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COMPARISON OF PLANKTON ASSEMBLAGES OF IDENTICAL SALINITY RANGES IN ESTUARINE TIDAL, AND STAGNANT ENVIRONMENTS II. ZOOPLANKTON*

by

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CONTENTS

I. INTRODUCTION

In a previous paper (Bakker & de Pauw, 1974), a comparison was made between the phytoplankton of the brackish water region of the Westerschelde estuary and Lake Veere, southwestern Netherlands. The present study deals with a comparison of the zooplankton of these regions.

Lake Veere was mesohaline (6 to 10‰ Cl′) during the years 1965 and 1966 and polyhaline (10 to 14‰ Cl′) during following years. As in the previous communication we have choosen the 6 to 10‰ and

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10 to 14‰ Cl′ periods of Lake Veere as a basis for comparison with the areas of the same chlorinity of the Westerschelde.

We are aware that comparison of the mesohaline period 1965–1966 of Lake Veere with the mesohaline area of the Westerschelde, investigated during 1972 and 1973, is perhaps not fully justified. Nevertheless, the comparison of the zooplankton of these waters seemed promising, as the results of the phytoplankton study provided strong arguments to extend the investigations in this direction.

Our aim is to compare a brackish water tidal area with a stagnant brackish water of the same salinity in relation to zooplankton species composition and abundance. Also other differences in environmental factors than salinity will be discussed in view of their influence on the zooplankton in both areas.

Acknowledgements.—Thanks are due to our assistants E. Biebout and W. J. Phaff and to A. A. Bolsius for the preparation of the figures.

II. METHODS

Plankton samples were collected on board of the R.V. "Jan Verwey" with a Pleuger pump (type no 64) with a capacity 200 l/min. As a maximum 200 litres of water were filtered through 63 μm gauze. This mesh size is small enough to retain most of the rotifers (abundant in Lake Veere) and naupliar stages of copepods (present in both areas). It is well known that a great variability may be found between replicate zooplankton samples by whatever technique used. Patchiness phenomena as well as inadequacies of sampling technique are the main causes. Pumping of water at the choosen capacity however, has given rather reliable results for most small zooplankton species. In Lake Veere numbers of adult copepods might be somewhat too low owing to avoiding movements of the animals. Avoidance behaviour plays a minor role in tidal areas where strong water movements level down the influences of pumping. With Raymont & Carrie (1964) we state that patchiness and tidal disturbances during pumping may cause far greater variation in the samples than pumping itself. A detailed analysis of the results of the pumping method used will be dealt with elsewhere.

Samples were taken once a month. In the turbulent tidal area of the Westerschelde only sampling of surface and near-bottom layers (depth approximately 20 metres) was performed to study the vertical zooplankton distribution. One sampling station was selected in the polyhaline zone, 2 in the mesohaline zone of the estuary (Fig. 1). Samples always were taken during the same tidal phase. When

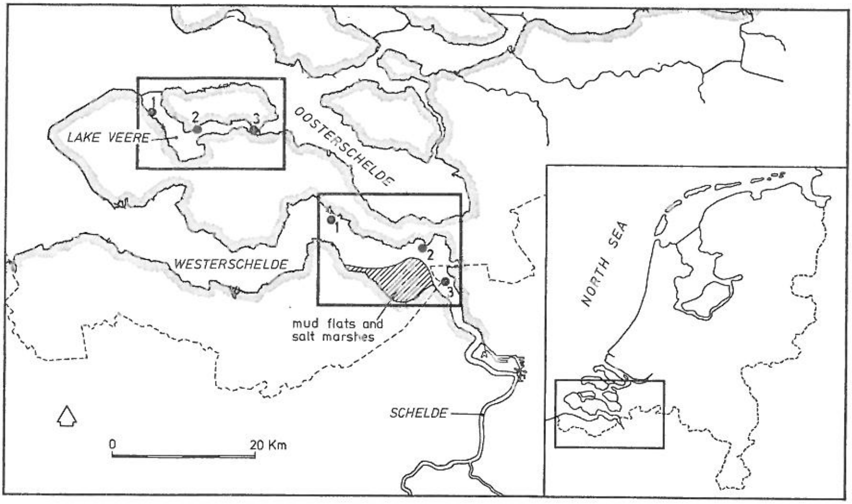

Fig. 1. Map of the areas investigated (rectangles) with sampling stations.

chlorinities did not fall within the choosen ranges (mesohaline or polyhaline) the plankton data were not used. In the stagnant waters of Lake Veere sampling took place at 3 stations (Fig. 1). Here it proved necessary to sample at 5 depths (0, 5, 10, 15, 20 metres) to investigate adequately the vertical zooplankton distribution. On board the samples were directly treated with neutralized formaldehyde up to a concentration of approximately 4%. Rotifers (*Synchaeta* spp.) were identified in their living state on board ship. Countings were carried out at low magnifications with an inverted microscope. As numbers of organisms of different species and of different stages of the same species cannot be used directly for biomass estimation, we calculated the volumes of the species concerned. This method, introduced by LOHMANN (1908), was followed more recently by HAGMEIER (1961), BAKKER (1964), HICKEL (1967) and BEERS & STEWART (1969). HAGMEIER arrived at an accuracy of approximately 20%. In Lake Veere 1 litre samples were also taken with a Hydrobios 5 l sampler for sedimentation. These samples were fixed on board with lugol and after sedimentation in the laboratory with formalin. Nannozooplankton organisms (mainly Protozoa) were counted at high magnifications, together with the phytoplankton. Countings of sedimented samples of the Westerschelde could not—or only with great difficulties—be performed owing to the presence of large quantities of silt and detritus. Detailed quantitative data concerning the seasonal development of the different zooplankton species are left out of consideration in this study.

In this paper we have restricted ourselves to the calculation of the average concentrations per unit volume of the most abundant organisms and of their average biomass during the years of investigation.

