The Westerschelde Estuary: two Food Webs and a Nutrient Rich Desert

O. HAMERLYNCK[1], J. MEES[1], J.A. CRAEYMEERSCH[2], K. SOETAERT[2],
K. HOSTENS[1], A. CATTRIJSSE[1] and P.A. VAN DAMME[3]

[1] Marine Biology Section, University of Gent
[2] Netherlands Institute for Ecology, Centre for Estuarine and Coastal Ecology
[3] Laboratory for Ecology, University of Leuven

Abstract.

Hummel *et al.* (1988) hypothesised the concomitant existence of two separate food chains in the Westerschelde: a photo-autotrophic coastal food chain in the marine part and a heterotrophic chain in the brackish part. The present study intends to re-examine the hypothesis on the basis of recently published data. Biomass gradients of the important functional units along an estuarine transect were observed to differ from those reported by Hummel *et al.* (1988) in some important aspects. The bimodal primary production gradient reported by Spaendonk *et al.* (in press) does not resemble the phytoplankton biomass curve, gradually increasing from the sea to Antwerp proposed by Hummel *et al.* (1988). Estimates of mesozooplankton biomass were found to be about an order of magnitude lower than reported by Hummel *et al.* (1988) and to display a completely different and more complex spatial pattern. However, the new gradient found is more in line with the hypothesis of two food chains than the gradient reported by Hummel *et al.* (1988). In the macrobenthos the biomass peak in the brackish part reported by Hummel *et al.* (1988) could not be confirmed. This finding does not falsify the original hypothesis as the function of this detritus dependent macrobenthic fauna is largely taken over by the hyperbenthic mysids, a group of previously unknown importance in the system. The existence of two food chains is also supported by the gradients observed in fish and epibenthic invertebrates, functional units not addressed by Hummel *et al.* (1988). In the zone between the two different food chains the dominant animal groups of the pelagic system have only a low biomass, this is the nutrient rich desert of the title. The zone upstream of the Dutch-Belgian border supports no hyperbenthos, no epibenthos and no mesozooplankton because of the low dissolved oxygen concentrations (less than 40% saturation), but there is a prominent peak in the microzooplankton. Clearly, in the brackish part, the richness of most functional units can only be explained on the basis of an input of organic matter from outside, consumed through a heterotrophic food chain. A second, smaller peak is observed close to the mouth of the estuary and is dependent on the primary production in the marine part of the estuary. Even for individual species this clear bimodal pattern can be observed. This disqualifies simplistic physiological models of estuarine succession as a basis for the findings. In the oxygenated part of the system there is no good general correlation between macrobentic biomass (mostly suspension-feeders) and primary production. Macrobenthic biomass is highly variable in this zone, probably as a result of local differences in current velocity maxima. The new data confirm the view of Hummel *et al.* (1988) but it is concluded that these authors must have formulated their hypothesis intuitively and could not have done so from the data available at the time.

1.– Introduction.

There has recently been renewed emphasis on food web theory in ecological studies (Lawton, 1989). Much of the thinking on this subject has been severely hampered by the lack of appropriate data on enough components of reasonably complex food webs. The claim by Briand and Cohen (1987), that food chains in two-dimensional areas such as estuaries tend to be shorter, was not confirmed by a recent, relatively well documented, study of an estuarine food web (Hall and Raffaelli, 1991). However, in studies of the properties of food webs (*e.g.* chain length, degree of omnivory, connectance, etc.) of a large area encompassing a diversity of habitats, such as an estuary, care should be taken not to confound different food chains or "compartments" *sensu* Paine (1980). Besides the theoretical aspects of compartmented webs regarding system stability (Pimm and Lawton, 1980), the elucidation of web infrastructure is a prerequisite for a correct evaluation of web properties (Rafaelli and Hall, 1992).

With the increased research effort into the dominant role of bacteria in secondary production in marine and estuarine ecosystems (Cole *et al.*, 1988) more insight has been gained into the distinction between detritus based food chains, termed heterotrophic (Smith *et al.*, 1989; Findlay *et al.*, 1991), where respiration exceeds production and phytoplankton dominated food chains, termed autotrophic, where primary production exceeds respiration. Unlike previously thought, the bacterial production does not simply result in a remineralisation of nutrients but also opens up a loop towards the zooplankton through the protozoans (Billen *et al.*, 1990). In estuarine systems it is thought this loop may support an important food chain sustained by the detrital organic carbon imported from the riverine system. Care should be taken with the term autotrophic food chain as around hydrothermal vents, methane sources, hypoxic parts of estuarine systems and elsewhere chemo-autotrophic food chains exist (*e.g.* Conway and McDowell, 1990). Photo-autotrophic would be a better term for the food chains termed autotrophic by Findlay *et al.* (1991).

Hummel *et al.* (1988) hypothesised the concomitant existence of two separate food chains in the Westerschelde. Their hypothesis was based on scattered and comparatively old data from the literature. In the meantime a concerted research effort has been developed by Dutch and Belgian scientists which has begun to make available more systematically collected and more reliable recent data for different functional units (phytoplankton, zooplankton, hyperbenthos, etc.) of the Westerschelde ecosystem. These data are now being used for the development and validation of an ecological model of the Westerschelde (Soetaert *et al.*, 1992; Herman *et al.*, unpublished). This paper will examine some of the input data for this model in relation to the Hummel *et al.* (1988) hypothesis. Additional data on the higher trophic levels in the Westerschelde, not to be included in the MOSES model are also presented.

