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COPEPOD BIOMASS IN AN ESTUARINE AND A STAGNANT BRACKISH ENVIRONMENT OF THE S.W. NETHERLANDS*

C. BAKKER[1], W. J. PHAFF[1], M. v. EWIJK-ROSIER[1] & N. DE PAUW[2]

[1] Delta Institute for Hydrobiological Research, Yerseke, The Netherlands.

[2] Laboratory for Biological Research of Environmental Pollution, State University, Gent, Belgium.

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Abstract

In the mesohaline zone of the Westerschelde estuary *Eurytemora affinis* is the dominant copepod, demonstrating large biomass values nearly throughout the year. In the meso-polyhaline Lake Veere *Acartia tonsa* is abundant, mainly during summer. In spring a small population of *Eurytemora americana* is found.

The tidal estuary harboured far denser copepod populations throughout the year than the stagnant brackish lake water. The average yearly copepodid + adult biomass in the Westerschelde estuary was approx. 850 mg/m^3 (wet weight), in Lake Veere approx. 130 mg/m^3.

Temporarily low oxygen values did not influence negatively the copepod populations in the Westerschelde estuary.

The seasonal distribution of the dominant copepods in both areas is explained in the light of recent litterature data.

Perennial *Eurytemora affinis* abundance in the Westerschelde estuary must be mainly caused by large concentrations of nannodetritus particles, bacteria included, throughout the year. *Acartia tonsa* in Lake Veere has to thrive mainly on nannophytoplankton.

Introduction

In previous papers (Bakker & De Pauw, 1974; 1975), comparisons were made between the phytoplankton resp. zooplankton of the brackish water region of the Westerschelde estuary and Lake Veere, southwestern Netherlands. The aim of these studies was to compare a brackish water tidal area with a stagnant brackish water of the same salinity in relation to species composition, seasonal distribution and size of the standing stocks. Plankton development in the investigated stagnant and tidal waters was quite different in all respects.

Rotifers and polychaete larvae constituted important groups in Lake Veere zooplankton and were nearly absent in the mesohaline zone of the Westerschelde. Important factors explaining these differences appeared to be food supply and water turbulence. Copepods on the other hand showed a better adaptation to the estuarine tidal environment of the Westerschelde than to stagnant Lake Veere waters.

The present study deals in more detail with the copepods, in both areas dominated by the genera *Eurytemora* and *Acartia.* The mesohaline area of the Westerschelde is characterized by *Eurytemora affinis,* which is perennial and nearly always dominating. In summer also *Acartia tonsa* is found in numbers. The meso-polyhaline Lake Veere harbours *Eurytemora americana,* occurring mainly during spring, and *Acartia tonsa,* abundantly in summer.

Our previous results (Bakker & De Pauw, 1975) indicated high standing stocks of naupliar stages, and relatively low numbers of copepodids and adults in the Westerschelde. Due to the sampling methods followed, however, we doubted the validity of our data on copepodid- and adult densities. We therefore reinvestigated our copepod data and performed an additional sampling program. Results of this study are presented in this paper.

Material and methods

Zooplankton samples were collected in 1974 with a submersible pump (type Pleuger no. 64) with a capacity 200 l/min. In Lake Veere the efficiency of the pump method was compared with that of a Schindler-Patalas self-closing transparant zooplankton trap (Schindler, 1969), see discussion. Because this light weight sampler is very sensitive to water currents, we made the trap heavier fixing lead strips on two opposite sides.

In the tidal area of the Westerschelde surface and near-bottom layers (depth 20 meters at the maximum) were sampled in three localities at high water. In stagnant Lake Veere sampling took place at 0, 5, 10, 15 and 20 metres, again in three localities (Fig. 1). We were not able to study the possible differences in distribution of the copepods between the main channels and the shallows. In both areas investigated, only the channels were sampled.

The samples were filtered through 63 μm gauze to study total netplankton. The copepod plankton was concentrated by refiltering the samples through 120 μm gauze in order to lose large quantities of diatoms, smaller zooplankton organisms, silt and detritus. The last two fractions were of great importance in the Westerschelde estuary where the sample volumes often had to be decreased from 100 to 25 litres in upstream direction to prevent clogging of the net. In Lake Veere always 100 to 200 litres of water could be filtered. The 120 μm filtrates did not contain any copepodids but only some early naupliar stages, already counted in the original samples.

Subsampling was performed by means of a wide-mouth calibrated pipette, immediately filled after thoroughly shaking of the sample. We used counting cells of own construction, consisting of bottom glass slides divided by parallel calibrations at a distance of 3 mm, with mounted perspex rectangles of 6.2 x 3.8 cm. In order to count ca. 100 animals per sample, the size and number of the subsamples was determined in relation to the densities of total suspended matter. Counting and measuring were performed by means of a stereomicroscope.