At the same stations and depths of zooplankton sampling, samples were taken for the determination of chlorinity (Knudsen), oxygen (Winkler) and *p*H.

III. SOME ENVIRONMENTAL FACTORS

For data about suspended matter and transparency we refer to BAKKER & DE PAUW (1974). In the context of zooplankton occurrence we will shortly discuss the factors water movement and water exchange, phytoplankton, oxygen and *p*H.

1. WATER MOVEMENT

In the brackish water region of the Westerschelde average current velocities, calculated for average tides, are 50 to 85 cm/sec; maximum values are 130 cm/sec (flood) and 165 cm/sec (ebb). These values increase up to 20% during spring tides and decrease to the same extent during neap tides (data Hydrographical Service, Den Haag). In connection with the complex bottom configuration in tidal areas this factor results in strong turbulence, tending to disperse the organisms homogeneously from surface to bottom. Mixing is enhanced by strong winds.

In Lake Veere vertical water movements are only induced by wind action. During periods of calm weather different zooplankton organisms tend to concentrate on different depths. Table I gives an example of the distribution of zooplankton in Westerschelde and Lake Veere at nearly the same time under calm weather conditions. In Lake Veere concentration of certain species or stages may occur at any depth. As a rule copepod nauplii are most numerous in surface layers, adults in deeper water layers. It is not unusual when concentrations on different depths differ 10 to 20-fold or more. In the Westerschelde zooplankton concentrations of surface and deeper water layers differ 2 to 3 times at the maximum.

2. WATER EXCHANGE

Average river discharge of the Westerschelde is about 90 m^3/sec. In summer discharge values may decrease to 60 m^3/sec, resulting in a retention time of several months. During the remainder of the year discharge may increase to 200 m^3/sec, exceptionally to 600 m^3/sec,

TABLE I

Vertical distribution of zooplankton in Lake Veere (station 1, 15 August 1974, 13.05 h) and Westerschelde (station 2, 16 August 1974, 13.00 h, ¾ h before HW); weak W wind.

Species (stage)	*Numbers per l, at depths:*				
	0 m	*5 m*	*10 m*	*15 m*	*20 m*
Lake Veere					
Acartia tonsa eggs	4	9	8	9	3
nauplii	133	27	6	5	8
copepodids	3	4	4	5	3
adults	4	5	5	23	41
Stenosemella ventricosa	745	1160	484	50	50
Alaurina composita	0.4	0.4	0.2	0.2	0.2
Polydora sp.	6	0.1	0.2	0.3	0.1
Gastropod larvae	2	4	4	3	1
Westerschelde					
Acartia tonsa nauplii	47				44
Cirriped nauplii	1				2
Eurytemora affinis nauplii	244				96
copepodids	40				24
Euterpina acutifrons nauplii	17				14
cop., ad.	4				2
Tintinnopsis campanula	8				18
Tintinnopsis fimbriata	3040				1660
Zoöthamnion clusters	220				100

lowering the retention time to some weeks (DE PAUW, 1975). Tidal exchange causes horizontal transport in seaward direction, shifting the animals out of the area they prefer. Optimum development of planktonic animals without special adaptation is only to be expected in summer during periods of small river discharge (and higher water temperature) (SCHULZ, 1961).

Retention time in Lake Veere is always longer. The mesohaline period was characterized by high discharges of fresh water, leading to retention times of 7 to 8 months. During the polyhaline period less fresh water came into the lake, resulting in retention times of 9 to 12 months.

3. PHYTOPLANKTON

Qualitative aspects.—BAKKER & DE PAUW (1974) demonstrated that phytoplankton of Lake Veere and the Westerschelde were totally different. The character species in the mesohaline area of the Westerschelde is the large diatom *Coscinodiscus commutatus*. Also the other predominant species nearly all are larger marine diatoms. The dominating species in the mesohaline period of Lake Veere were mainly nannoplanktonic: Cryptophycean flagellates (*Rhodomonas* sp.), a ciliate with zooxanthellae (*Mesodinium rubrum*) and μ-algae. Marine diatoms were scarce during this period, except the small species *Sceletonema costatum* and *Detonula confervacea*. During the polyhaline period the number of species increased strongly (BAKKER, 1972).

Quantitative aspects.—In Lake Veere strong blooms developed during spring in the mesohaline as well as in the polyhaline period. In the Westerschelde spring development within both salinity areas was not of significance. Maximum densities of standing stocks were found here during summer. Standing stocks in the mesohaline area never reached the level of those in the mesohaline period of Lake Veere. Summer levels of standing stocks in the polyhaline area sometimes exceeded those of Lake Veere.

Westerschelde waters are characterized by high sediment contents, low transparencies and, consequently, unfavourable light conditions. Turbidity was seldom caused by dense concentrations of living phytoplankton, but mainly by inorganic and dead organic material (detritus) from the bottom and littoral zone, kept in suspension by the tides. Lake Veere waters were found to show low transparencies too, but the cause was always strong blooming of nannophytoplankton.

Absence of tidal turbulence in Lake Veere created the opportunity for quick stabilisation of the water mass and, consequently, for development of small pelagic (often motile) phytoplankton species. In the Westerschelde turbulence permanently prevents stabilisation. Consequently, small motile phytoplankton species do hardly occur; development is hampered by turbulence and does not proceed logarithmically.

4. OXYGEN AND PH

At the mesohaline stations of the Westerschelde (Fig. 2) minimum values of oxygen saturation were 10 to 20%. Average values showed decreasing tendencies, demonstrating the increasing pollution of the estuary. At the polyhaline station 100% values were usually reached, minimum values were about 50%, and decreasing averages were demonstrated here too. The values, taken from surface waters, are indicative for the whole water column of the well-mixed estuary.

