptions, the following observations seem reliable. Primary production in situ and import of organic detritus from the coastal sea appear to be the most important food sources. Detritus imported from salt marshes or other terrestrial systems is relatively unimportant.

This type of food budget, which also has been found in the Dutch Wadden Sea, is very different from the benthic food budgets of American estuaries where the benthos depend primarily on salt marsh or mangrove detritus and primary production in situ.

The mechanisms causing high benthic secondary production in estuaries are reviewed and categorized into three types (1) those in which the supply of dissolved nutrients from various sources causes high primary production; (2) those with supply of particulate organic matter from various sources to estuarine waters; and (3) those in which the shallow nature of the estuary causes rapid sinking of particulate organic matter, as well as rapid transport of particulate organic matter by turbulent diffusion.

INTRODUCTION

Estuaries are well known for their high benthic secondary production, and throughout the world they sustain important shell-fish cultures and fisheries. Their high benthic production is also reflected in the role estuaries play as nursery grounds for juvenile fishes and other nektonts, and in the multitude of shorebirds that feed in these areas.

The high benthic production of estuaries has been attributed to a number of food sources, primarily detritus from various macro-

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phytes (Schelske and Odum 1961; Odum 1971; De la Cruz 1973; Day et al. 1973). However, during a study of a Dutch estuary we found high benthic production in a water body with insignificant salt marshes and eelgrass beds. Apparently other mechanisms may also cause high benthic production values.

In this paper I propose a food budget in the form of a particulate organic carbon budget for the benthos of the Grevelingen estuary. In comparing this budget with similar budgets for other estuaries, the discussion centers on differences between these waters and the mechanisms causing high benthic secondary production in various estuaries.

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PARTICULATE ORGANIC CARBON BUDGET FOR THE BENTHOS IN THE GREVELINGEN ESTUARY

The Grevelingen estuary lies in the southwestern part of The Netherlands (Fig. 1) and has an area of about 140 km^2. Prior to our study the slight fresh-water input from the rivers Rhine and Meuse was cut off and tributaries of these rivers were dammed. During our study salinity did not fall below 15.0 °/₀₀ Cl^- (Peelen 1974). The average tidal amplitude is about 2.6 m, and the tidal currents have a maximum speed of 1.5-2.0 $m.sec^{-1}$ locally. Of the 140 km^2 4 km^2 are covered by salt marshes and 55 km^2 are tidal flats without erect vegetation. The remaining 81 km^2 of water have an average depth at low tide of 6 m, 9% of this area is deeper than 20 m, and the maximum depth is about 50 m.

Wolff and De Wolf (in press) estimated secondary production by the macrobenthos to be 50.3-57.4 g ash-free dry weight$\cdot m^{-2} \cdot year^{-1}$ (weighted average for the whole estuary). In the following discussion I use a value of 57.4 g ash-free dry weight based on the most probable values of these earlier data. An ash-free dry weight/carbon ratio of 1.9 (Winberg 1971) results in an estimate of about 30.3 g $C \cdot m^{-2}.year^{-1}$ (Table 1).

Reported values of salt-marsh production are often very high. Keefe (1972) and Gabriel and De la Cruz (1974) recorded aboveground net production values for *Spartina alterniflora* marshes ranging from 445 to 3300 g dry weight.$m^{-2}.year^{-1}$. European values range from about 200-1000 g dry weight.$m^{-2}.year^{-1}$ (Joenje 1974;