2.- Materials and Methods.

The Westerschelde estuary (figure 1) is the lower part of the river Schelde. It is the last remaining true estuary of the Delta area and is characterised by a marked salinity gradient. The estuarine zone of the tidal system extends from the North Sea (Vlissingen) to Antwerp, 80 km inland. Further upstream the system can be termed riverine, though the tidal influence extends to Gent. The water in the estuarine part is virtually completely mixed and the residence time in the brackish part is rather high: about 60 days (Soetaert and Herman, submitted). Consequently fresh water (average inflow 100 $m^3 s^{-1}$) dilution is gradual and downstream transport is relatively slow. Shifts in salinity zone distribution occur in accordance with seasonal variations in the freshwater inflow. The abiotic environment is discussed in Heip (1989) and Eck *et al.* (1991). The estuary carries high pollution loads, both in anorganic and organic contaminants. The riverine part is anoxic throughout most of the year (Herman *et al.*, 1991).

Spatially the estuarine system under consideration in the present study was divided into 12 compartments according to the MOSES model (Soetaert *et al.*, 1992). The MOSES model contains an extra compartment in the riverine system. Therefore the 12 estuarine compartments are numbered 2 to 13 when going from Antwerp to the North Sea (figure 1). Functionally the units considered are phytoplankton (Spaendonk *et al.*, in press), zooplankton comprising mesozooplankton, benthic larvae and part of the microzooplankton, *i.e.* Rotatoria and *Noctiluca miliaris* (Soetaert and Rijswijk, in press), macrobenthos (Craeymeersch *et al.*, 1992), hyperbenthos (Mees and Hamerlynck, 1992; Mees *et al.*, in press a), epibenthos and fish (Hamerlynck *et al.*, in press). The reader is referred to these publications for detailed descriptions of the sampling methodologies. Table 1 shows a matrix of the spatial compartments and the functional units for which data were available.

The primary production data are based on fortnightly measurements taken in 1989 (Spaendonk *et al.*, in press). The zooplankton data are annual means from approximately fortnightly samples from April 1989 through March 1991 (Soetaert and Rijswijk in press). The macrobenthos data refer to a stratified random sampling in the autumn of 1990 according to the grid shown in figure 2.

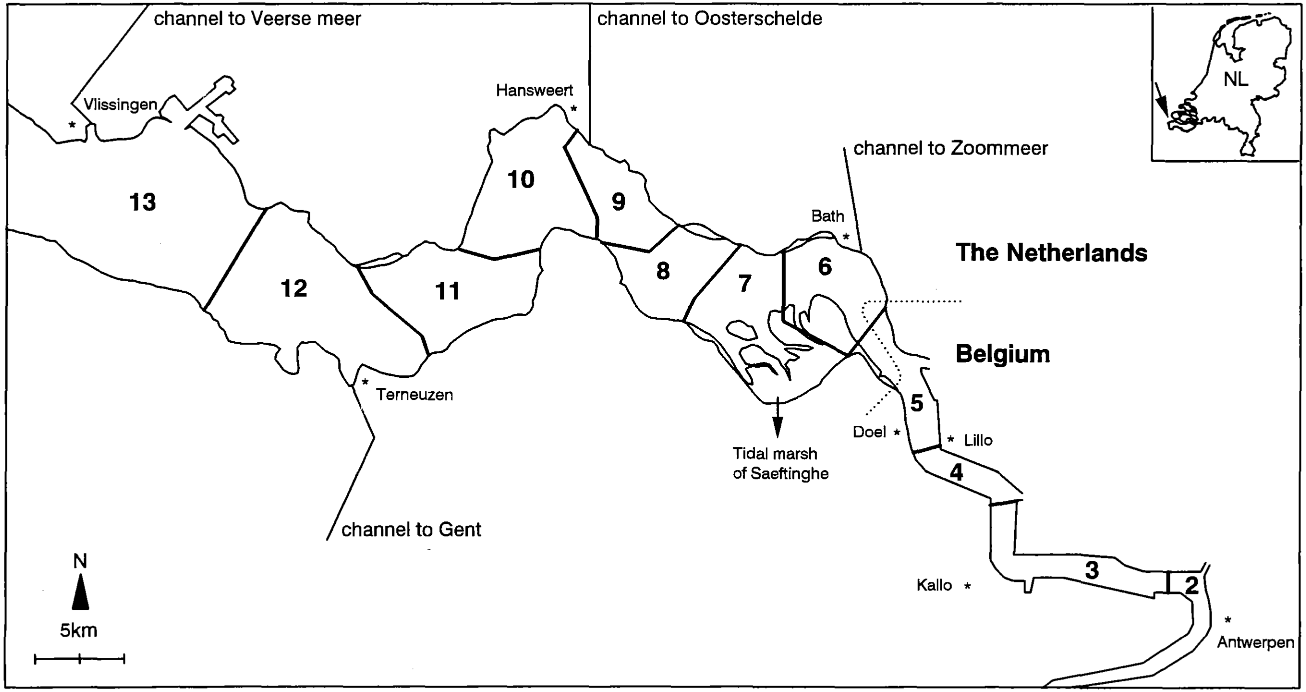
channel to Veerse meer
channel to Oosterschelde
Vlissingen
Hansweert
channel to Zoommeer
NL
13
10
9
Bath
The Netherlands
12
11
8
7
6
Belgium
5
Terneuzen
Doel
Lillo
Tidal marsh of Saeftinghe
4
channel to Gent
N
3
2
Kallo
Antwerpen
5km

Fig. 1.