In Lake Veere vertical oxygen profiles were determined monthly, using data from samples of 0, 2.5, 5, 10, 15 and 20 m depths. Calculations have been made of the average quantities of oxygen, taking into account the volumes of the successive water layers concerned. The ranges figured (Fig. 2) are composed of these monthly averages. Maximum surface values sometimes were increasing far above the maximum value of Fig. 2 (140%), *e.g.* 280% in 1965. Minimum values of bottom layers sometimes approached zero during summer. Yearly average values (Fig. 2) fluctuated around 100% saturation.

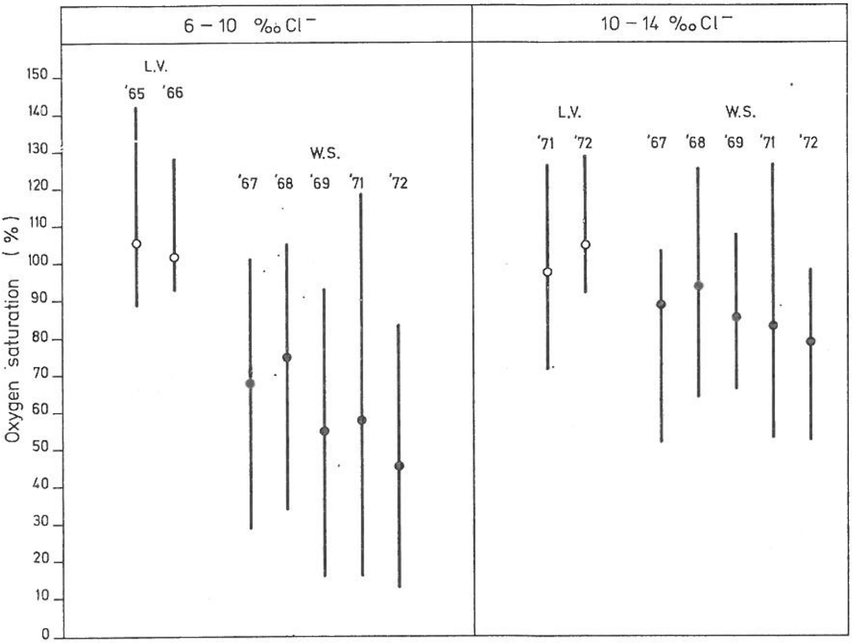

Fig. 2. Means and ranges of oxygen saturation percentages in Lake Veere (LV) and the Westerschelde (WS) in mesohaline (6–10‰ Cl′) and polyhaline (10–14‰ Cl′) zones.

In accordance with the oxygen values, *p*H of Lake Veere (8.0 to 9.2) was higher than of Westerschelde water (7.1 to 8.4) as a result of the higher primary productivity in Lake Veere.

IV. RESULTS

1. SPECIES COMPOSITION AND RELATIVE ABUNDANCE

The zooplankton is divided in the following 4 groups (Figs 3 and 4): Protozoa, Rotatoria, Crustacea, and other forms.

The differences between the zooplankton assemblages of Lake Veere

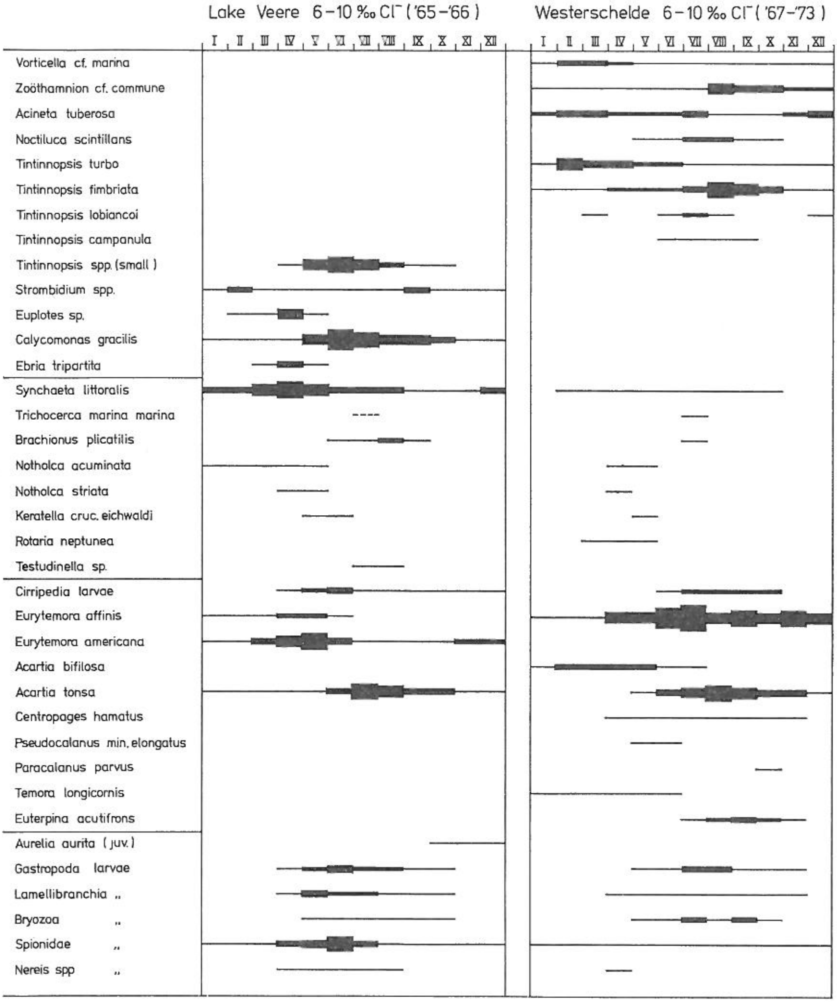

Fig. 3. Characteristic species composition, relative abundance and seasonal distribution of zooplankton in the mesohaline range of Lake Veere and the Westerschelde.

and the Westerschelde in the 6 to 10‰ Cl′ range (Fig. 3) are clear, as is the case with the phytoplankton. Just as the phytoplankton organisms from Lake Veere are dominated by the nannoplankton, the zooplankton is characterized by small species. This especially applies for the Protozoa; small Tintinnida and the flagellate *Calycomonas gracilis* reached large concentrations during early summer. Mass development of the rotifer *Synchaeta littoralis* was observed nearly throughout the year with peak numbers in spring.