We made biomass estimations, following the method of Lohmann (1908), by calculating copepod volumes. A clay model of the cephalothorax of *Eurytemora affinis* was made, based on figures from Sars (1902) and on measurements of our own material. Contents of the model were converted into contents of a cylinder with corrections for abdomen (furca included), antennulae and feet. The calculation was applied to *Acartia tonsa*

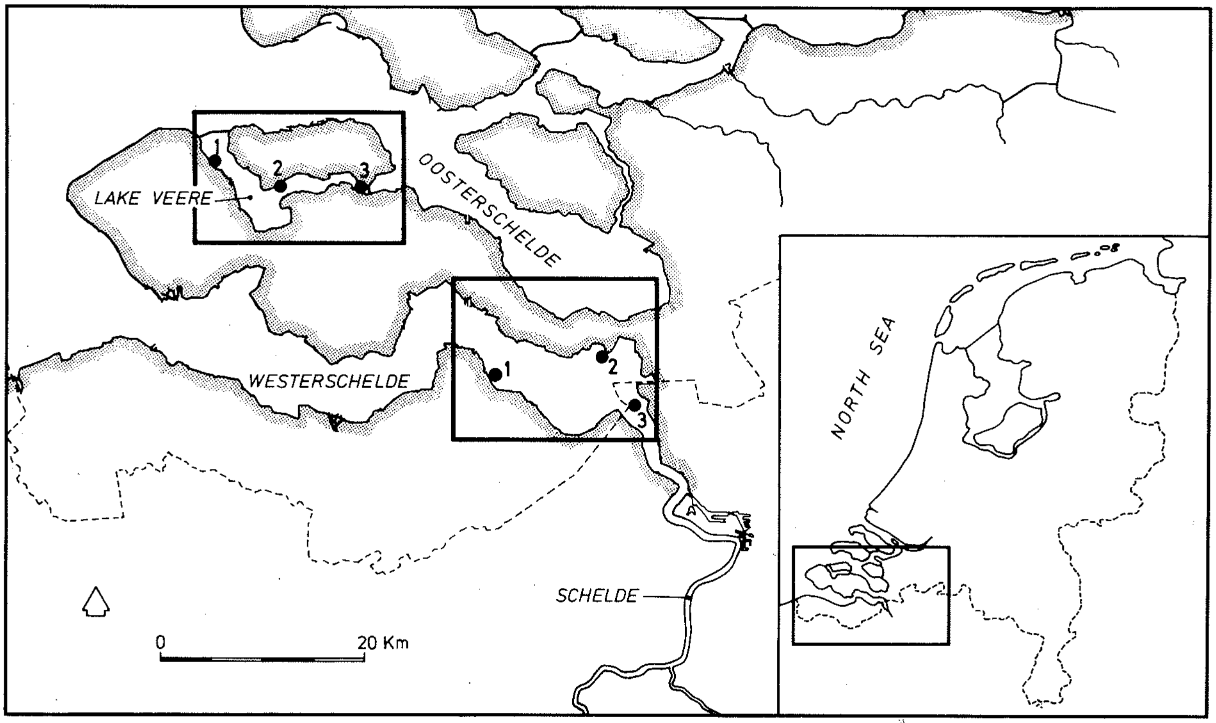

Fig. 1. Map of the areas investigated, Lake Veere and Westerschelde estuary (rectangles), with sampling localities.

too, because of the similar (cylindrical) body form of this species. Cephalothorax lengths of approx. 100 animals were measured. The length/diameter relation was estimated in 10 to 20 specimens at each sampling date. Volume determinations of the different size classes (copepodid stages and adults) were performed, expressed as wet weight in $mm^3/m^3 = \mu g/l$ (assuming a zooplankton volume of 1 mm^3 to be equivalent to 1 mg). For both areas average biomass values were calculated from all data of the three stations.

Results

Some environmental factors

In this study the copepod zooplankton component of the year 1974 is treated. Therefore average monthly values are given from this year of the factors temperature and salinity (Figs. 2 and 3), oxygen and pH (Figs. 4 and 5), transparency and suspended matter (Figs. 6 and 7). Westerschelde locality 2, the middle station of the brackish water zone of the estuary, was selected for graphical presentation. In Lake Veere curves were composed from the data of locality 1, the most representative sampling station in the northwestern lake section containing 62% of the total lake volume.

1. *Temperature* (Fig. 2). Highest Westerschelde temperatures were always found in locality 3, the upstream station. The longitudinal temperature gradient was small, in the range of 0.5 to 1.5°C and vertical differences were still smaller in this tidal area. Temperatures of both areas were nearly constant and relatively high (6 to 7°C) from January to March. In summer (July, August), Westerschelde temperatures exceeded those of Lake Veere with approximately 1°C and maintained this difference during autumn.

Vertical differences of temperatures in Lake Veere were small in locality 1, owing to thorough mixing of the water column by wind action. During the vernal rise of temperature from April to May, large vertical differences arose under calm weather conditions, especially in locality 3. In this station lowest temperatures were demonstrated in the deepest waters where salinity stratification occurred nearly throughout the year as a consequence of regular entrance of high salinity water via the locks, separating the lake from the marine tidal area of the Oosterschelde (Fig. 1). Higher deep water temperatures in this locality during October and November were caused by the same phenomenon.

2. *Chlorinity* (Fig. 3). In Lake Veere average chlorinity was found to increase gradually during spring and summer, reaching a maximum value of 13.3‰ in August/September. The average chlorinity range of locality 1 from January to September was less than 3‰.

During the same period increase of chlorinity in the Westerschelde was twice as large (6‰, locality 2) and proceeded less regularly (May to July) than in Lake Veere. Heavy rainfall during the last months of the year caused the chlorinities to decrease strongly in both areas, notably in the Westerschelde: in locality 2 a drop of 10‰ was found. Maximum values were always measured in the most seaward station. Vertical salinity stratification is

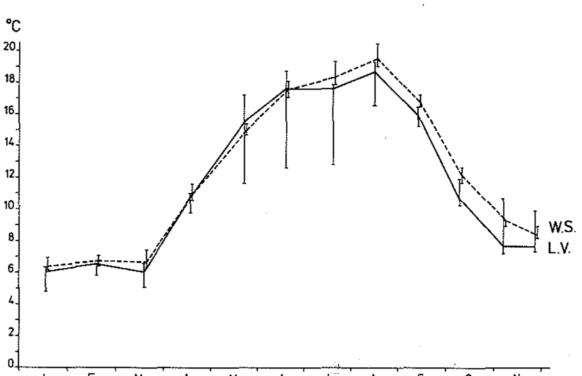

Fig. 2. Average water temperature (°C) during 1974 in Lake Veere (L.V., solid line) at locality 1, and in the Westerschelde estuary (W.S., broken line) at locality 2. Ranges of samples from localities 1, 2 and 3 are indicated by vertical lines.

