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Consumption and assimilation by zooplankton related to primary production in the baltic coastal water inlet Barther Bodden

With 7 Figures and 3 Tables

Abstract

Data about the annual fluctuation of the main planktic biomass components, primary production and zooplanktic consumption and assimilation are presented for a swallow brackish coastal water inlet. Primary production was about 2000 mgC m^{-2} · d^{-1} during the spring bloom in April. From May — September it was 1500 — 1000 mgC m^{-2} · d^{-1}. The consumption by zooplankton amounted to about 10% of the primary production in May, but less than 3% from June — September. In May the secondary production reached a maximum of 3% of the primary production. Simulation of the field data in a mathematical model indicates that the main reason for the low efficiency of trophic transfer is the dominance of blue-green algae in summer.

1. Introduction

The planktic food web in the highly eutrophic Barther Bodden (mean depth 1.8 m, area 19.4 km^2, Fig. 1) is generally characterized by low efficiency (Schnese & Heerkloss 1978, Heerkloss et al. 1980). This gives rise to the question of the factors that limit trophic transfer between primary producers and consumers. To clarify this, the annual fluctuations of planktic primary production and consumption were comparatively studied and feeding and assimilation rates were used to set up and check a mathematical model of the annual fluctuation of the copepods biomass.

2. Methods

All biomass determinations were done by counting fixed samples in an inverted microscope and using mean volume equivalents for the different species. Primary production was measured at 4 stations in the Barther Bodden by means of the in-situ ^{14}C-method (Steemann Nielsen 1952).
A ^{14}C-method described by Schnese & Heerkloss (1978) was used to measure the feeding rates at sampling sites. The animals were caught in nets, cleaned by means of a light trap (Heerkloss & Arndt 1981) and imme-
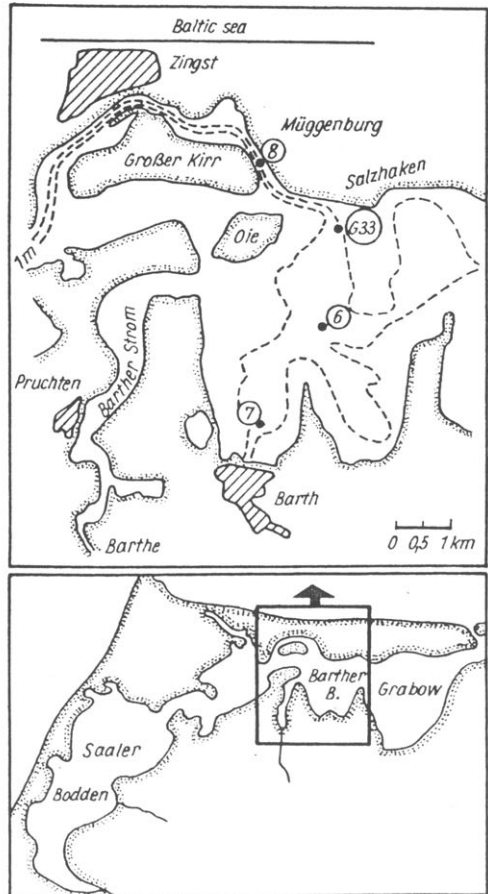

Fig. 1. Area of investigation (6, 7, 8 and G 33 indicate locations of in-situ primary production measurement)

diately placed in site water labelled with ^{14}C-bicarbonate for two days. The animals were handled with great caution during the transfer operation in order to avoid startingstress. The animals were fed for a short period of 10−20 minutes. The feeding rates related to the weight of the animal (specific feeding rate) was then calculated from the relationship between the radioactivity per unit dry weight in the food and in the animals. The animals were divided into a larger and a smaller size class by means of nets with appropriate mesh size (115 μm and 65 μm respectively). As a rule over 95 % of the biomass in the larger fraction was composed of adult copepods and copepodids. Rotifers predominated in the smaller fraction, but this fraction also contained nauplii of copepods and cirripedes, protozoans, and other small zooplankters. The consumption of suspended organic matter by zooplankton expressed as feeding activity per square meter (absolute feeding rate) was calculated by multiplying the specific feeding rates with the standing crop of zooplankton.