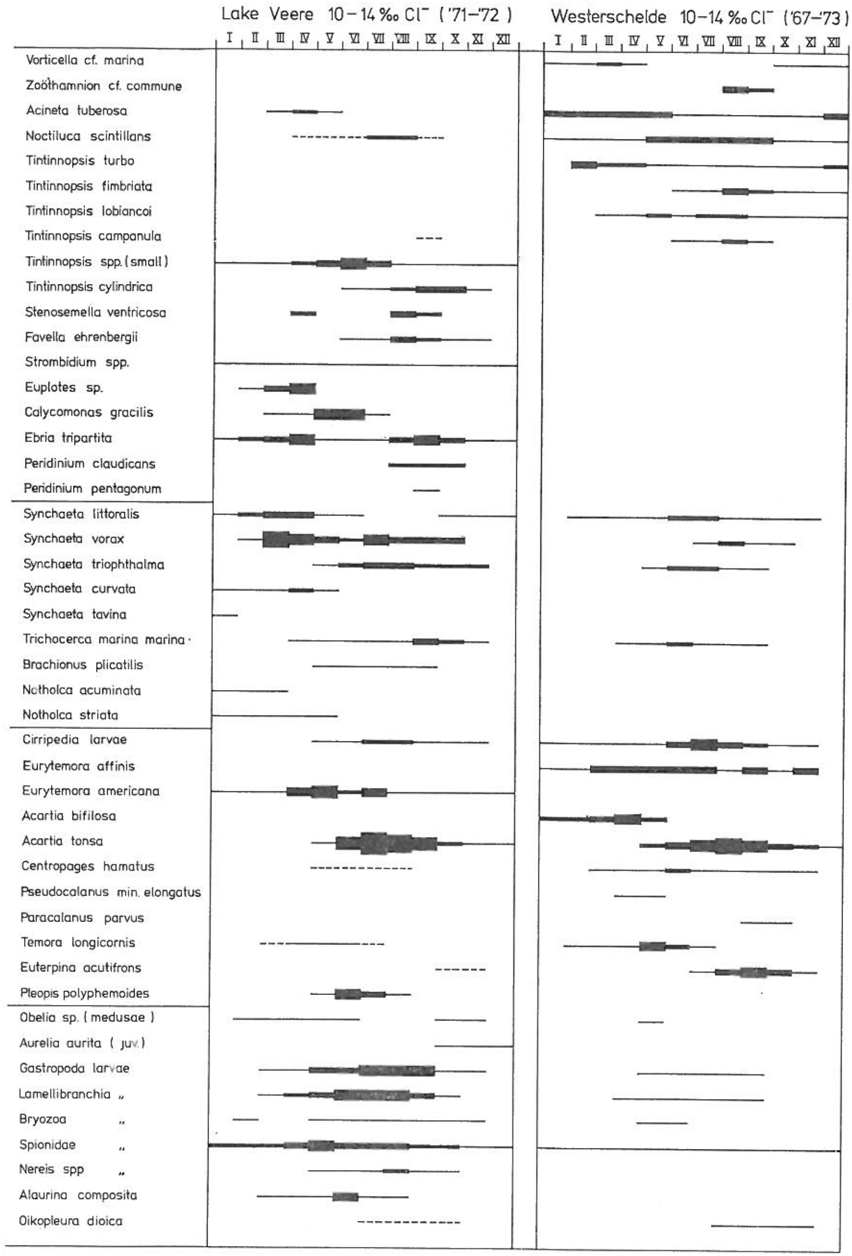

Fig. 4. Characteristic species composition, relative abundance and seasonal distribution of zooplankton in the polyhaline range of Lake Veere and the Westerschelde.

In the Westerschelde larger tintinnids generally are dominating: *Tintinnopsis turbo* during spring, *T. fimbriata* during summer. The last species can be considered a character species of the mesohaline zone. The peritrichous ciliates *Zoothamnion* and *Vorticella* are characteristic for the self-purification zone, extending in the mesohaline range. These species appear sessile (on detritus) or free in the plankton, just as Suctoria (*Acineta*). The rotifer plankton is weakly developed.

The copepods are dominated by the genera *Eurytemora* and *Acartia* in both areas. In the mesohaline period of Lake Veere the *Eurytemora* species *E. americana* and *E. affinis* were found. During these wet years the large quantities of fresh water discharged on the lake, contained many specimens of *Eurytemora affinis* and a small lake population was built up. *E. americana* however, introduced into the lake soon after the closure of the former sea arm, remained dominating. This species has not been found (yet) in the Westerschelde; here we deal exclusively with *E. affinis* which is present every month and nearly always dominating. Of the genus *Acartia* 2 species occur in the Westerschelde, *A. bifilosa* in spring, *A. tonsa* in summer, while in Lake Veere only *A. tonsa* is found, being present throughout the year with a maximum in summer. Thus in Lake Veere the spring population consists of the *Eurytemora* species and the summer population of *Acartia tonsa*. In the Westerschelde *Eurytemora affinis* is accompanied by *Acartia bifilosa* during spring (not frequent) and by *A. tonsa* during summer (numerous). The remainder of the marine copepods in the Westerschelde is not characteristic. The species *Temora longicornis*, *Centropages hamatus* and *Euterpina acutifrons*—rather frequently found during spring, summer and late summer, respectively—are euryhaline and their maintenance depends on continuous import from the sea.