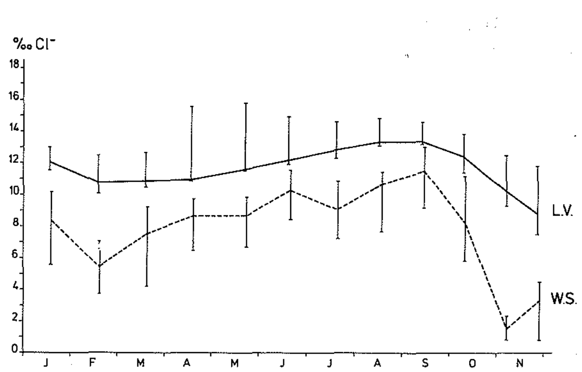

Fig. 3. Average chlorinity (‰ Cl') during 1974 in Lake Veere (L.V.) at locality 1, and in the Westerschelde estuary (W.S.) at locality 2. Ranges of samples from localities 1, 2 and 3 are indicated by vertical lines.

generally unimportant in the well-mixed Westerschelde estuary. In locality 2 the average chlorinity difference between surface and near-bottom layers was 0.5‰. This difference increased to 2‰ in October when freshwater discharge suddenly rose to much higher values than the mean (90 m^3/sec). Consequently, the lengths of the vertical bars of the Westerschelde curve indicate mainly horizontal chlorinity differences. The brackish water zone is characterized by a fairly strong longitudinal chlorinity gradient, in the order of 3-5‰, except during the first week of November after the period of strongly increased river discharge. The tidal chlorinity variation in Westerschelde locality 2 is approximately 3‰, with maximum values of 4.5‰ (De Pauw & Peters, 1975).

In Lake Veere vertical stratification phenomena are common, especially in the eastern lake section (locality 3), as mentioned above. Therefore the lengths of the vertical lines of the Lake Veere curve represent mainly vertical chlorinity differences.

3. *Oxygen* (Fig. 4). In the Westerschelde estuary the higher salinities of locality 1 always coincided with higher oxygen contents, both factors showing lower values in upstream direction. Oxygen values in Westerschelde locality 3 may fall below 1 mg/l (November). One hundred percent saturation values were not reached in 1974; only in January the 90% level was crossed (10 mg/l). Obviously influences of phytoplankton blooming in this zone of the estuary were less significant than strong wind effects (cf. end of November).

In Lake Veere average oxygen contents of locality 1 were higher than in the Westerschelde throughout the year. In winter, values were 10-11 mg/l (approximately 100% saturation), remaining nearly constant in spring although saturation values gradually increased to a mean value of 115% due to phytoplankton blooming). Average

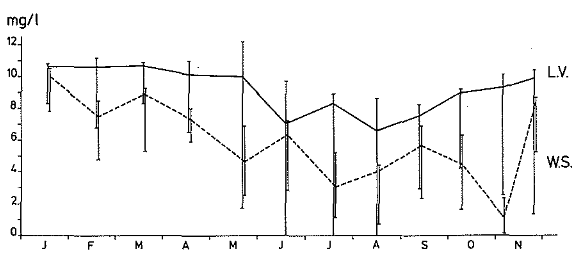

Fig. 4. Average oxygen contents (mg O_2/l) during 1974 in Lake Veere (L.V.) at locality 1, and in the Westerschelde estuary (W.S.) at locality 2. Ranges of samples from localities 1, 2 and 3 are indicated by vertical lines.

summer values fluctuated between 6.5 and 8.3 mg/l (equalling ± 80 and ± 100% saturation). Very low oxygen values were found in the deeper water layers in spring (notably May), mainly caused by stratification in locality 3; total oxygen depletion was demonstrated during summer in the bottom water layers of this station.

4. *pH*. (Fig. 5). pH values of locality 1 in Lake Veere roughly fluctuated between 8.0 and 8.6, at a higher level than in the Westerschelde (viz. between 7.1 and 8.0). The general picture of the pH curve of the Westerschelde resembles that of the oxygen curve. The high primary production in Lake Veere in spring and early summer (Bakker & Vegter, in prep.) is clearly reflected in high pH values during that period. Westerschelde waters did not demonstrate such a relationship: dense phytoplankton standing stocks develop in summer (Bakker & De Pauw, 1974), but are not accompanied by increasing pH values. The lower pH of the Schelde river (De Pauw, 1975) is responsable for the minimum values, all measured in locality 3, and became evident in November.

5. *Transparency* (Fig. 6) *and suspended matter* (Fig. 7). Transparency, measured as Secchi disc visibility, and suspended matter show clearly the large differences between a brackish water tidal area and a brackish lake.