The assimilation rate was determined under field conditions by a method similar to that described by Sorokin (1968). The animals were fed for a longer period (100 to 200 minutes) with ^{14}C-labelled natural phytoplankton whereupon their guts emptied by means of food containing no tracer. The assimilation efficiency was calculated as the quotient of the assimilation and the feeding rate. To determine the assimilation efficiency directly the ^{51}Cr-indicator method described by Carlow & Fletscher (1972) was used. In these experiments the food was marked with two tracers: ^{14}C and ^{51}Cr. In double labelled samples these two kinds of tracers can easily by distinguished because they emit different kinds of radiation. When they are included in the food source it are mainly the components marked with ^{14}C that are resorbed, while the ^{51}Cr passes through the gut virtually without quantitative change. In *Eurytemora affinis* (Poppe) 1−5 % of the ^{51}Cr consumed was resorbed in the gut. If the ^{51}Cr activity in the fecal pellets was corrected to compensate for chrome resorption, the quotient ^{14}C/^{51}Cr for the fecal pellets and food could be used to calculate the assimilation efficiency for ^{14}C. To avoid toxic effects caused by the chromium the algae used as food were separated from the

medium containing the tracer by centrifugation before the experiment and resuspended in medium containing no chromium. Furthermore the chromium concentration of 10 μg/l was below the toxicity limit given in the literature (Jørgensen 1979).

The seston content was determined by filtration of 10−50 ml through membrane filters with a pore size of 0.4 μm and weighting on a microbalance.

To express rates and biomass concentrations in appropriate dimensions the conversion factors according to Heerkloss & Vietinghoff (1981) were used (Table 1).

3.   Results and discussion

The quality and quantity of the zooplankton in the Barther Bodden was ascertained by means of a routine programme conducted over 11 years. The means show a characteristic annual fluctuation for the development of the population that is regularly repeated every year (Fig. 2). The copepod population increases and thrives in April and May, the typically brackish species *Eurytemora affinis* (Poppe) being almost the sole species involved. The copepod population declines in June to reach almost the level of February and March. A second copepod peak composed of the more thermophile species *Acartia tonsa* Dana in addition to *E. affinis* appears in August. In the meantime the considerable reduction in copepod biomass in June and July is partly compensated for by the rapid development of rotifers. The dominant species are *Brachionus calyciflorus* Pallas, *B. quadridentatus* Hermann, *B. plicatilis* (O. F. Müller), *Kertella cochlearis* (Gosse), *K. quadrata* (O. F. Müller) and *Filinia longiseta* (Ehrenberg). The remainder of the zooplankton consists mainly of phyllopods and ciliates.

Table 1. Conversion factors according to Heerkloss & Vietinghoff (1981)

	dry:fresh weight	ash:dry weight	carbon:organic dry weight	Joule/mg C
Cyanophyta	0.3	0.09	0.5	40
Chlorophyta	0.3	0.12	0.6	38
Bacillariophyceae	0.4	0.4	0.55	42
Zooplankton	0.17	0.1	0.5	48
Detritus	—	0.4	0.5	32