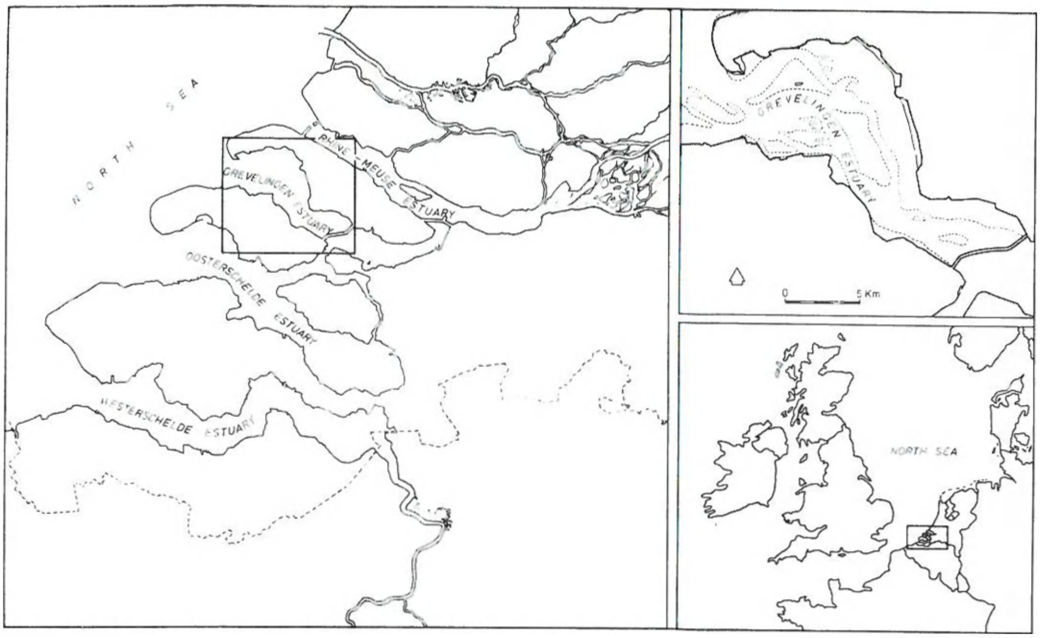

Fig. 1. Survey of the Grevelingen estuary.

Table 1. Weighted mean for the annual benthic secondary production in the Grevelingen estuary. Values from Wolff and De Wolf (in press) are divided by 1.9 to give carbon weight.

Species	Type of feeder	Amount
Hydrobia ulvae	(grazer)	2.4 g $C \cdot m^{-2} \cdot yr^{-1}$
Mytilus edulis	(filter-feeder)	8.5 " " " "
Cardium edule	(filter-feeder)	16.9 " " " "
Macoma balthica	(deposit-feeder)	0.5 " " " "
Arenicola marina	(deposit-feeder)	1.2 " " " "
All other macrobenthic species		0.8 " " " "

Ketner 1972; Wallentius 1973). For the 4 km^2 of salt marshes along the Grevelingen estuary this means a production of 100-500 g $C.m^{-2}.year^{-1}$. Teal (1962) reported that 45% of the net production of a Georgia salt marsh is exported as detritus to the open water system of the estuary, whereas the remainder is consumed in the marsh, while Nixon and Oviatt (1973) assumed that 23% is exported from a New England marsh. Along the Grevelingen estuary, however, part of the net production is transported by storm floods to levels above the normal spring high tide level. Part of this material is removed by the agencies maintaining the sea walls, and it is not known whether the remaining part ever returns to the estuary. Therefore it is assumed that 10-45% of the above-ground net production of the Grevelingen marshes is exported as detritus to the aquatic system and the salt marsh contribution to the aquatic part of the estuary is thought to be about 0.3-7 g $C.m^{-2}.year^{-1}$. Even if the complete production of the salt marsh went to the estuary, the yield would only be about 15 g $C.m^{-2}.year^{-1}$, an insignificant quantity.

Dense beds of *Zostera marina* in the Grevelingen estuary cover about 2 km^2 (unpublished observations Delta Institute) and less dense beds cover another 10 km^2 (Nienhuis 1970; unpublished observations). Mann's (1972, 1973) summary of what is known about the production of *Zostera marina* indicated that except for a high value of 1500 g $C.m^{-2}.year^{-1}$ based on extrapolation of short-term observations, all values range between 58 and 340 g $C.m^{-2}.year^{-1}$ and the *Zostera* primary production for the entire estuary is estimated at 696-4080 $ton.year^{-1}$. Grazing of the *Zostera* is negligible, except for feeding by wigeon (*Anas penelope*) and brent geese (*Branta bernicla*). Regular counts indicate that these species consumed maximally about 50 tons of *Zostera* expressed as carbon weight per year. The maximal amount available as detritus for the aquatic food web, then, is 5-30 g $C.m^{-2}.year^{-1}$. The actual figure is probably much closer to the former value than to the latter one.

For the tidal flats of the western Wadden Sea, Cadée and Hegeman (1974) determined the mean annual primary production of the benthic microalgae at 101 (± 38.5) g $C.m^{-2}.year^{-1}$. Since the tidal flats of the Grevelingen estuary are very similar in sediment composition and appearance to the flats of the Wadden Sea, and since the distance between the two areas is only 150 km, the benthic microflora in the Grevelingen estuary probably has a similar production. Since the area of tidal flats is 55 km^2, the total annual production is estimated at 5555 ± 2118 tons C. Averaged over the whole estuary, benthic microflora may contribute 41 ± 16 g $C.m^{-2}.year^{-1}$ to the benthic food web.