In Lake Veere values of Secchi disc visibility in winter were 1 to 2 metres, during periods of algal blooms approximately 2-3 metres and in summer and early spring 3 to 5.5 metres. The highest Secchi values were generally found in locality 1, whereas the upper water layers of locality 2 and 3, being influenced regularly by discharged polder water, showed lower visibilities. Suspended mat-

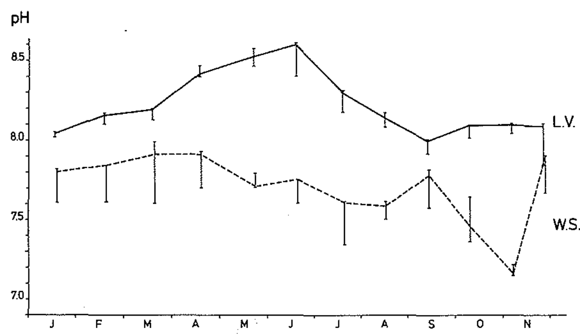

Fig. 5. pH-values during 1974 in Lake Veere (L.V.) at locality 1, and in the Westerschelde estuary (W.S.) at locality 2. Ranges of samples from Westerschelde localities 1, 2 and 3 (surface data only) and from Lake Veere locality 1 are indicated by vertical lines.

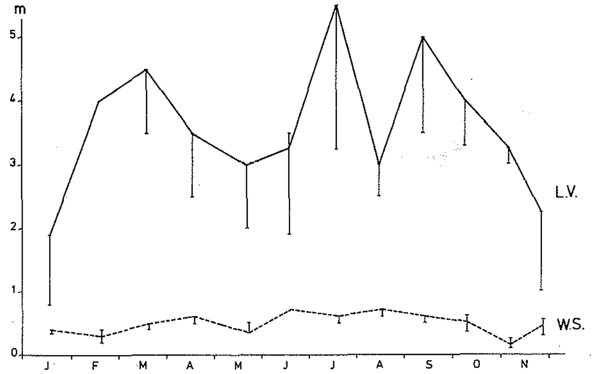

Fig. 6. Secchi disc visibility (metres) during 1974 in Lake Veere (L.V.) at locality 1, and in the Westerschelde estuary (W.S.) at locality 2. Ranges from localities 1, 2 and 3 are indicated by vertical lines.

ter contents in Lake Veere were always low (less than 10 mg/l).

Transparency values in the Westerschelde fluctuated between 0.2 and 0.7 metres. Suspended matter consisted mainly of silt and detritus, with values fluctuating between 20 and 220 mg/l. As a rule maximum values were measured in winter during stormy weather, minimum values (20-40 mg/l) in summer when algal blooms prevailed indeed, but at the same time sedimentation of heavier material proved important.

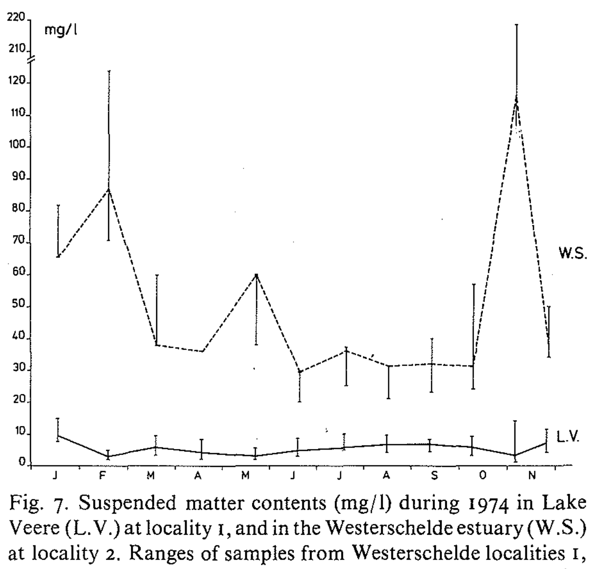

Fig. 7. Suspended matter contents (mg/l) during 1974 in Lake Veere (L.V.) at locality 1, and in the Westerschelde estuary (W.S.) at locality 2. Ranges of samples from Westerschelde localities 1, 2 and 3 (surface data only) and from Lake Veere locality 1 are indicated by vertical lines.

Size and biomass of the copepod standing stocks

Numerical densities of copepodid stages + adults, together with total biomass figures (wet weights), have been presented in Tables I and II. From the Westerschelde data (Table I) follows that average densities of *Eurytemora affinis* were always considerably larger than those of *Acartia* (*A. bifilosa* in winter, *A. tonsa* in summer). Only in September at locality 1 *A. tonsa* reached higher numbers than *E. affinis*. In most cases copepod numbers in the near-bottom samples were larger than in the surface samples. The detailed data about the abundance, dimensions and biomass of the different size classes will be dealt with elsewhere (Bakker, in prep.) In general, the deeper water layers contained more advanced copepodid stages and adults, the surface layers more young stages. Consequently, highest biomass values were found in the deeper water layers (with a few exceptions: station 2, May; station 1 and 2, September, *E. affinis;* station 3, October). *E. affinis* concentrations increased in the upstream direction, reaching maximal values in station 3 at high tide.

Lake Veere summer data have been presented in Table II. October and November values were of importance only in station 3. Biomass values during the remainder of the year, being on average less than 10 mg/m^3, were omitted as these data had no significance in comparison with those of the Westerschelde. Maximum copepod densities were found at different depths during the summer season. Large concentrations of animals were sampled in the top layers of localities 2 and 3 in July, but generally numbers increased in deeper layers. Older stages were found in deeper layers than young stages, just as in the Westerschelde. During summer copepods could not or hardly be found in the 15-20 m water layers of the stratified Lake Veere locality 3 as a consequence of oxygen depletion.