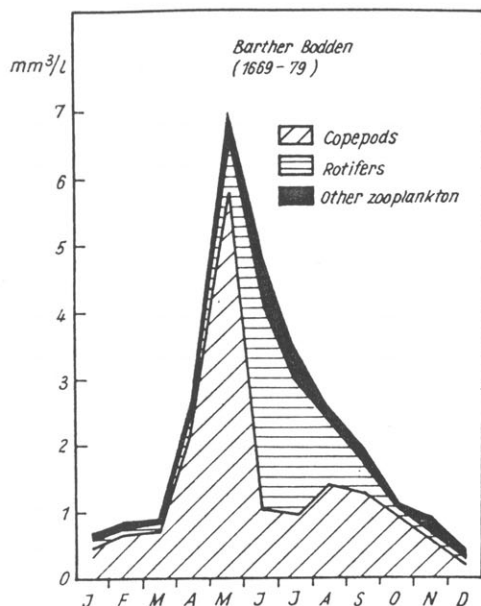Specific weight: Bacillariophyceae 1.1; other phyto- and zooplankton 1.04

Fig. 2. Annual fluctuation of mean zooplankton biomass, Barther Bodden 1969—1979

Fig. 3. Annual variation of the specific feeding rate of zooplankton; size class >115 μm (mainly copepods); mean and S. D. 1976—1980; long-term mean of temperature from BROSIN (1965)

The annual variation in the specific feeding rate of the copepods was plotted and compared with the curve of the annual mean temperature variation (Fig. 3). Although there was a correlation between the two parameters, some differences between the curves indicate that temperature alone cannot be the cause for the different feeding rates in spring and summer. A more feasible explanation would be differences in the quality of food.

The specific feeding rates of small zooplankters were measured only in June and July, the time when rotifers dominate. Their feeding rates were on average 2.3 times as high as those of the copepods during the same period.
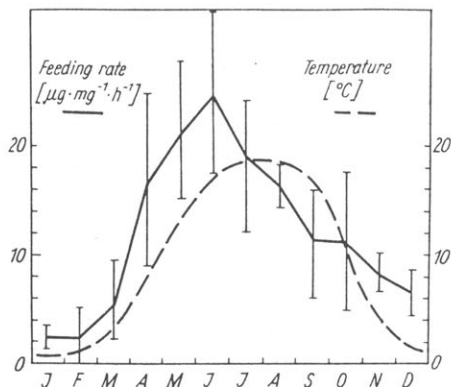
The fact that the feeding activity of many zooplankters is subject to diurnal variations (DUVAL & GEEN 1975, HANEY & HALL 1975) had to be considered. Three experiments conducted at different times of the year were therefore used to investigate diurnal variations in the feeding and filtering activity of copepods. The curves obtained from all three experiments were similar (Fig. 4 A—C). Activity was especially high in the evening, declined rapidly during the night to reach a minimum in the early morning, increased to a second small maximum around midday and then declined again. As a rule our short term experiments (Fig. 3) were conducted between 9 a.m. and 11 a.m. During this period the curve did not differ substantially from the daily mean. It therefore seemed justified to calculate the daily feeding rates directly from the rates obtained during the short term experiments.

We shall take one year as an example to compare

Table 2. Assimilation efficiency of E. affinis with different kinds of food; mean and 5%-confidence level