During our study primary production by phytoplankton was 179 g $C.m^{-2}. year^{-1}$ (Vegter personal communication): a value obtained in the main tidal channel where the depth of the channel was greater than the compensation depth. Since the compensation depth was similar to the tidal amplitude, corrections had to be made for the phytoplankton production over the submerged tidal flats. Assuming that all other conditions remain the same, we subsequently estimated the average phytoplankton production, the area of tidal flats included, to be about 130 g $C.m^{-2}.year^{-1}$.

The amount of organic matter supplied to the estuary by sewers may be estimated from the number of inhabitants contributing to untreated sewage. Klomp and Speksnijder (1973) estimated the number of inhabitants to be 11,625 and assuming that 52.5 g dry organic matter per capita is produced daily (Liebmann 1960), we arrive at a total supply of 223 ton dry matter to the Grevelingen area in 1972. This is equivalent to about 117 tons of carbon, i.e., a supply of about 1 g $C.m^{-2}.year^{-1}$. The supply by land drainage (5305 ha) is not known, but using the phosphorus budget proposed by Klomp and Speksnijder (1973), we arrive at a similar amount. Thus the total supply from land drainage and sewers is about 2 g $C.m^{-2}.year^{-1}$.

The total amount of particulate organic carbon from all sources is then 317-451 g $C.m^{-2}.year^{-1}$ (Table 2).

Table 2. Benthic food budget, expressed as particulate organic carbon, for the aquatic part of the Grevelingen estuary.

Food Source		Amount
Contribution salt marshes		0.3- 7 g $C\cdot m^{-2}\cdot yr^{-1}$
Production seagrass beds		5 - 30 " " " "
Production microphytobenthos		25 - 57 " " " "
Production phytoplankton		130 " " " "
Land run-off		2 " " " "
Import from North Sea		155 - 225 " " " "
	Total	317 - 451 g $C\cdot m^{-2}\cdot yr^{-1}$

The net transport of living plankton and detritus between the estuary and the North Sea is the only source or sink which is difficult to quantify. Seaward net transport of floating parts of phanerogams and macroalgae does occur but is probably unimportant because most winds blow landward. Entrapment of detritus by salinity stratification does not occur since the estuary always is well mixed. The only mechanism which may cause a landward net transport of detritus and may counteract a seaward transport, is the tidal mechanism described by Postma (1954, 1961, 1967) for the Wadden Sea. Postma (1954) estimated that the western Wadden Sea received about 80 g $C.m^{-2}.year^{-1}$ in 1950 by means of this mechanism, and De Jonge and Postma (1974) inferred that owing to the increasing pollution of the southern North Sea, this amount had increased to about 240 g $C.m^{-2}.year^{-1}$ in 1970.

If the same mechanism is acting in the Grevelingen estuary, Postma's (1954) method may be used to quantify its effect. From monthly observations (May 1967-April 1971) it was determined that the average concentration of dissolved phosphorus at three sampling localities well within the Grevelingen estuary was 3.35 μgat P.liter^{-1}. During the same period, the average concentration of dissolved phosphorus in the two entrance channels of the estuary was 2.76 μgat P.liter^{-1}. Hence, a gradient of 0.59 μgat P.liter^{-1} exists between the inner part of the estuary and its entrances. Therefore at high tide the surplus of dissolved phosphorus in the estuary amounts to $0.59 \times 0.8 \times 10^{12} \approx 0.47 \times 10^{12}$ μgat, or about 14.600 kg dissolved P. The high tide volume of the estuary is about 0.8×10^{12} liter.