Comparison of average monthly biomass values from the Westerschelde with those from Lake Veere is given in Fig. 8. In the Westerschelde estuary *Eurytemora* biomass was high throughout the year, showing large values not only in spring (May: 2350 mg/m^3) and summer (August: 1940 mg/m^3), but also in winter (February: 1400 mg/m^3). The high winter biomass coincided with a low chlorinity (see Fig. 3), indicating a shift of *Eurytemora*-rich waters from the river in downstream direction. During August-October a marked decrease of population density took place. The lowest value (200 mg/m^3) was found in the beginning of November. The yearly

Table I. Abundance and biomass figures (wet weight) of *Eurytemora* and *Acartia* in the Westerschelde estuary. For location of the stations see Fig. 1. Data of nauplii are only given for locality 3. In December no samples were taken.

1974	species	copepodids + adults												nauplii			
		locality 1				locality 2				locality 3				locality 3			
		surface		depth		surface		depth		surface		depth		surface		depth	
		N/100L	mg/m^3	N/100L	mg/m^3	N/100L	mg/m^3	N/100L	mg/m^3	N/100L	mg/m^3	N/100L	mg/m^3	N/ L	mg/m^3	N/L	mg/m^3
18/1	E. affinis	494	62	1638	440	978	117	1575	778	1054	236	1833	1617	12	10	10	10
	A. bifilosa	0	0	325	55	108	13	125	37	0	0	0	0	0	0	0	0
19/2	E. affinis	650	168	1300	385	1520	330	2100	824	4500	2243	7800	4432	140	112	80	59
19/3	E. affinis	1165	169	1100	228	2481	262	1300	294	3850	598	2240	1091	82	125	100	143
	A. bifilosa	84	5	47	2	13	1	0	0	0	0	0	0	0	0	0	0
18/4	E. affinis	1710	275	2510	840	1520	178	4130	1341	4600	697	1400	597	190	192	84	61
22/5	E. affinis	8633	1893	10400	2976	12400	3412	3925	1277	2275	303	14400	4252	217	175	136	106
19/6	E. affinis	0	0	0	0	275	39	320	53	2883	258	13600	5253	308	465	95	96
19/7	E. affinis	300	20	1400	174	1200	147	3217	819	232	79	10650	3073	108	75	176	211
16/8	E. affinis	1095	81	2618	678	2288	151	2233	220	1600	543	31470	9972	338	282	272	295
	A. tonsa	150	8	436	89	300	14	300	19	120	10	0	0	0	0	0	0
13/9	E. affinis	250	67	50	12	738	78	600	72	1413	203	4275	1805	145	150	10	11
	A. tonsa	488	25	575	157	538	31	750	66	163	24	250	34	0	0	0	0
9/10	E. affinis	0	0	2075	497	198	30	560	237	992	359	500	295	40	56	7	8
	A. tonsa	288	31	375	145	255	32	0	0	0	0	0	0	0	0	0	0
6/11	E. affinis	1050	460	975	504	200	78	273	93	63	11	56	22	4	5	4	4
26/11	E. affinis	2100	145	1050	370	1917	191	1667	260	550	227	3070	1662	90	123	116	151

average was about 850 mg/m^3. Westerschelde values of *Acartia tonsa* were only of some importance during the period August-October but did not reach *Eurytemora* levels: peak numbers of *A. tonsa* in September represented an average of 56 mg/m^3, a value of only 15% of the *Eurytemora* biomass during that time. The average value of *A. bifilosa* biomass (Table I) was 18 mg/m^3 in January.

Copepod biomass in Lake Veere was mainly represented by the summer population of *A. tonsa,* showing a sharp increase during early summer, peak numbers in July and decreasing densities in late summer (Fig. 8).

Table II. Abundance and biomass (wet weight) figures of *Eurytemora* and *Acartia* (copepodids + adults) in Lake Veere. For location of stations see Fig. 1. Further explanations in the text.

1974			depths.										
			0 m		5 m		10 m		15 m		20 m		average bio-
date	locality	species	N/100L	mg/m^3	N/100L	mg/m^3	N/100L	mg/m^3	N/100L	mg/m^3	N/100L	mg/m^3	mass mg/m^3
18-6	1	E. americana	60	3	0	0	600	29	1500	107	4100	377	16
		A. tonsa	320	12	120	4	1800	52	760	40	3700	249	19
	2	E. americana	50	2	220	10	200	10	1460	94	40	4	10
		A. tonsa	520	16	460	18	1320	53	1800	147	8	0	26
	3	E. americana	100	6	220	18	1240	81	0	0	0	0	22
		A. tonsa	900	51	1020	80	2560	94	0	0	0	0	68
18-7	1	A. tonsa	11000	546	6600	327	4600	279	3100	257	2100	244	382
	2	A. tonsa	32200	1557	54000	2554	3300	247	1500	135	2220	271	1786
	3	A. tonsa	28800	2485	24900	1756	14900	979	0	0	0	0	1818
15-8	1	A. tonsa	2300	122	1650	131	2100	159	5800	955	8600	1848	194
	2	A. tonsa	1880	116	1620	103	2360	174	3440	351	2250	443	126
	3	A. tonsa	1230	38	2270	64	1460	50	0	0	0	0	50
12-9	1	A. tonsa	120	4	1740	62	1140	48	1120	71	1900	317	44
	2	A. tonsa	640	24	700	36	810	38	1680	169	2820	462	38
	3	A. tonsa	880	24	1120	32	760	31	370	22	4000	698	33
8-10	3	A. tonsa	70	2	490	17	850	34	1830	104	560	26	18
5-11	3	A. tonsa	40	1	890	39	950	50	11700	725	480	23	56