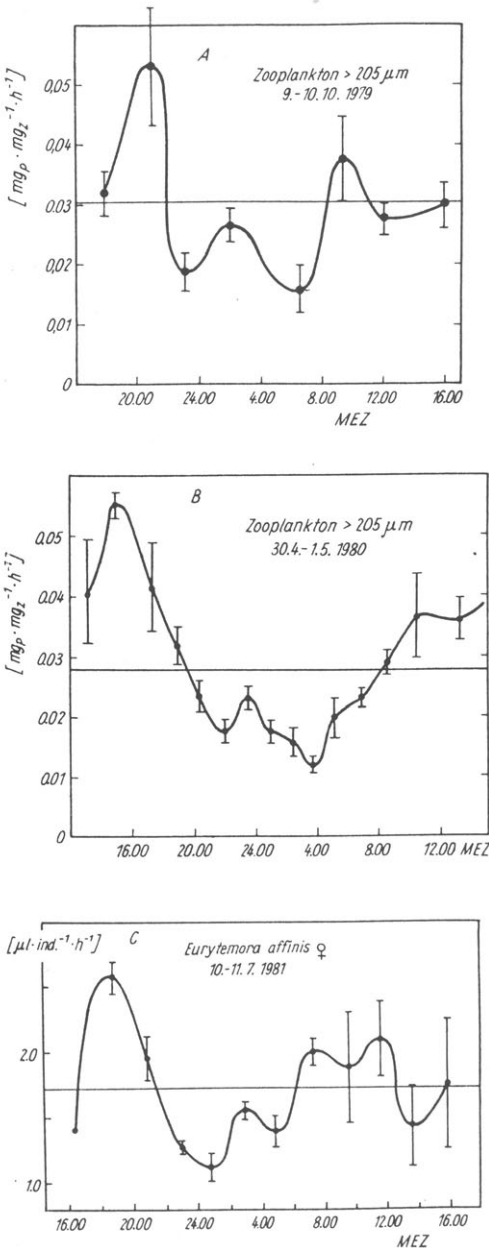| Kind of feed	$^{14}C/^{51}Cr$-method	^{14}C-method
Natural phytoplankton	75.7 (±18.6)%	—
Dunaliella tertiolecta	59.0 (±15.3)%	—
Dunaliella viridis	43.3 (±15.6)%	—
Chlorella vulgaris	78.0 (±5.4)%	53.3 (±25.1)%
Microcystis firma	60.7 (±6.1)%	—

Fig. 4. Diurnal variation of the specific feeding and filtering rates respectively of copepods: mean and S.D. of 2—3 experiments:

A and B: Mixed samples of adults and copepodit stages: C: Females of *E. affinis* (the horizontal line corresponds to the daily mean)

planktic primary production and consumption. Fig. 5 shows the annual variations of the different rates. The absolute feeding rate of the copepods as well as of the whole zooplankton was considerably lower than primary production for the whole year. The relation between the two, the "utilization efficiency" (Hall & Hyatt 1974), reached its maximum of 9.8 % in May. The relation in July, August and September after the decline of the copepod population was much worse (Fig. 6). It can be concluded that the energy flow through the gracing food chain becomes unimportant in summer.

Assimilation efficiencies determined under field conditions with the method according to Sorokin (1968) exhibited major statistical fluctuations so that it was impossible to calculate the annual variation of this parameter with any certainty. The only apparent trend was that copepods had higher values in summer than in winter. From April—September their mean assimilation efficiency was 43.9 ($\pm$ 19.2) % compared with 21.4 ($\pm$ 20.5) % for the period from October—March. A mean of 24.4 ($\pm$ 17.2) % was calculated for the small zooplankters.