The larvae of *Polydora* spp. are well represented in Lake Veere, with maximum numbers about May-June. In the Westerschelde these larvae are not important. Small concentrations of lamellibranch veligers in Lake Veere mainly came from *Cardium glaucum*, in the Westerschelde from *C. edule* and *Mytilus edulis*. The gastropod veligers in both areas mainly belong to *Littorina littorea*.

In the 10 to 14‰ Cl′ range (Fig. 4) the zooplankton shows similar relations as the phytoplankton. While the number of species in the Westerschelde remained almost the same as in the mesohaline area, the number of species in Lake Veere increased considerably. So some polyhalobe tintinnids were added to the Protozoa (a.o. *Favella ehrenbergii*), as well as some marine dinoflagellates (a.o. *Peridinium claudicans*). A diversification was noticed in the rotifers of the genus *Synchaeta*; the leading role of the mesohalobe *S. littoralis* was taken over by the polyhalobe *S. vorax*, also during spring. *S. triophthalma* became abundant in summer. Among the marine copepods *Temora longicornis* started settling in the lake. The cladoceran *Pleopis* now became numerous in June, together with the turbellarian *Alaurina composita*. The silicoflagellate *Ebria tripartita* and also veligers of molluscs became more abundant in the polyhaline period (increase of *Mytilus edulis*). The differences between the zooplankton composition of the 2 salinity ranges in the Westerschelde are of a quantitative rather than qualitative nature (as are the differences in phytoplankton composition). The characteristic brackish water components (*Eurytemora affinis*, *Tintinnopsis fimbriata*) also occur in the polyhaline range, though less numerous than in the mesohaline range. Poly- to euhaline species (*Temora longicornis*, *Euterpina acutifrons*), on the other hand, show greater abundance in the 10 to 14‰ Cl′ area.

2. PERCENT COMPOSITION

A clear picture of the differences between the zooplankton of Lake Veere and of the Westerschelde is obtained by a calculation of the percent composition (Table II). It has to be emphasized that only pumped samples (netplankton) could be used for these calculations. Total values for the main groups demonstrate that the plankton of the mesohaline area of the Westerschelde is monotonous and can be characterized as a crustacean-protozoan community. The mesohaline period of Lake Veere is mainly characterized by rotifers, accompanied by polychaet larvae and crustaceans. In the polyhaline area of the Westerschelde crustaceans are still important, but protozoan numbers are higher as a result of blooming of *Noctiluca* during summer. The other groups, rotifers and larvae of polychaets and molluscs, are all well represented here, though in smaller percentages. The polyhaline period of Lake Veere is still characterized by rotifers, crustaceans and polychaet larvae, but larger protozoans and larvae of molluscs are also rather numerous here. Incidentally we will point out the rather constant proportions of the main zooplankton groups, when successive years are compared, for Lake Veere as well as for the Westerschelde. GIERE (1968) demonstrated similar relations for the Elbe zooplankton.

3. SIZE AND BIOMASS OF THE STANDING STOCKS

The differences between Lake Veere and Westerschelde in densities of rotifers, polychaet larvae and protozoans are obvious (Table III). More copepod nauplii have been found in the Westerschelde than in Lake Veere, especially in the mesohaline area.

TABLE II

Percent composition of net zooplankton of Lake Veere and the Westerschelde in 2 salinity ranges during 2 years, calculated from average numbers of individuals in samples of 100 l.

Group (stage)	*Percentage at 6–10‰ Cl′*				*Percentage at 10–14‰ Cl′*			
	Lake Veere		*Westerschelde*		*Lake Veere*		*Westerschelde*	
	1965	*1966*	*1972*	*1973*	*1972*	*1973*	*1972*	*1973*
Copepod nauplii	9.1	11.1	60.7	54.3	9.4	10.1	25.8	37.9
copepodids	5.3	10.6	8.9	8.4	2.4	9.5	3.0	2.9
adults	1.4	1.8	3.5	1.4	0.5	0.7	0.7	0.9
Cirriped larvae	0.1	0.2	0.0	0.9	0.1	0.4	4.3	2.2
Cladocerans, *Pleopis*	0.0	0.0	0.0	0.0	1.0	0.5	0.0	0.0
Crustaceans, total	15.9	23.7	73.1	65.0	13.4	21.2	33.8	43.9
Rotifers, *Synchaeta*	56.2	49.0	1.8	1.9	40.8	28.5	9.5	2.7
eggs	5.2	1.2	0.0	0.0	12.8	13.1	0.0	0.0
total	61.4	50.2	1.8	1.9	53.6	41.6	9.5	2.7
Polychaets, nektochaets	21.8	19.1	0.0	0.8	15.5	13.5	0.6	5.7
trochophores	0.0	4.7	0.0	0.0	2.4	1.1	0.0	0.0
total	21.8	23.8	0.0	0.8	17.9	14.6	0.6	5.7
Molluscs, gastropods	0.1	0.1	0.0	0.0	7.2	5.1	0.5	0.3
lamellibranchs	0.7	1.4	0.0	0.0	2.6	7.5	6.3	1.1
total	0.8	1.5	0.0	0.0	9.8	12.6	6.8	1.4
Turbellarians, *Alaurina*	0.0	0.0	0.0	0.0	0.2	1.0	0.0	0.0
Protozoans, tintinnids	0.0	0.0	20.9	17.9	5.0	8.9	33.5	18.8
Zoöthamnion	0.0	0.0	3.1	5.6	0.0	0.0	0.0	0.0
Noctiluca	0.1	0.6	0.3	8.5	0.0	0.0	14.7	26.6
total	0.1	0.6	24.3	32.0	5.0	8.9	48.2	45.4
Remaining groups	0.0	0.2	0.8	0.3	0.1	0.1	1.1	0.9

Zooplankton numbers mentioned in Table III are converted to plankton volumes in Table IV. *Noctiluca* was not taken into account here owing to its strong vacuolisation. According to LOHMANN (1908) the plasma volume only amounts to $0.004 \cdot 10^6$ μm^3 (total volume $70 \cdot 10^6$ μm^3), which means that average densities of 7 to 35 per litre (Table III) are of little importance to biomass. The volumes of the other species are given in the legend of Table IV. From Table IV it follows that in the Westerschelde copepods represent 83 to 98% of the total average standing stock. In the polyhaline range the Westerschelde and Lake Veere demonstrated nearly the same copepod biomass, in the mesohaline area of the Westerschelde values were 2.5 to 3.5 times larger. In Lake Veere crustaceans account for 41 to 44%

TABLE III

Average numbers of zooplankton in 2 salinity ranges of Lake Veere and Westerschelde; figures of dominating nannoplanktonic protozoans from Lake Veere included.