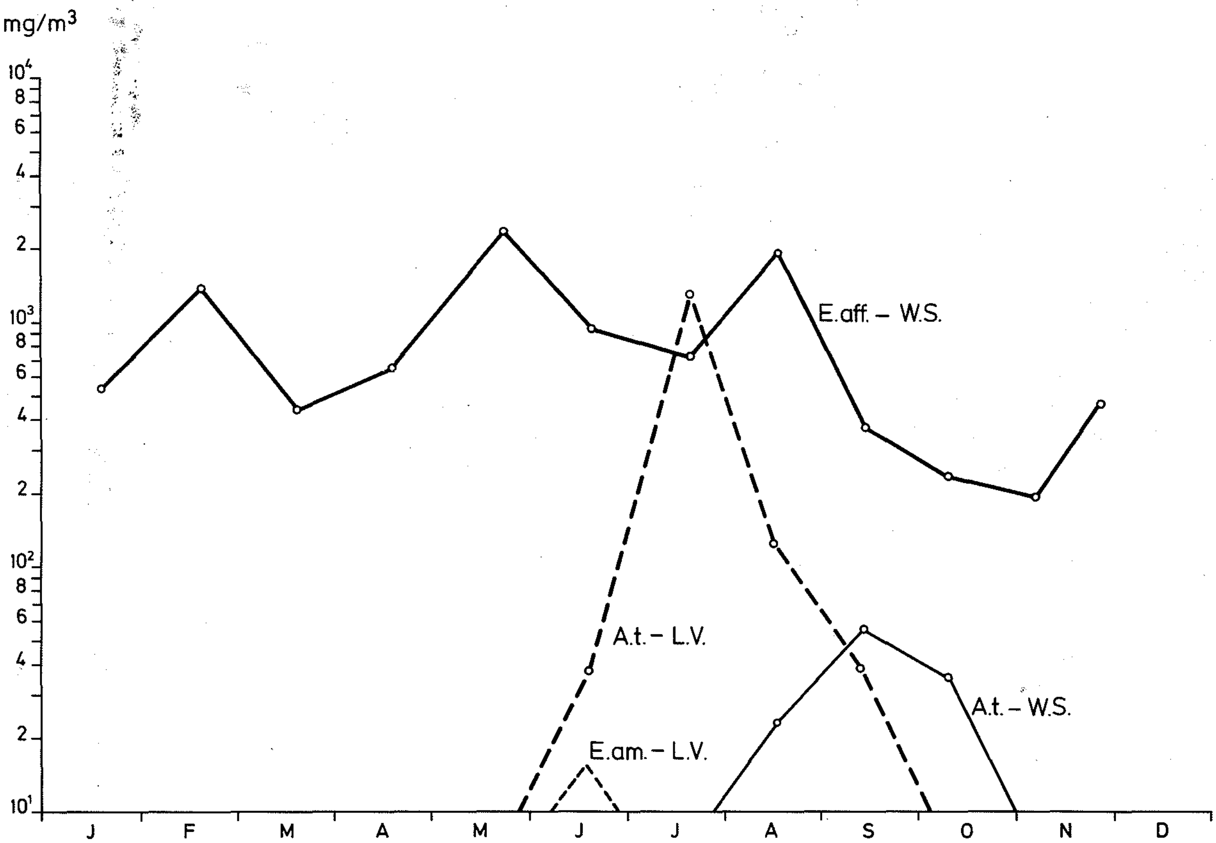

Fig. 8. Copepod biomass, expressed as mg/m³ wet weight values of copepodid + adult stages, during 1974 in the Westerschelde estuary (*Eurytemora affinis:* E. aff.; *Acartia tonsa:* A.t.) and in Lake Veere (*Acartia tonsa;* A.t. broken line; *Eurytemora americana;* E.am., idem).

Only in June the biomass of *Eurytemora americana* was of some importance, amounting to 16 mg/m³. Spring biomass (March-May) of *E. americana* was less than 10 mg/m³ in 1974. Only in summer Lake Veere reached standing stock levels equaling those in the Westerschelde estuary. The average yearly copepod biomass of Lake Veere was approximately 130 mg/m³, strikingly lower than the average Westerschelde value of 850 mg/m³. Evidently the tidal estuary harboured dense copepod populations nearly throughout the year whereas the stagnant lake water did so only during a short summer period.

Besides information on copepodid and adult copepod biomass we tried to get an impression of the naupliar biomass. Only in the Westerschelde counts and measurements of nauplii were performed in the samples of locality 3 (Table I). Abundance of nauplii was nearly always far greater than of the older stages. High numbers of all stages occurred already in February. The yearly average of nauplii was about 120 individuals/litre, representing a high percentage (71%) of the total numerical density (copepodids and adults amounted to an average of 50 individuals/litre = 29%). Calculation of the average yearly biomass of Westerschelde locality 3 resulted in 1660 mg/m³ for copepodids + adults and in 125 mg/m³ (less than 8%) for the naupliar stages. Biomass values for both categories differed maximally in January when reproduction of the rather large remaining stock of copepods hardly had been started and very low numbers of nauplii were found, even below the level of copepodids + adults. The bulk of total copepod biomass, up to 90-99%, consisted of copepodids and adults. The portion of naupliar stages in the surface water samples increased from 17% in March to 63% in June. In the nearbottom water nauplii always played a minor role (mostly less than 10% of total copepod biomass).