The ^{14}C-method to measure the assimilation has drawn critism from some authors (Johannes & Satomi 1967, Conover & Francis 1973, Lampert 1977). They argue that some of the ^{14}C is rapidly reliberated in the course of feeding, attention being drawn especially to the fact that some of the low-molecular ^{14}C-compounds will be liberated by respiration immediately after resorption in the gut. We therefore undertook parallel experiments involving another method for measuring assimilation efficiency. We used the ^{51}Cr-indicator method described by Carlow & Fletcher (1972). With this method the problem of ^{14}C-losses due to respiration does not arise. It has also the advantage of lower statistical variability because it measures assimilation efficiency directly. With the ^{14}C-method, in contrast, two separately measured quantities, the feeding and assimilation rate, are compared. Table 2 shows the initial results obtained with different cultured algae and phytoplankton. The efficiency values obtained were significantly higher than in experiments with only ^{14}C. We adopted an assimilation efficiency of 75 %
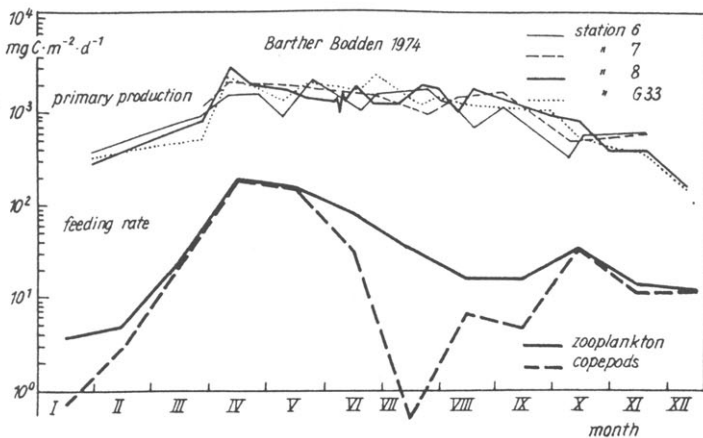
Fig. 5. Planktic primary production and consumption by zooplankton in the Barther Bodden in 1974
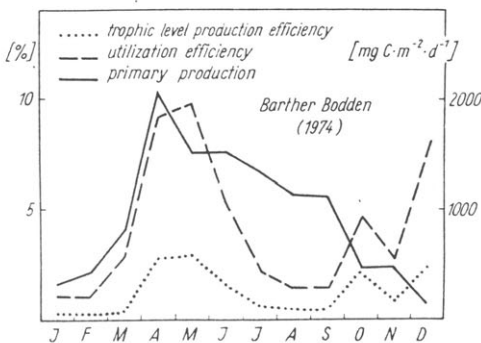

Fig. 6. Primary production and its relation to consumption and production of zooplankton

to calculate the absolute assimilation rate of zooplankton and, taking a net production efficiency coefficient of $K_2 = 0.4$, secondary production. Secondary production relative to primary production, the "trophic level production efficiency", reached its maximum of 2.9 % in May. From July—September it was less than 1 % (Fig. 6).

An attempt has been made to simulate our in-situ results for copepods in an mathematical model of the Barther Bodden ecosystem. It has proved difficult to simulate the extremely rapid decline of the copepod biomass in June. Possible factors that had to be taken into account were temperature, predation, food

quantity and food quality. It seems unlikely that the increase of water temperature from a mean of 13.5 °C in May to 17.0 °C in June (with maximum values of 25 °C) is the cause. BRADLEY (1975) states that the upper limit to the temperature tolerance of E. affinis is around 30 °C and furthermore, that the adaptability of this species to temperature fluctuations is very good. Predation will play some role, but the estimated grazing rates of juvenile fish, herring, smelt and the mysid Neomysis integer are so low that this factor, too, can scarcely be considered the sole cause. Food quantity can also not be regarded as a plausible reason because, as shown in Table 3, there is an increase of phytoplankton biomass and seston content from May—June. So the animals should not have a shortage in food. The main cause seems to be the qualitative composition of phytoplankton. The portion of blue-green algae in the particulate organic matter increases from 9.04 % in May to 15.30 % in June whereas the portion of green algae and diatoms decreases (Table 3).

The following assumptions were made for the mathematical model:

1. Copepods use only diatoms and green algae as energy sources, only the nanoplankton among these algae coming into question as a food source.

2. Copepod mortality is correlated to the blue-green algae biomass.

Table 3. Phytoplankton, zooplankton and seston content and percentage composition of suspended particulate organic matter in the Barther Bodden phytoplankton biomass mean 1971—1979; zooplankton biomass mean 1969 - 1979; seston content mean 1978 - 1981; 5 % -confidence level in brackets; data about phytoplankton from S. Nasev (unpubl. research report, Rostock 1980)