Group (stage)	*Numbers/litre*			
	6–10‰ Cl′		*10–14‰ Cl′*	
	Lake Veere	*Westerschelde*	*Lake Veere*	*Westerschelde*
Netplankton				
Copepod nauplii	11	129	17	46
copepodids	7	11	10	4
adults	2	4	2	1
Cirriped larvae	0.1	1	0.4	4
Cladocerans, *Pleopis*	0	0	1.5	0
Rotifers, *Synchaeta*	61	5	67	8
eggs	6	0	24	0
Polychaets, nektochaets	24	1	32	5
trochophores	4	0	4	0
Molluscs, gastropods	0.1	0	12	1
lamellibranchs	1	0	8	5
Turbellarians, *Alaurina*	0	0	1	0
Protozoans, tintinnids	1	44	12	39
Zoöthamnion	0	9	0	0
Noctiluca	0	7	2	35
Nannoplankton				
Ebria tripartita	1750		16000	
Euplotes spec.	1350		4000	
Calycomonas gracilis	500000		50000	
Tintinnopsis spec.	40000		3000	

of total biomass, polychaet larvae for 30 to 35%, rotifers for 17 to 21%. The larger average standing stock of the netplankton in the mesohaline range is found in the Westerschelde, *viz.* 460 mm^3/m^3. This value is caused mainly by copepods as the relatively small cell volumes of the larger Protozoa (*Tintinnopsis*) are negligible. The netplankton of the polyhaline area of Lake Veere reaches a value of 415 mm^3/m^3. Therefore the areas show opposite tendencies: the stagnant brackish environment of Lake Veere contains more net zooplankton in its polyhaline stage whereas the tidal brackish environment of the Westerschelde contains more biomass in its mesohaline part.

Figures of net zooplankton biomass have to be completed with those of the nannoplankton. Table IV demonstrates that nannoplankton in Lake Veere is of quantitative importance. Nannoplankton biomass in the Westerschelde could be measured only incidentally and was considerably smaller; present results are still too scarce to determine average values for comparison with those of Lake Veere.

TABLE IV

Average biomass (mm^3/m^3) composition in Lake Veere and Westerschelde. As volumes (in 10^6 μm^3) for the different categories were calculated: 2 for copepod nauplii, 5 to 10 (average 7) for copepodids (mainly *Eurytemora* and *Acartia*), 25 for adults of *Acartia*, 30 for adults of *Eurytemora*, 5 to 12 for cirriped nauplii, 5 for *Pleopis*, 1 for *Synchaeta*, 0.1 for *Synchaeta* eggs, 2 for small specimens of *Polydora* larvae (mostly 80% of total volume), 10 for large specimens of *Polydora* (remainder), 3 for polychaet trochophores, 3.5 for gastropod veligers, 0.6 for lamellibranch veligers, 0.05 for large *Tintinnopsis*, 0.0005 for small *Tintinnopsis*, 0.004 for *Ebria*, 0.015 for *Euplotes*, 0.0001 for *Calycomonas*.

Group (stage)	*Plankton volume (mm^3/m^3)*			
	6–10‰ Cl′		*10–14‰ Cl′*	
	Lake Veere	*Westerschelde*	*Lake Veere*	*Westerschelde*
Netplankton				
Copepod nauplii	22	258	34	92
copepodids	49	77	70	28
adults	55	110	55	30
Cirriped larvae	1	5	4	20
Cladocerans, *Pleopis*	0	0	7	0
Crustaceans, total	127	450	170	170
Rotifers, *Synchaeta*	61	5	67	8
eggs	0.6	0	2.4	0
total	62	5	69	8
Polychaets, nektochaets	88	2	112	18
trochophores	12	0	12	0
total	100	2	124	18
Molluscs, gastropods	0.4	0	42	3.5
lamellibranchs	0.6	0	5	3
total	1	0	47	7
Turbellarians, *Alaurina*	0.4	0	4	0
Protozoans, tintinnids	0	3	0.6	2
Total netplankton	290	460	415	205
Nannoplankton				
Ebria tripartia	7		64	
Euplotes spec.	20		60	
Calycomonas gracilis	50		5	
Tintinnopsis spec.	20		2	
Total nannoplankton	97		131	

V. DISCUSSION

We will discuss the observed differences between zooplankton development in the stagnant and tidal brackish waters investigated, paying special attention to the influences of the different environmental factors on the main zooplankton groups. We will treat these groups separately.

Protozoa.—Several small forms were regularly found in Lake Veere. High numbers were reached during periods when suitable algal food was abundant. During the mesohaline period, when μ-algae dominated nearly throughout the year (BAKKER & DE PAUW, 1974), a relatively small average biomass of *Ebria tripartita* was found (Table IV). The minute flagellate *Calycomonas gracilis* and some tintinnids however, thrived well on these algae and became numerous. During the polyhaline period *Sceletonema costatum* was the dominating alga. This species is the preferred food for *Ebria* that now could increase to a nearly 10-fold average density (Table IV). We conclude that the nannophytoplankton species spectrum and notably species abundance dictate to a high degree species composition and especially biomass of the nannozooplankton in the lake.