This phosphorus surplus is exchanged during the tidal exchange with the North Sea, which is estimated at 7-10% per tidal cycle (Eysink 1974; D. Gersie personal communication). Thus 0.07-0.10 x 14.600 kg P = 1022-1460 kg of dissolved P is exchanged with the North Sea per tidal cycle. This flux of dissolved phosphorus towards the North Sea has to be balanced by the land runoff, estimated at 18.40 kg P.year^{-1} ≈ 26 kg P.tidal cycle^{-1} (Klomp and Speksnijder 1973), and a flux of particulate P from the North Sea towards the estuary as described by Postma (1961) of (1022-1460) - 26 = 996 - 1434 kg P.tidal cycle^{-1}, a value equivalent (De Jonge and Postma 1974; Manuels and Postma 1974) to about 31-45.000 kg C.tidal cycle^{-1}, or to 155-225 g C.m^{-2}.year^{-1}. Similarly the flux of particulate organic matter during the shorter period we studied the production of the macrobenthos, was computed from the P-values at 210-298 g C.m^{-2}.year^{-1}. Although these figures are subject to probable error, their substitution in Table 2 shows that the tidal transport of particulate organic matter is of paramount importance to the benthic community of the Grevelingen estuary. The value found may be compared to Terwindt's (1967) calculations that in the Oosterschelde estuary adjacent to the Grevelingen estuary some 0.2 - 0.3.10^{-6} tons of mud are deposited annually in an area of about 150 km^2. Assuming that on the average 5% of the mud consists of organic C (Manuels and Postma 1974), about 67 g C.m^{-2}.year^{-1} is deposited in this area. The difference from the Grevelingen estuary values may be due to the many uncertainties in the calculations and to the greater stretch of coastal water between the estuary and the mouth of the rivers Rhine and Meuse.

COMPARISON WITH OTHER ESTUARIES

Budgets of particulate organic carbon comparable to that for the Grevelingen estuary are not numerous. A similar budget for particulate organic phosphorus may be constructed for the Western Wadden Sea, The Netherlands, from data by De Jonge and Postma (1974) (Table 3). This budget is very similar to mine for the Grevelingen estuary.

Data from Day et al. (1973) may be used to construct a similar budget for the aquatic part of the estuarine system of Barataria Bay, Louisiana, USA (Table 4). Their data expressed as dry organic

Table 3. Benthic food budget, expressed as particulate organic phosphorus, for the western Wadden Sea, The Netherlands (from De Jonge and Postma 1974).

Food Source		Amount
Contribution salt marshes		insignificant
Contribution seagrass beds and macro algae		insignificant
Primary production *in situ* (phytoplankton and microphytobenthos)		$2\ g\ P \cdot m^{-2} \cdot yr^{-1}$
Land run-off and sewers		insignificant
Import from North Sea		$6\ g\ P \cdot m^{-2} \cdot yr^{-1}$
	Total	$8\ g\ P \cdot m^{-2} \cdot yr^{-1}$

Table 4. Annual budget of particulate organic carbon, for Barataria Bay, Louisiana (from Day et al. 1973).

Source and Sink		Amount
Contribution saltmarshes		$297\ g\ C \cdot m^{-2} \cdot yr^{-1}$
Production phytobenthos		244 " " " "
Production phytoplankton		209 " " " "
	Total	$750\ g\ C \cdot m^{-2} \cdot yr^{-1}$
Consumption in estuary		$432\ g\ C \cdot m^{-2} \cdot yr^{-1}$
Export to Gulf of Mexico		318 " " " "
	Total	$750\ g\ C \cdot m^{-2} \cdot yr^{-1}$

matter weights, have been divided by 2 to obtain carbon weights. A comparable budget probably could be established for the Georgia estuaries, where Teal (1962) and Odum and De la Cruz (1967) indicated an important contribution of detritus from the salt marshes and a net transport of particulate organic matter from the estuary to the shelf waters. Nixon and Oviatt (1973) proposed an annual energy budget for a marsh embayment in New England with a tidal range up to 3 ft (Table 5) and although their data are expressed as $kcal.m^{-2}.year^{-1}$, the behavior of the system they studied is similar to that of the estuarine systems in Louisiana and Georgia. Barsdate et al. (1974), who presented a carbon budget for Izembek Lagoon, Alaska, found a tremendous export to the Bering Sea of floating eelgrass, but did not mention possible import of suspended detritus. Odum and Heald (1975) described in qualitative terms the export of detritus from mangrove forests to nearby coastal and estuarine waters in Florida, USA. Their findings are similar to those of Golley et al. (1962) in a Puerto Rico mangrove forest.

Hence, a picture of two different types of estuaries arises, one deriving detritus from salt marshes, mangroves or eelgrass beds

Table 5. Annual energy budget for the Bissel Cove marsh embayment, New England (from Nixon and Oviatt 1973).