Table 1

Compartment	2	3	4	5	6	7	8	9	10	11	12	13
Zooplankton	•	•	•	•	•	•	•	•	•	•	•	•
Primary production	•		•	•	•	•		•	•	•	•	•
Macrobenthos					•	•	•		•	•	•	•
Hyperbenthos	•	•	•	•	•	•	•	•	•	•	•	•
Epibenthos & fish			•	•	•	•	•	•	•	•	•	•

The strata were intertidal, subtidal and gully (more than 10 m below Mean Tidal Level) stations. During the macrobenthos survey no data were collected upstream of compartment 6, but it is known that in the upstream (hypoxic) zone only some oligochaetes survive (P.M. Meire, pers. comm.). For the hyperbenthos the data are the averages per station of the 1990 seasonal data reported in Mees *et al.* (in press a). The area upstream of compartment 6 was explored for hyperbenthos in March, April and May 1990 and in August 1991 but no animals were found. The epibenthos and fish data are annual means based on monthly samples collected in 1989. The data in compartments 4 and 5 refer to samples collected from the intake screens of Doel power station. Between April and July virtually no fish were recorded in this area (P.A. Van Damme, unpublished).

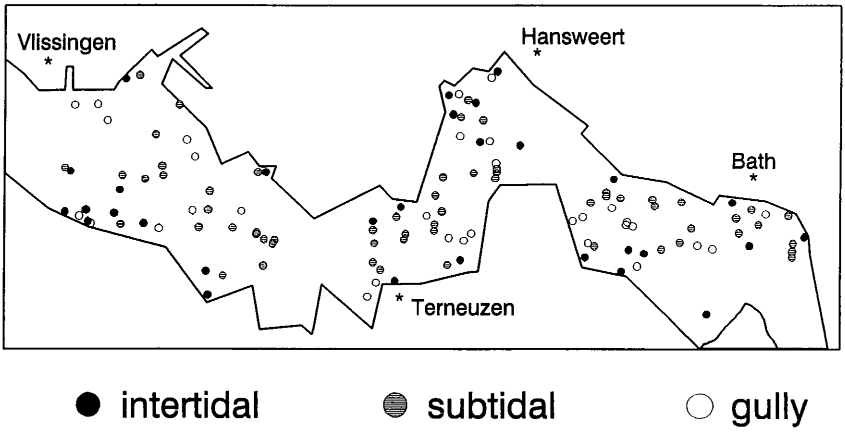

Fig. 2.

Values reported as Ash-free Dry Weight (ADW) were converted to g C using the same 0.4 conversion factor as in Hummel *et al.* (1988). Dry Weight data from the zooplankton study (Soetaert and Rijswijk, in press) were first converted to ADW by subtracting 10%.

3.– Results and discussion.

The results of the present data compilation and the biomass patterns reported by Hummel *et al.* (1988) are shown in Figs. 3 through 7.

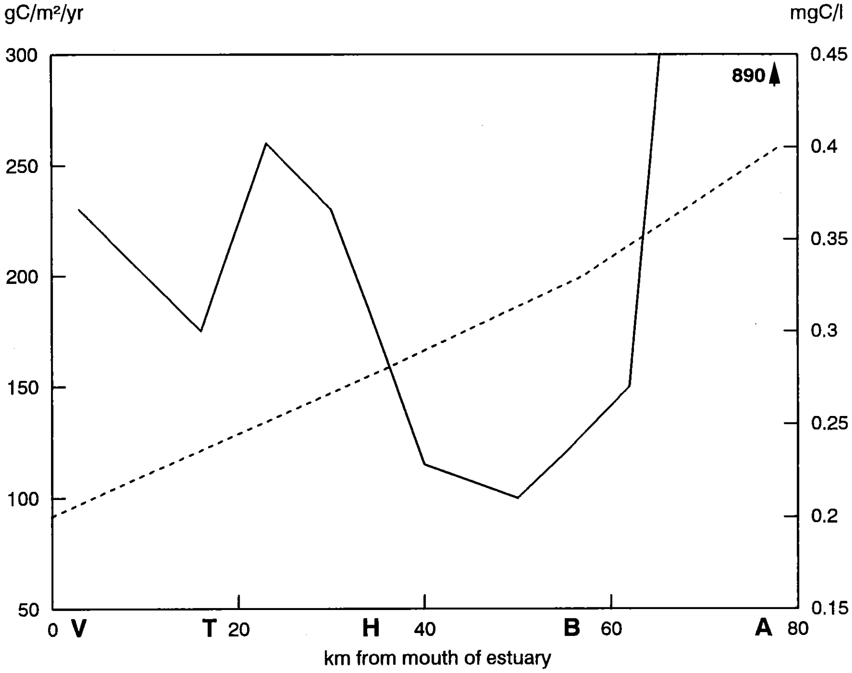

Fig. 3.

Besides proposing the two food chain hypothesis Hummel *et al.* (1988) also split the tidal part of the river into three zones: a fresh water tidal zone from Gent to Antwerpen which falls outside the scope of the present study, a brackish tidal zone (Antwerpen to Hansweert) and a marine tidal zone (Hansweert to Vlissingen). This second division was confirmed in the community structure of the zooplankton (Soetaert and Rijswijk, in press), the macrobenthos (Meire *et al.*, 1991), the hyperbenthos (Mees and Hamerlynck, 1992; Mees *et al.*, in press a) and the epibenthic invertebrates and fishes (Hamerlynck *et al.*, in press) and therefore seems very robust.