The mesohaline area of the Westerschelde contained less nannophytoplankton. Substantial amounts of detritus prevailed throughout the year and larger diatoms occurred during summer. Small protozoan species were found sparsely but larger species, particularly *Tintinnopsis fimbriata*, predominated. These species were thus bound to feed mainly on small detritus with bacteria. *T. fimbriata* may be especially adapted to estuarine tidal conditions, for the species was never found in Lake Veere. The species also dominated in the brackish tidal waters of the former Zuiderzee during summer (HOFKER, 1922). In the Elbe, on the contrary, *T. fimbriata* occurs only sparsely (SCHULZ, 1961). Here *T. lobiancoi*, *T. subacuta* and *T. turbo* temporarily may characterize the meso- and polyhaline areas (SCHULZ, 1965). GIERE (1968) omitted the tintinnids in his survey of Elbe zooplankton.

The high numbers of larger tintinnids and *Noctiluca* in the Westerschelde (Tables II and III), reached only less than 1% of the total biomass. The small forms of Lake Veere, however, provided important contributions (24 to 25%) to total biomass (Table IV). Here nannozooplankton represents an important link in the food chain besides the phytoplankton. Extensive data about biomass of nannozooplankton are rather scarce in literature and therefore comparisons with other areas are difficult to make. BEERS & STEWART (1969) found protozoans to form 13 to 28% of microzooplankton biomass in the northern Pacific.

Rotifers.—The high percentage of rotifers in Lake Veere (Table II) account for roughly 20% of total average biomass of the netplankton (Table IV). The animals tend to migrate in the direction of the surface (positive phototaxis) and are able to perform this reaction owing to the absence of regular strong vertical water movements. In spring and summer when the upper water layers provide a rich algal food, concentration of the rotifers may occur in this zone. Under these optimal growth conditions multiplication proceeds rapidly. The rotifers therefore prove to be well adapted to stagnant brackish waters.

In the brackish water zone of the Westerschelde rotifers are sparsely represented (*cf.* DE PAUW, 1975). The portion of rotifers in total biomass amounted to only 1 to 4% (Table IV). In the Elbe *Synchaeta littoralis* sometimes is abundant (GIERE, 1968), but the data of SCHULZ (1961) indicate that average densities of this rotifer were the same as in the Westerschelde. Strong tidal turbulence and much lower densities of small algal cells explain why these animals are much less numerous in the Westerschelde than in Lake Veere.

Polychaet larvae.—Larvae of Polychaeta, mainly the planktotrophic larval stages of *Polydora ciliata* and *P. ligni*, constitute another important part of Lake Veere zooplankton: 15 to 24% of total average numbers corresponding to 30 to 34% of total average biomass (Tables II and IV). High numbers of larvae in spring, summer and autumn, together with a long pelagic life time account for the large average biomass. The lecithotrophic larvae of *Nereis diversicolor* constitute only a few percents of the biomass of polychaet larvae. Also polychaet larvae concentrate in phytoplankton-rich surface layers. Development appears to proceed optimally in Lake Veere. So, just as with the rotifers, the main factors causing good development of polychaet larvae in Lake Veere appear to be absence of intensive vertical turbulence and abundance of algal food.

The unimportance of polychaet larvae in the mesohaline area of the Westerschelde (less than 1% of total numbers and of biomass), is caused primarily by low numbers of adults in the mud. Larvae penetrating this zone will have difficulties to settle because of the permanently moving substrate (W. J. WOLFF, personal communication). This explains the low abundance of the mud-dwelling and euryhaline (1 to 16.5‰ Cl′) *Polydora ligni*. The presence of *P. ciliata* —not occurring anymore in the Westerschelde below 10‰ Cl′—might be limited by the absence of molluscs as their suitable substrate (WOLFF, 1973). *Nereis diversicolor* and *N. succinea*, though rather common in the mesohaline reaches of the Westerschelde (WOLFF, 1973), are of little importance to the plankton biomass owing to their lecithotrophy including a short larval period. The 10 to 14‰ Cl′ area of the Westerschelde contained more polychaets (8 to 9% of total biomass), but also here this group is much less important than the copepods. In this respect the Westerschelde differs rather strongly from other estuaries, *e.g.* the Elbe, owing to different hydrographical and geomorphological features. In the Elbe mouth the polyhaline area is characterized by extended mud flats. The 10 to 14‰ Cl′ area of the Westerschelde is not situated in the mouth, is much smaller and contains less shallows. KÜHL & MANN (1963) and GIERE (1968) found the polyhaline zone of the Elbe strongly characterized by polychaet and lamellibranch larvae. GIERE qualifies this region as the area of "euryhaline meroplankton".

Levels of oxygen concentration might be of significance for polychaet larvae. Some indications of the degree of tolerance to low oxygen concentrations can be given in relation to the situation in Lake Veere. Here *Polydora* larvae still have been found alive at oxygen saturation values between 0 and 1% and therefore we assume that negative influences of low oxygen contents on *Polydora* larvae in the Westerschelde may be excluded.

Copepods.—The bulk of Westerschelde zooplankton is represented by copepods; a general rule for estuaries. JEFFRIES (1967) stated that "estuarine holoplankton is a monotonous assortment of calanoid copepods" and mentioned values higher than 60% in 3 estuaries along the American east coast. CRONIN, DAIBER & HULBERT (1962) found up to 84% copepods in the Delaware River estuary. Their figures of the average biomass of *Eurytemora affinis* and *Acartia tonsa* are in the same order of magnitude as our data. According to JEFFRIES' ecological classification of estuarine copepods, *E. affinis* and *E. americana* belong to the "true-estuarine category", characterized by organisms reproducing exclusively in brackish water. *Acartia tonsa*, usually limited by chlorinities less than 6‰ Cl′, propagates throughout the major portion of the estuary and is considered "estuarine and marine".