Source and Sink	Amount	
Contribution saltmarshes	240 – 470	$Kcal \cdot m^{-2} \cdot yr^{-1}$
Net immigration of fish and shrimp	3.5	" " "
Contribution from streams (dissolved organic matter)	15	" " "
Primary production phytoplankton and benthos	9,600	" " "
Total	9,858.5–10,088.5	$Kcal \cdot m^{-2} \cdot yr^{-1}$
Consumption within embayment	9,800	$Kcal \cdot m^{-2} \cdot yr^{-1}$
Storage and export to Narragansett Bay	58.5 – 288.5	" " "
Total	9,858.5–10,088.5	$Kcal \cdot m^{-2} \cdot yr^{-1}$

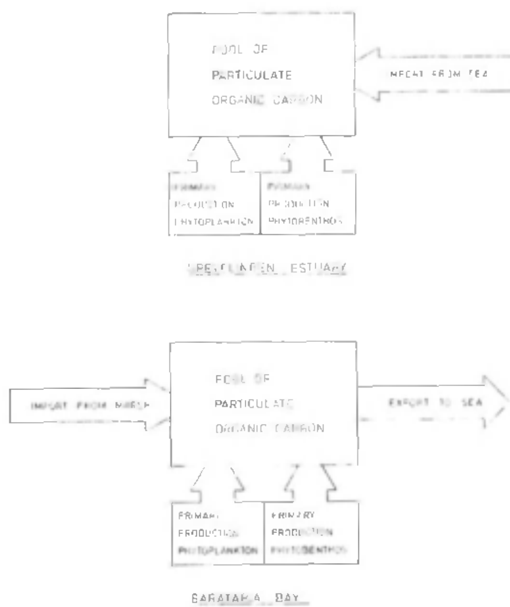

Fig. 2. The main characteristics of the benthic food budgets for the Grevelingen estuary, The Netherlands, and Barataria Bay, Louisiana, USA.

and fertilizing the adjacent sea with detritus, the other deriving detritus from the sea and not exporting detritus to any other system (Fig. 2).

These differences can be partly attributed to the following factors: (1) On the American coasts the marsh grass *Spartina alterniflora* occupies about two-thirds of the intertidal zone below the high water mark (Redfield 1972) while on European coasts, *Spartina maritima* and *S. townsendii* as well as other salt-marsh plants hardly descend below high tide level (Beeftink 1965). Thus, at relatively the same places where European estuaries show bare tidal flats American estuaries contain extremely productive *Spartina* marshes. (2) Detritus floating at the surface will move down a concentration gradient, unlike detritus kept in suspension by turbulent water movements which in tidal estuaries moves up the concentration gradient. Since in the European estuaries described here floating detritus is of little importance, inshore transport will predominate. In many American estuaries, however, the possible inshore transport of suspended detritus will be counteracted by the offshore transport of floating material, since its concentration in the estuary will be higher than in the coastal sea. (3) The European estuaries described here are characterized by onshore winds, whereas the American counterparts experience more offshore winds, which influence the transport direction of floating detritus. (4) The European estuaries possess tidal mechanisms that transport particulate organic matter in an inshore direction. The tidal range at Barataria Bay, Louisiana, and at Bissel Cove, New England (maximally about 0.9 m), may be too small to support this mechanism, but the tidal range in the Georgia marshes (about 2 m) should be sufficient for it. (5) The Atlantic Ocean along the American east coast is in general less rich in nutrients, and hence in phytoplankton, than the North Sea.

MECHANISMS MAINTAINING HIGH BENTHIC PRODUCTION

Schelske and Odum (1961) have already reviewed the mechanisms maintaining high productivity in estuaries in general, and pointed out that in the Georgia estuaries primary production is organized very efficiently in that production by *Spartina*, benthic algae and phytoplankton is largely complementary and is maintained on a high level year round. They considered rapid turnover of nutrients and release of dissolved nutrients by the sediment to be the mechanism maintaining this production. They also stated that the estuary acts as a nutrient trap through vertical mixing of waters of different salinities and biological removal of nutrients by the benthic fauna. They did not specify, however, the source of trapped nutrients. They excluded a fresh-water source of dissolved nutrients and an oceanic source of particulate organic matter and/or sediment, although Odum (1971) pointed to a marine origin of nutrients.

I propose that the following mechanisms support high secondary production in estuaries:

High Primary Production in situ

1. Supply of dissolved nutrients by river discharge (Ketchum 1967).--According to Riley (1967) and Pomeroy et al. (1972) this is a relatively rare phenomenon; clean rivers tend to flush the estuary and thus also decrease the amount of nutrients from other sources.