Though it is difficult to compare chlorophyll *a* concentrations from Hummel *et al.* (1988) with production figures given in Spaendonk *et al.* (in press), these authors also provide peak concentrations of chlorophyll *a* at a few stations which broadly confirm the link between phytoplankton biomass, expressed as chlorophyll *a* concentrations and primary production. Peak concentrations in the marine part (Hansweert) are higher than in the brackish part (Bath), but the biomass peak in Antwerpen is 10 to 20 times higher than those peaks (Spaendonk *et al.*, in press). In the Hummel model phytoplankton biomass was essentially increasing from the mouth up to Antwerpen even if they also stated that primary production was low in the turbid brackish zone (figure 3). According to Spaendonk *et al.* (in press) the high primary production around Antwerpen in 1989 was mostly due to salinity intolerant freshwater species that would not survive transport to the turbid brackish zone. In the rest of the estuary primary production was found to be essentially light limited. However, as there may be a high variability in the patterns of chlorophyll *a* and primary production among years, more data are still required to come to more robust conclusions regarding this functional unit in the Westerschelde.

For the zooplankton (which in their definition corresponds to the mesozooplankton) Hummel *et al.* (1988) also reported a gradual increase in biomass from Vlissingen to Antwerpen (and a steep decline further upstream). Besides the fact that the biomass reported by Hummel *et al.* (1988) seems an order of magnitude too high (figure 4a) (they even reported more zooplankton than phytoplankton in the brackish part, possibly their zooplankton data refer to the spring bloom only?), a very clear bimodal pattern in mesozooplankton biomass could be found with the peak in the brackish part (predominantly *Eurytemora affinis*) about double (figure 5a) the peak at the mouth of the estuary (a mixture of coastal species). The mesozooplankton decreases rapidly east of Bath as a consequence of hypoxia. The peak in primary production and the peak in *Eurytemora affinis* are separated by about 30 km. In between (figure 5b) there is a clear peak in the microzooplankton—as quantified by Soetaert and Rijswijk (in press)—, which in this part of the system consists mostly of Rotifera, a group relatively resistant to hypoxia and an essential link for opening up the microbial loop (Azam *et al.*, 1983) for higher trophic levels. According to Fenchel (1988) the bacterial production is consumed by heterotrophic nanoflagellates and protozoans (all associated to the particulate detritus), which in turn are taken by ciliates, heterotrophic dinoflagellates and Rotifera.

A clear representative of the coastal food chain in the zooplankton are the meroplankton (planktonic larvae of benthic animals) which decrease gradually from the mouth to the brackish part (figure 5c).

A trend line through the macrobenthos biomass (figure 4b) would more or less conform to the bimodal pattern reported by Hummel *et al.* (1988) except that the average biomass in the marine part reported in the present study is about four times higher than the biomass in the brackish part. Hummel *et al.* (1988) reported a 1.5 times higher mean biomass in the brackish part than in the marine part. Even going back to the original data used by Hummel *et al.* (1988) this higher peak in the brackish zone could not be retrieved. It is well documented

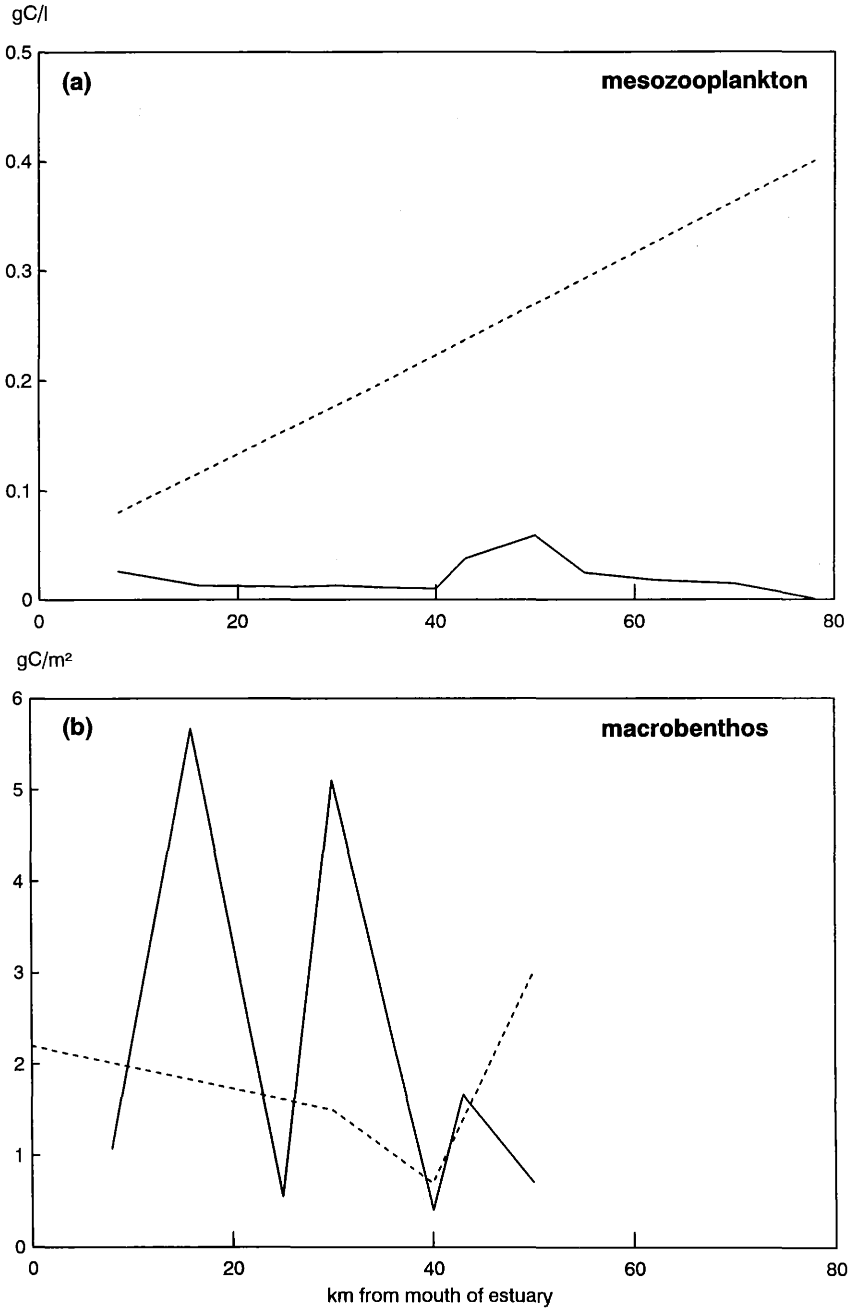
gC/l
0.5
0.4
0.3
0.2
0.1
0
(a)
mesozooplankton
0
20
40
60
80
gC/m2
6
5
4
3
2
1
0
(b)
macrobenthos
0
20
40
60
80
km from mouth of estuary