	Jan.	Febr.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Seston content (mg dwt l)	15.1 (±2.5)	28.0 (±14.8)	30.5 (±8.5)	34.4 (±2.6)	42.2 (±3.2)	51.0 (±2.1)	45.2 (±2.4)	42.6 (±6.9)	38.2 (±1.5)	41.2 (±8.9)	44.9 (±7.1)	29.1 (±25.0)
Phytoplankton biomass (mm^3/l)	6.87 (±4.2)	5.42 (±3.2)	11.39 (±2.5)	18.57 (±18.7)	15.20 (±5.1)	22.37 (±11.6)	21.63 (±6.9)	27.21 (±17.2)	14.30 (±6.5)	13.65 (±7.6)	9.08 (±11.9)	8.08 (±12.1)
Zooplankton biomass (mm^3/l)	0.66 (±0.35)	0.86 (±0.22)	0.89 (±0.42)	2.78 (±1.41)	6.90 (±3.52)	4.88 (±1.91)	3.45 (±1.21)	2.54 (±0.97)	1.90 (±0.64)	1.16 (±0.36)	0.92 (±0.44)	0.47 (±0.43)
Percentage composition of particulate organic matter:												
Cyanophyta	16.72	3.16	6.33	8.50	9.04	15.30	20.12	28.25	15.19	12.91	5.16	7.10
Chlorophyta	3.32	2.44	4.30	6.97	5.78	4.30	2.09	1.21	1.68	1.35	3.86	4.36
Bacillariophyceae	1.24	2.87	5.83	8.62	1.66	0.85	0.45	0.66	0.83	0.31	0.37	1.22
Other phytoplankton	0.15	0.29	0.41	0.31	0.30	0.50	0.09	0.22	0.04	1.12	0.11	0.15
Zooplankton	1.17	0.82	0.78	2.16	4.38	2.56	2.05	1.60	1.33	0.73	0.55	0.43
Detritus and microorganismus	77.46	90.42	82.36	73.44	78.81	76.77	75.21	68.07	80.93	83.55	89.96	86.40

3. Detritus as a food source can be neglected.

The special importance of green algae and diatoms as food source for copepods was also stressed by BOSSELMANN (1975) in the case of Lake Esrom. The second assumption may be supported by the fact that in Gdansk bay the chlorophyll content of the gut of copepods is very low when blue-green algae are dominant among the phytoplankton (E. STYCZYNSKA-JUREWICZ, pers. comm.). The third assumption could be made because the detritus in the Barther Bodden is mainly resuspended from the sediment with a high degree of degradation. BOWEN (1979) reports that detritophagous fishes show signs of protein deficiency when fed on old, greatly degraded detritus.

Using these assumptions it was possible to fit the curves from the model sufficiently closely to those derived from measured values (Fig. 7). In the model however, the copepod population collapses somewhat later.

Further experiments are necessary to check the validity of these assumptions in order to refine the quantities used in setting up and checking the model. The results show how modelling can draw the attention of the experimenter to new problems. It can be concluded, that the dominance of blue-green algae in summer is an important factor that limits the trophic transfer from primary producers to secondary producers to secondary producers in the planktic system of the Barther Bodden.
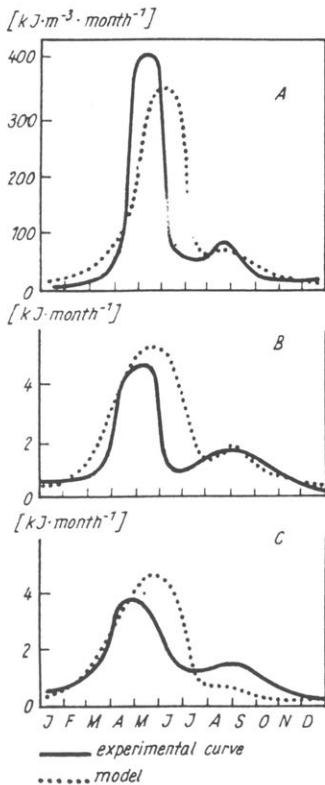

Fig. 7. Comparison of the experimental and model curves of the annual fluctuation of biomass and consumption of copepods;

A: Absolute feeding rate of juvenile and adult copepods; B: Biomass of adults; C: Biomass of juvenils

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