Discussion

Discussing the large differences in relation to size and biomass of copepod standing stocks between Lake Veere and the Westerschelde estuary, we have to return to the evaluation of our sampling methods. We supposed that avoidance behaviour of copepods plays a neglible role in tidal areas where strong water movements level down the influences of pumping. Values of the Westerschelde therefore, based on pumped samples, were supposed to be adequate. In Lake Veere, however, numbers of larger copepodids and adults might be somewhat too low owing to avoiding reactions of the animals as a result of the water movements caused by pumping. Patalas (1954) demonstrated that quickly swimming planktonic crustaceans (*Leptodora, Eudiaptomus*), were sampled in too low numbers with a plankton pump in comparison with a planktontrap. Comparing synchronous copepod catches of the two devices in Lake Veere, we could demonstrate that the trap was 2.5 times as efficient as the pump. Consequently, our copepod data obtained by pumping alone were corrected with this factor in Lake Veere. A detailed analysis of the results of the pumping method compared with those of the plankton trap will be given elsewhere (Bakker, in prep.). The plankton trap could not be used in the turbulent tidal waters of the Westerschelde estuary. Generally, however, any systematic sampling error will probably result in rather too low than too high densities of zooplankton organisms (Heinle, 1966), sampled by whatever technique. Larger Westerschelde values therefore would only cause an increase of the demonstrated differences between both areas. Moreover, some pump series of detailed vertical sampling during 1975 in the Westerschelde showed that mostly zooplankton was more abundant on a depth of 5 metres and below than at the surface. Thus, the presented Westerschelde averages will again result in rather too low than too high values. Therefore, the large differences in average copepod standing stock between the estuary and the lake, have to be at least as large as calculated, being probably larger.

In relation to the environmental factors being of importance to copepods, the oxygen values show that *Eurytemora affinis,* as well as *Acartia tonsa,* must be extremely tolerant to (very) low oxygen levels. They were counted in numbers within the total oxygen ranges figured; the animals disappeared only after total oxygen depletion occurring temporarily in the deeper water layers of locality 3 in Lake Veere (Fig. 4, Table III: 18/6, 18/7, 15/8). *E. americana* and *A. tonsa* were still found in water with 0.4 mg O_2/l (Lake Veere, locality 2, 18/6, 20 m). Maximum densities of *A. tonsa* still occurred when 3 mg O_2/l was present (Lake Veere, locality 3, 12/9, 20 m.). *E. affinis* abundance was even large at the 1.5-1.6 mg O_2/l level (Westerschelde, locality 3, July and August); some animals were still found alive in the presence of 0.1 mg O_2/l (Westerschelde, locality 3, 6/11). Hoos (1970; in Davis, 1975) observed several species of pelagic invertebrates inhabiting an oxygen minimum layer (approx. 0.57 mg O_2/l) in a British Columbia inlet. The copepod *Calanus plumchrus* even showed tendencies to remain there. In his discussion about the oxygen requirements of aquatic invertebrates Davis (1975) stated that (p. 2318) tolerance tends to be correlated with habitat so that individuals normally living in well-oxygenated water are less tolerant of low dissolved oxygen values than those encountering it periodically. The tolerance of the species involved and the duration of low oxygen conditions are of prime importance to survival.

Low oxygen values thus gave no indications to influence negatively the copepod populations in the Westerschelde. Possible high concentrations of harmful substances (heavy metals, pesticides), not measured by us, evidently had negative effects either. Not only *E. affinis* has proved a surprising adaptation to the strongly polluted environment of the Westerschelde estuary, but, as we showed earlier (Bakker & De Pauw, 1975), several other characteristic components of the brackish water plankton assemblage too. The question arises how long estuarine pollution may increase before aquatic life will become seriously affected.

In the northeastern estuaries of the U.S.A. *E. americana* and *E. affinis* occur together (congeneric associates: Jeffries, 1967). The main factor regulating the relations in time and space between the two species appeared to be their different temperature requirements or tolerances. According to Katona (1971) different salinity requirements or tolerances may have modified that pattern. As a rule *E. americana* is not found in water of very low salinity and prefers lower temperatures. *E. affinis* on the other hand is able to tolerate even fresh water and tolerates or prefers higher water temperatures to certain limits (Katona, 1970, 1971; Jeffries 1967; Bradley, 1975). This is the explanation for the absence of *E. americana* in the mesohaline zone of the Westerschelde as well as the presence of this copepod in the meso-polyhaline Lake Veere in spring. *E. affinis* is the prominent estuarine copepod as was demonstrated by its almost perennial occurrence and

dominance in the Westerschelde estuary.

In Lake Veere temperature-salinity combinations seemed only suitable for *E. affinis* when salinity fell below 8‰ Cl′ during longer periods (Bakker & De Pauw, 1975). During polyhaline periods of Lake Veere *E. affinis* could not be demonstrated. Its absence however might partly be caused by the fact that only a few individuals of the species were able to enter the lake during that time, due to the strongly decreased discharges of oligohaline polder-water, introducing *E. affinis* in the lake. Polyhaline conditions as such cannot be the main reason for the absence of *E. affinis* because von Vaupel-Klein and Weber (1975) demonstrated from field data that the species is able to reproduce in chlorinities up to 12.5‰. In their laboratory fresh water grown animals rapidly acclimated to intermediate salinities (8‰ Cl′), and obtained an increasing tolerance to higher salinities (18‰ Cl′) in which survival for considerable time was possible. Moreover, Bradley (1975) demonstrated that resistance of *Eurytemora affinis* to higher temperatures increased with rising salinities. His results seemingly conflict with the usual seasonal distribution of the species. Bradley (l.c.) suggested that competition with *Acartia tonsa*, the dominant summer copepod, might be an important factor influencing the distribution of *Eurytemora affinis* in summer. Essential for this assumption were the findings of Heinle (1969) that the growth rate of *E. affinis* is equal to that of *A. tonsa* at 12°C, but only half as great at 25°C. Moreover, abundance of *A. tonsa* may be closely related to phytoplankton densities, whereas abundance of *E. affinis* is not, resulting in additional competitive advantage to *A. tonsa* in summer and autumn. The foregoing considerations explain the dominance of *A. tonsa* in Lake Veere.