2. Supply of dissolved nutrients from deep offshore waters (Ketchum 1967; Riley 1967).

3. Supply of dissolved nutrients from sediments and interstitial waters.--This has been described by Schelske and Odum (1961) and by Pomeroy et al. (1965, 1972), who considered mainly chemical and microbiological processes. McRoy et al. (1972) described a mechanism by which submerged *Zostera* supplied dissolved phosphate from the sediment to the water. However, ultimately such a supply depends on an import of sediment or dissolved nutrients from some other source.

4. Rapid turnover of nutrients due to tidal action (Schelske and Odum 1961).

5. Supply of dissolved nutrients from sewage.

Import of Particulate Organic Matter

1. River discharge and land runoff containing fresh-water plankton and/or detritus (Copeland 1970; Meade 1972).--Windblown material may also be placed in this category (Darnell 1967).

2. Tidal mechanisms causing an inshore transport of marine plankton and detritus as described by Postma (1954, 1961, 1967) and Groen (1967).--This paper assumes that the mechanism also acts in the Dutch Grevelingen estuary. Although Pomeroy et al. (1972) attributed the high concentration of organic matter in the estuaries of Georgia to a supply from the marshes, the tidal import mechanism might also play a role in the Georgia estuaries.

3. Entrapment of particulate organic matter from various sources in a salt wedge system (Odum 1971; Meade 1972).

4. Tidal flushing from extensive salt marshes and mangrove forests (Teal 1962; Day et al. 1973; De la Cruz 1973; Golley et al. 1962).

5. Sewage.

None of these mechanisms excludes any of the others. Hence in some estuaries a very large food supply for the primary consumers may be created from various sources. However, no mechanism is common to all estuaries and coastal inlets, so that in arid regions there probably exist non-tidal coastal systems without any extra food source - like the open sea. In conclusion, estuaries and coastal inlets may be very rich in food for all primary consumers, but are not necessarily so.

Mechanisms providing a larger share of food to the benthos than to the zooplankton or the nekton seem to be related to either the shallow nature of estuaries or to the tidal currents.

It is generally accepted that the marine benthos feeds on that part of the surface production left behind by the pelagic consumers, i.e., bacteria, zooplankton and nekton (Sanders 1956; Steele 1973). Thus the amount of food available for the benthos should correlate negatively with the depth of the water column. Indeed, Rowe (1971) found a positive relationship between benthic biomass and surface productivity and a negative relationship between benthic biomass and depth in the deep sea; Spärck (1935) reached a similar conclusion for coastal waters. Hargrave (1973), however, established a significant positive relationship between surface primary production and amount of phytoplankton reaching the bottom, and a significant negative correlation between depth of the mixed layer and the amount of phytoplankton reaching the bottom. A correlation with total depth was not significant. Because Hargrave (1973) did not use data from very great depths in his regression analysis, and because in the other data his "remaining-depth" factor is relatively small in comparison to his "mixed-layer depth" factor, his conclusions are not contrary to the conclusion of Spärck (1935) and Rowe (1971). In shallow estuaries with average depths of only a few meters sinking phytoplankton therefore may form a large source of food for the benthos. However, living phytoplankton species usually have sinking rates under 1 $m.day^{-1}$ (Smayda 1970), so the zooplankton is left ample time to exploit the living phytoplankton. Tidal currents, on the other hand, make the phytoplankton production much more readily available to the benthos. In the Grevelingen estuary, for example, tidal currents in the range 0.1-1.0 $m.sec^{-1}$, would cause the vertical component of the turbulent diffusion coefficient to be approximately 50-500 $cm^2.sec^{-1}$, implying that surface production becomes available to benthic filter-feeders at a few meters depth within an hour or less. Furthermore, in conjunction with this vertical transport due to the tidal currents there is a continuous horizontal transport of plankton-loaded water. This places the benthos in a more favorable position than the zooplankton, because in such a situation the benthos is able to compete for food on an almost equal basis.

The possibility that the often high yield of benthic secondary production is partly caused by a larger share of r-selected species in estuaries than elsewhere, has not yet been investigated in detail. The unpredictable nature of the abiotic factors in many estuaries makes this a likely possibility.

Summarizing, the mechanisms causing high benthic secondary production in estuaries are: (1) supply of dissolved nutrients from various sources causing a high primary production; (2) supply of particulate organic matter from various sources and (3) the shallow nature of estuaries. The possible preponderance of r-selected species would convert this high production into a high yield.

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