Food conditions in Lake Veere have to be considered favourable in view of the great numbers of several species of small algal cells. The size of food particles is important for copepods as NASSOGNE (1970) demonstrated in a laboratory culture of *Euterpina acutifrons*: only medium-sized algae (of approximately 10 μm) offered the best chances as food for a population to reach the adult stage. In this light the more balanced composition of the copepod stock in Lake Veere (more than 50% of the nauplii develops to copepodids) is understandable. One may wonder whether the food requirements of the older stages in the Westerschelde can be met completely. Dominance of detritus and shortage of nannophytoplankton during long periods of the year, may be indicative for a less varied food supply. This might partly explain the relatively low copepodid numbers (only 10 to 12% of nauplii develops to older stages), provided these data are completely adequate (see below). The high standing stocks of nauplii evidently do not guarantee a further optimal development. MARSHALL & ORR (1955) purport that the nauplius stages I and II of *Calanus finmarchicus* do not eat. In the laboratory many nauplii even reach stage III, but then die off. Applied for copepods in general, this observation would imply that conditions for nauplii may be considered favourable only if larvae of stage IV are present in numbers. A detailed regular analysis of the composition of the naupliar standing stock in the Westerschelde has not yet been completed. However, mortality of the younger stages (I to III) appears to be high, especially of *Eurytemora affinis*, and the dense stocks have thus to compensate for severe losses in the course of development. *Acartia tonsa* is omnivorous (ANRAKU & OMORI, 1963) and may have fed also on its own larval stages (CONOVER, 1956).

Turbulent water movement coupled with tidal exchange could be supposed to influence negatively the establishment and maintenance of estuarine copepod populations. Stagnant waters on the other hand, giving the animals the opportunity to persist during longer periods in preferred zones, might offer more favourable conditions than tidal waters. The observed distribution of copepod stages in Westerschelde and Lake Veere (Table II) demonstrate that these suppositions are too simple. Evidently standing stocks of nauplii in the Westerschelde are considerably larger than in Lake Veere, suggesting a successful adaptation to the estuarine environment. The numbers of copepodids and adults however, evolving from these dense naupliar stocks, appear surprisingly low, suggesting high mortality in the course of the development from nauplius to adult. The relatively low abundance of copepodid stages and adults in the samples may depend on the influence of the turbulent tidal movement and water exchange on the animals. Gradual washing out in seaward direction is partly prevented by the fact that the older stages are not dispersed homogeneously, but tend to concentrate along the river banks and the bottom after dispersion of the younger stages over a large area (CRONIN, DAIBER & HULBERT, 1962; DE PAUW, 1973, 1975). *Eurytemora affinis* therefore does not behave in turbulent tidal waters as a truly pelagic copepod, but as a more benthic-littoral species, staying preferably in more shallow and less turbulent water. Possible concentrations in the upper muddy bottom layers as well as occurrence along the banks might have resulted in inadequate quantitative sampling because most samples for this study have been taken at the stations in the deeper channels with higher current velocity. Therefore, in the Westerschelde sampling of nauplii will have been adequate, sampling of the older stages may have been not. The numbers of adult copepods in Lake Veere might be too low owing to avoiding movements of the animals caused by pumping. As a result of these complications the differences found between percentage composition and biomass of the copepod plankton of Lake Veere and the Westerschelde can not be analyzed any further on basis of our present data. Comparison of the preliminary findings with the results of a special sampling program will be the subject of a following study.

Little is known about the influences of lowered oxygen contents on copepods. In nature one single factor will seldom be responsible for an eventual stress situation of an organism. In polluted estuaries doubtless a combination of factors causes the general deterioration of the environment. In the mesohaline area of the Westerschelde minimum oxygen saturation values were as low as 10 to 20%. *Eurytemora affinis* must be extremely tolerant to low oxygen levels. The species disappeared from the River Tyne, U.K., only after total oxygen depletion (BULL, 1931). The still dominant appearance of *E. affinis* in the brackish water zone of the Westerschelde, thus, is not unusual. Even the marine copepod *Pseudocalanus minutus elongatus* is able to tolerate oxygen levels of less than 0.1 mg/l as was found by ACKEFORS (1966) at depths below 100 metres in the Landorts Deep, Baltic. As yet there are no indications that composition and abundance of the actual characteristic *Eurytemora-Tintinnopsis-Coscinodiscus* assemblage are influenced harmfully by the strong pollution. It might be possible that *E. americana* requires higher oxygen concentrations than *E. affinis*, as the first species is absent in the Westerschelde and dominates in Lake Veere during spring when saturation is always higher than 100%. Data on oxygen-limited distribution of this copepod are not known to us. About possible influences of a lowered *p*H on brackish water zooplankton in general nothing is known either.

VI. SUMMARY

A comparison was made between the zooplankton assemblages of the meso- and polyhaline ranges of the Westerschelde estuary and Lake Veere (SW Netherlands). Species composition and density of the zooplankton of brackish water ecosystems depend not only on salinity but on several other factors too. Zooplankton development in stagnant

Lake Veere and tidal Westerschelde waters of the same salinity is quite different. Important factors appeared to be food supply, water movement and water exchange.

Lake Veere zooplankton subsists on a diversified and dense phytoplankton as source of food during long periods of the year. Continuous turbulent water movement is absent. The combination of these factors is favourable for rotifers and polychaet larvae. Several groups, *i.e.* protozoans, rotifers, larvae of polychaets and molluscs, copepods, constitute important parts of total average biomass.

Westerschelde zooplankton in the mesohaline area of the estuary subsists on detritus as the only important source of food throughout the year. Phytoplankton is densest in summer but small species, essential as food, are quantitatively rare. Strong tidal turbulence tends to disperse the organisms in the whole water mass. Tidal exchange causes transport of organisms in seaward direction. These conditions are unfavourable especially for rotifers. Copepods show successful adaptation to the estuarine environment. Average standing stocks in the mesohaline area are much larger than in Lake Veere.

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