Fig. 4.

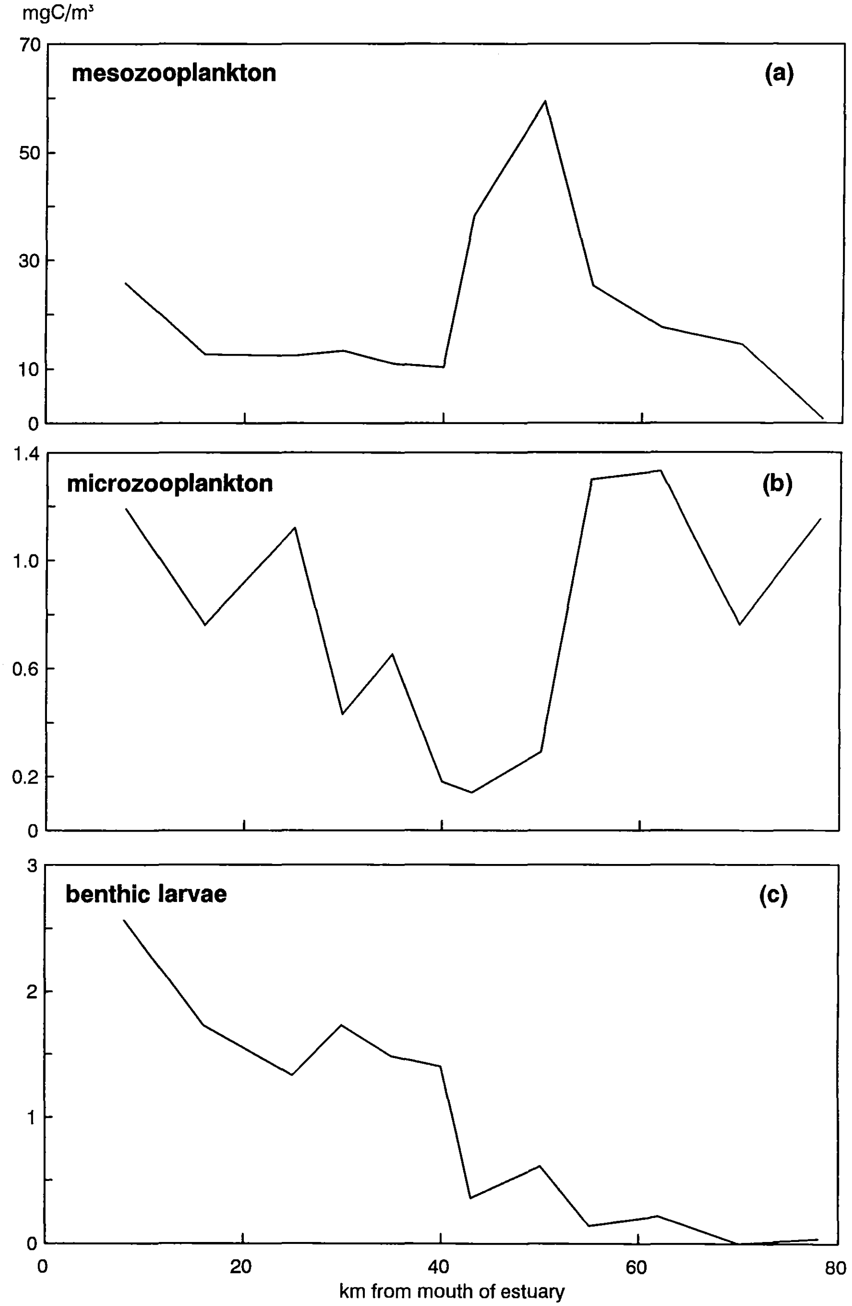
mgC/m³
70
50
30
10
0
mesozooplankton
(a)
1.4
1.0
0.6
0.2
0
microzooplankton
(b)
3
2
1
0
benthic larvae
(c)
0
20
40
60
80
km from mouth of estuary