In the investigated stretch of the Westerschelde estuary *A. tonsa* densities of 1974 were not large. The species, abundant in the polyhaline region from August to September, was able to extend in upstream direction (Fig. 8, Table I), when in August water temperature passed 19°C (Fig. 2) and chlorinity of locality 1 and 2 was ± 11‰ (Fig. 3). In the same area *E. affinis* biomass strongly decreased at the same time. In previous years *A. tonsa* even reached absolute dominance in the geographic region normally occupied by *E. affinis* (unpublished data). Therefore the seasonal development of both copepods in the Westerschelde is explained again by the results of Heinle (1969) and Bradley (1975).

The copepod year cycle of 1974 was studied in the mesohaline area of the Westerschelde estuary, whereas Lake Veere was polyhaline during the greater part of the year (Fig. 3). Bakker & De Pauw (1975) demonstrated that the polyhaline periods of Lake Veere were not characterized by smaller biomass values than the mesohaline periods and therefore we are allowed to exclude salinity as a factor causing the relatively small copepod biomass of Lake Veere.

What factors influence the copepod development in the Westerschelde estuary in such a positive way in comparison to Lake Veere, especially in spring? Food conditions for copepods have to be considered of prime importance. In Lake Veere favourable food conditions exist during the period of increasing and relatively high water temperatures. In spring and summer therefore the best combination of favourable physical and biological conditions for the development of copepod plankton is found. However, the early phytoplankton spring peaks in Lake Veere (Bakker & De Pauw, 1974) are not, or hardly used by *E. americana*. Food competition with the dense rotifer plankton (*Synchaeta* spp.) in early spring and with polychaete larvae somewhat later may be a cause for the poor response of this copepod. Rotifer and polychaete reproduction in Lake Veere, starting in February, are apparently less dependent on rising water temperatures in spring, whereas copepod reproduction did not start under the same low temperature conditions. When in March-April water temperature rises, rotifers and polychaetes have already reached large concentrations and thus may represent serious competitors for the copepods. In the mesohaline area of the Westerschelde on the other hand, rotifers and polychaetes never play an important role (De Pauw, 1975; Bakker & De Pauw, 1975) and competitive power of these groups can thus be excluded. Low water temperatures in spring did not prevent the start of the *E. affinis* reproduction, evidenced by increasing percentages of naupliar biomass in March (Table I).

Spring phytoplankton biomass in the Westerschelde estuary is small (Bakker & De Pauw, 1974). The *Eurytemora affinis* populations, however, are remarkably abundant almost throughout the year in the estuary, showing even high winter levels. A wellknown feature of the estuarine environment is the always large amounts of suspended matter. Although large fluctuations occurred in the Westerschelde (Fig. 6), sediment quantities were always considerably higher than in Lake Veere. Microscopical examination of the suspended material demonstrated, besides sand and silt, a large variety of particulate organic detritus. The material consisted partly of smaller and larger fragments of higher plants, not

suitable as copepod food owing to the difficult digestion of the cellulose walls. Initially these particles represent mainly a source of carbohydrates, but the older detrital stages, occupied by bacteria, are also of significance as nitrogen source (Darnell, 1967). Besides plant debris dead marine and freshwater plankton organisms were always present. The largest part of the detritus source consisted of 'nannodetritus' particles (Odum & de la Cruz, 1967), probably a sort of organic aggregates, small flocculate particles, diam. 10-30μ, occupied with bacteria and/or μ-algae. In Lugol fixed 1 litre samples these particles were initially considered artefacts, clotted during the sedimentation process. Freshly sampled material, not fixed but immediately studied, appeared to contain the same flakes. Odum & de la Cruz (1967) showed that this form of detritus represented 95% of total detritus content in a salt marsh-estuarine ecosystem (Georgia, U.S.A.). This form of bacteria impregnated detritus was characteristic for the studied area of the Westerschelde estuary. The detrital aggregates were present throughout the year in large amounts, representing in this way, in our opinion, an important stable factor in the otherwise so unstable estuarine tidal environment. We have not observed the actual utilization of these particles by the copepods, but it would be a remarkable feat of selection for estuarine animals to avoid ingesting this material in quantitites (Darnell, 1967, p. 379). The continuous supply of this highly qualified detrital food may explain the constantly high copepod population densities in this part of the estuary. Other food sources during the phytoplankton-poor period were not available. In this way the significance of eventual phytoplankton peaks may be restricted in such a food regime, although small phytoplankton cells must be qualitatively of great value. Darnell (1967) argues that estuarine areas of zooplankton abundance are correlated with centers of detritus abundance, rather than with phytoplankton abundance.

The above mentioned findings and considerations are in full agreement with the recent investigations of Heinle & Flemer (1975) who published an important paper about the *Eurytemora affinis* dynamics in the Patuxent River (U.S.A.). In the upper part of this estuary the water is highly turbid, as in the Westerschelde, and no pronounced spring phytoplankton maximum could be demonstrated here as well. Heinle & Flemer showed that gross algal production was 5-75 times smaller than the carbon requirements of the local *Eurytemora* population. Detrital carbon on the other hand was always present in large amounts. Thus, this organic detritus probably constitutes an important link between primary and secondary production in the estuarine ecosystem, bacteria being essential for the transfer of energy through this food chain. The constantly large amount of detritus present will have a stabilizing effect by leveling out the results of changing rates of primary production due to seasonal or other variations in external factors (Fenchel, 1972).

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