Fig. 5.

that the macrobenthos in the brackish part is dominated by deposit-feeders dependent on sedimenting detritus for their food supply (Meire *et al.*, 1991). In the marine part the suspension-feeders dominate and these depend mostly on primary production filtered from the water column (Herman and Scholten, 1990). In spite of this, there does not seem to be a good correlation between primary production and macrobenthic biomass in the marine part. Though both rise steeply west of Hansweert there is a primary production peak spatially coinciding with a deep macrobenthic biomass trough at about 25 km from the mouth, east of Terneuzen. The variability in macrobenthic biomass in the marine part seems to be extremely high and would at first sight seem to make any conclusions about this functional unit impossible. However, suspension-feeders do not only need primary production, they also need relatively stable sediments and not too many indigestible particles in the water column. They therefore prefer areas with current velocities below 0.6 $m\,s^{-1}$ (Dijkema, 1988). Preliminary data from the 2D hydrodynamical model of the Westerschelde (Portela *et al.*, 1992) suggest the two peaks coincide with two compartment subareas (both at the outer curve of a relatively sharp turn in the main ebb channel) where current velocities are consistently lower than in other parts of the marine zone (Ramiro Nevez, pers. comm.).

The hyperbenthos has only recently been discovered to be an important component of the Westerschelde ecosystem, both structurally (Mees and Hamerlynck, 1992; Mees *et al.*, in press a) and functionally (Mees *et al.*, submitted a). Most of the biomass pattern shown in figure 6a consists of Mysidacea. Coming from the sea a first peak in hyperbenthos biomass occurs in the vicinity of Hansweert. A second, larger peak coincides with the trough in primary production and the copepod peak in the vicinity of Bath. It is at present unclear what may be the cause of the bimodality within the peak in the brackish part. Some of this may be smoothed out when true annual means, based on the monthly samples taken (Mees, unpublished) instead of the seasonal data reported here, become available. Alternatively the presence of the large tidal marsh of Saeftinghe or some aspect of the hydrodynamics in the brackish part may be involved. Within some species groups a clearly bimodal pattern, with a peak close to the mouth of the estuary and a second peak in the brackish part, can be observed, an example are the gammaridean amphipods (figure 6b).

Data on fish and epibenthic invertebrates were also not available to Hummel *et al.* (1988). The brown shrimp *Crangon crangon* is the dominant epibenthic invertebrate in the system (Hamerlynck *et al.*, in press) and both the adult shrimp (figure 7a) and the hyperbenthic living juvenile postlarval shrimp of less than 20 mm total length (figure 6c) display a clearly bimodal pattern with a smaller peak close to the mouth of the estuary and a large peak in the brackish part. The biomass pattern of the demersal fish is rather similar to the pattern in the adult

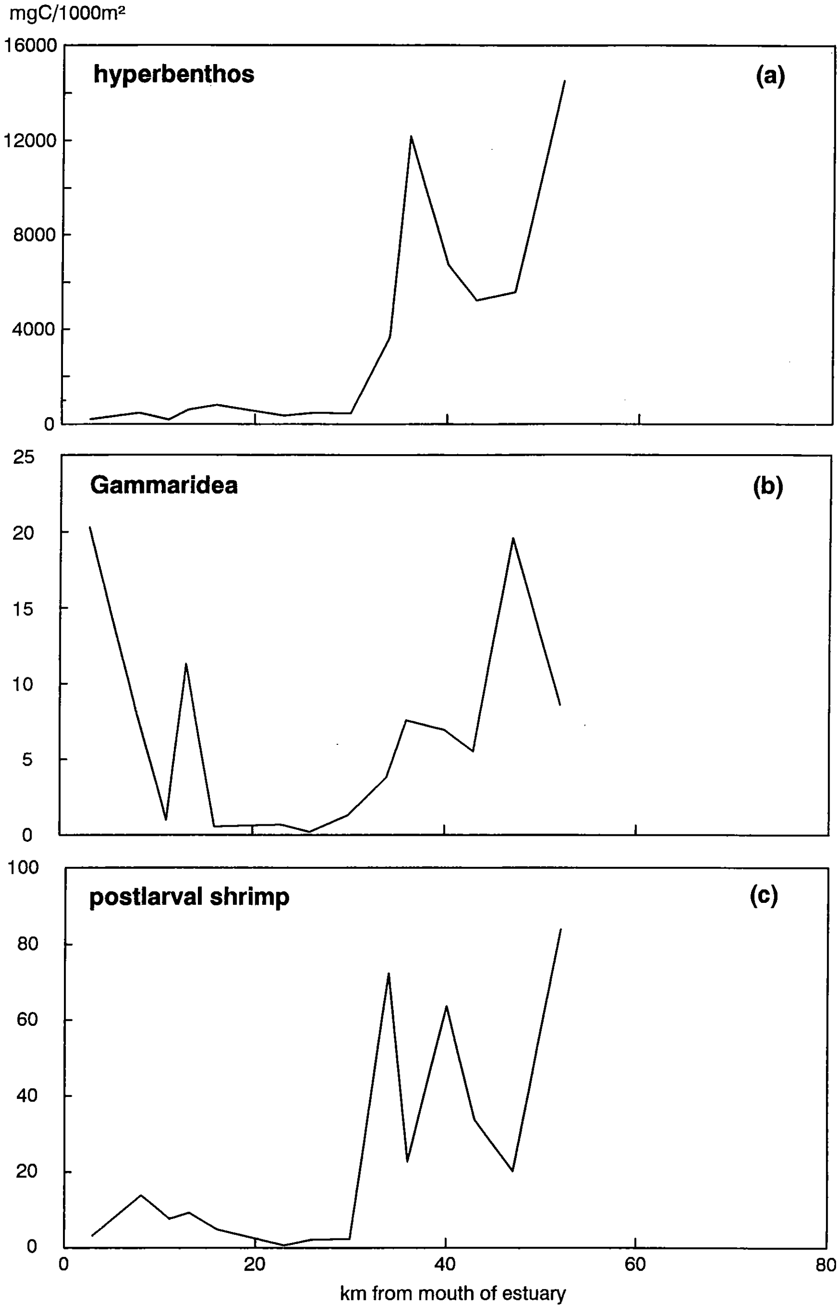
mgC/1000m²
16000
12000
8000
4000
0
hyperbenthos
(a)
25
20
15
10
5
0
Gammaridea
(b)
100
80
60
40
20
0
postlarval shrimp
(c)
0
20
40
60
80
km from mouth of estuary

Fig. 6.

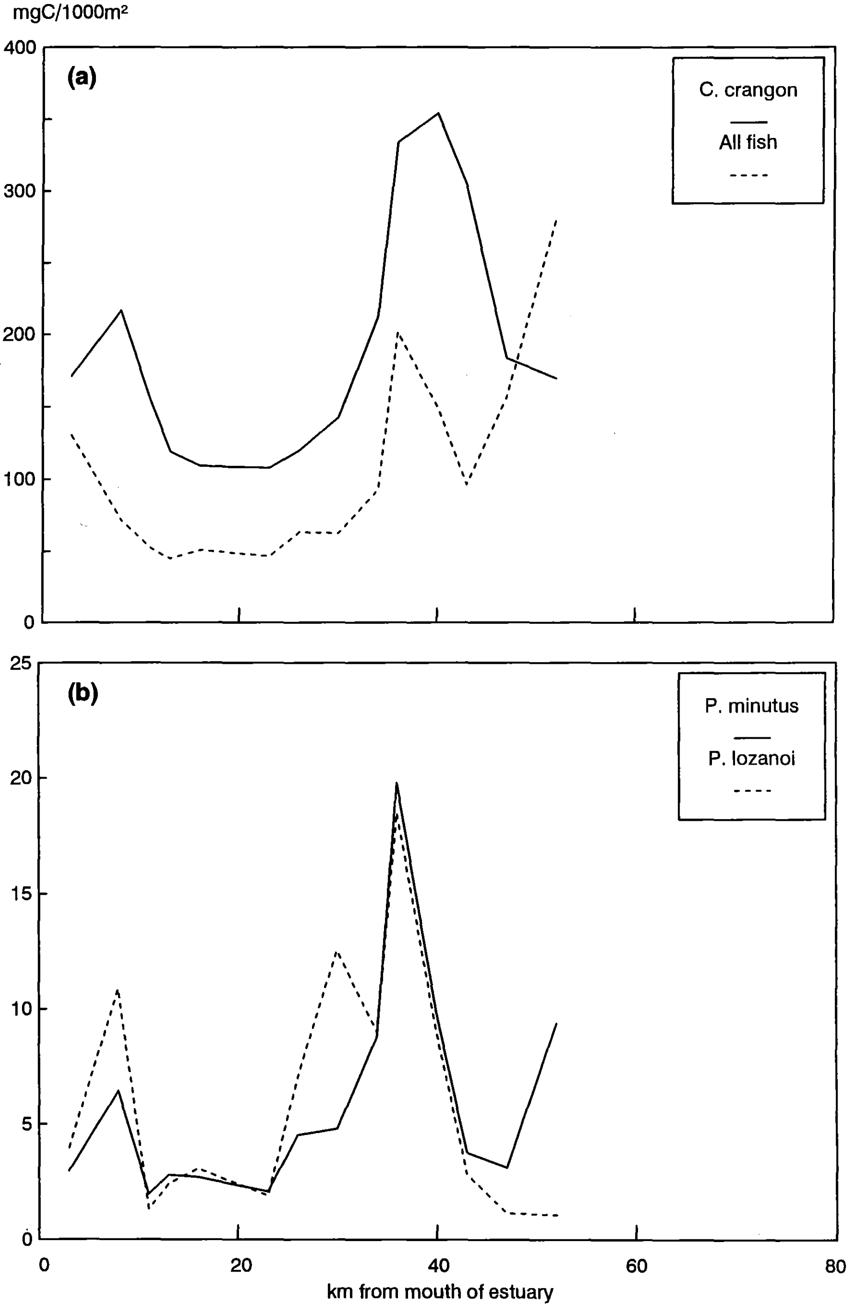
mgC/1000m2
400
300
200
100
0
(a)
C. crangon
All fish
25
20
15
10
5
0
(b)
P. minutus
P. lozanoi
0
20
40
60
80
km from mouth of estuary

Fig. 7.

shrimp (figure 7a). The two-peaked structure within in the brackish part is very similar to the observed pattern in the hyperbenthos (figure 6a). Possibly the fish fauna is entirely dependent on the hyperbenthos in this part of the system. Within the fish the dominant components are flatfish and gobies (Hamerlynck *et al.*, in press). Within the gobies the bimodal pattern is clear, both in *Pomatoschistus minutus* and *Pomatoschistus lozanoi* (figure 7b).

At present there are insufficient data on piscivorous birds to extend the analysis to that unit (Stuart *et al.*, 1990). Also, though anecdotal observations suggest seals are predominantly recorded around the Hooge Platen close to the mouth and on the Plaat van Valkenisse in the brackish part, as for the birds, coverage in the middle part of the estuary is too low to allow any firm conclusions to be drawn at present.

The results of the present study suggest that there are indeed two separate food chains in the Westerschelde as suggested by Hummel *et al.* (1988) and that a bimodal pattern of biomass distribution along the estuarine gradient is present, at least in the pelagic functional units. This pattern propagates through to the higher trophic levels. It is unclear how Hummel *et al.* (1988) arrived at their hypothesis from the data they had compiled. Hummel *et al.* (1988) stated that most of the biomass trends found show an increase from the sea to Antwerpen and that this may seem contradictory. They claim this contradiction will be explained in § 3.3.1 of their paper, but such a section can not be found.

There seems to be no gradual transition between the two purported food chains and they are separated by an intermediate "desertic" zone of over 20 km width. As an explanatory mechanism it is suggested, in accordance with Hummel *et al.* (1988), that the richness of brackish part is supported by a detritus based food chain. Virtually all of the non-refractory organic material in this zone would be either re-mineralised by the intense heterotrophic bacterial activity (Goossen *et al.*, 1992) or consumed by the zooplankton and the hyperbenthos, either directly or through the microzooplankton. Part of the material also settles on the bottom and sustains the deposit-feeding macrofauna. Possibly part of the energy requirements of shrimp are also sustained directly by detritus (or detritus plus bacteria and other micro-heterotrophs). This "second trophic level" in turn supports the rich community of epibenthic invertebrates (crabs and shrimp) and fish.

In the "desertic" zone the remaining organic matter is presumably mainly refractory. There is still a surplus of nutrients available and primary production is relatively high. Possibly as a consequence of high current velocities this primary production cannot be used very efficiently by the macrobenthos, except in a few relatively low turbulence sites where the suspension-feeders thrive. Still, it remains unclear why the zooplankton is not capable of exploiting the primary production in this zone.

Towards the mouth of the estuary primary production remains high and a coastal food chain flourishes. At the second trophic level species composition differs substantially in some groups, *e.g.* the zooplankton (Soetaert and Rijswijk, in press) and the hyperbenthos (Mees *et al.*, in press b). At the next trophic level the dominant species in both food chains are rather similar. That the observed bimodal pattern is caused by the underlying food chains and not by the physiologic limits of the respective organisms can be seen from the distribution in shrimp and gobies where the bimodal pattern can be observed within single species. Secondary support for the subordinate (if any) role of physiological limitation is provided by the fact that *Neomysis integer* has its peak distribution at much higher salinities in the Westerschelde than in the other European estuaries (Mees *et al.*, submitted b). Fecundity and growth in the Westerschelde are comparable or higher than those recorded in the other areas (Mees *et al.*, submitted b) indicating that the animals are not particularly stressed.

The role of the tidal marshes within the brackish part is less clear at present. At high tide they are intensively used by both hyperbenthic crustaceans (Cattrijsse *et al.*, in press; Mees *et al.*, in press b) and juvenile stages of fishes (Cattrijsse, unpubl.; Frid and James, 1988) and may thus form an integral part of the food web of the estuary. Logically, as tidal marshes are sinks for mud they should be net importers and not net exporters of organic matter. This high input of organic matter may be one of the attractants for the mobile fauna. Presumably added to that there is a substantial primary production by the diatom phytobenthos in the sheltered tidal creeks. It is also possible that there may be a qualitative edge to foraging in a tidal marsh related to the characteristic lipid quality reported for a nearby coastal marsh by Hemminga *et al.* (1992). Several mysid species, both coastal zone species and estuarine endemics, move into the tidal marshes to release their larvae (Mees *et al.*, in press b). In view of the high densities of fish and shrimp in the marsh (Cattrijsse, unpublished), instead of being a strategy of predator avoidance, this behaviour may also be related to food quality.

The obvious next step for a better understanding of the system and especially of its characteristic heterotrophic food chain in the brackish part is the detailed investigation of the link between the bacterial production and the higher trophic levels. Are it really the detritus-associated bacteria that form the basis of the food chain and are they consumed as such by the next links, *i.e.* the mesozooplankton and the mysids? It seems unlikely that copepods and mysids, in view of their short and uncomplicated digestive systems are able to incorporate unmodified plant detrital material with its characteristic C/N ratio to a great extent. However, it is also known that mysids possess cellulases (Mann, 1988) so the alternative hypothesis, namely that bacteria and metazoa compete for the same detritus can as yet not be ruled out. The heavily polluted Westerschelde may be a particularly interesting system for the analysis of the energy transfers under consideration here because some of the important functional units are spatially segregated due to the gradient in dissolved oxygen (and not as a result of transport processes because of the high residence time of the water). This should facilitate the analysis of the underlying processes.

4.- Conclusions.

Except for the bimodality in the macrobenthos biomass reported by Hummel *et al.* (1988) none of the patterns in their other functional units were suggestive of the existence of two separate food chains. They have therefore probably proposed their model intuitively. As is often the case they were right but for the wrong reasons.

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