Abundances and Production of Copepods in the Rhode River Subestuary of Chesapeake Bay

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ABSTRACT: Seasonal fluctuations in zooplankton abundance between July 1973 and July 1974 showed a clear peak in total copepods and rotifers in February-March, and a less pronounced peak in July-August. Standing crop and production estimates for the two dominant copepods, Acartia tonsa and Eurytemora affinis, revealed that the February-March peak was primarily E. affinis and sustained far higher biomass (218.6 mg/m³) and production (20.5 mg/m³·day) than did the August peak of A. tonsa (biomass 16.3 mg/m³, production 7.5 mg/m³·day). The Rhode River has low standing crop and production of copepods relative to the much larger Patuxent estuary. These results are consistent with the theory of Williams et al. (1968) that shallow embayments have lower standing crops; however, the statistical basis for their statement is shown to be spurious.

Introduction

The maximum standing crops of copepods in Atlantic and Gulf Coast estuaries vary over nearly an order of magnitude (Williams, Murdoch and Thomas 1968; Heinle 1966). Studies of production dynamics are still relatively few to say whether production varies to the same degree. During 1973-74 we had the opportunity to study the annual production cycle of copepods in Rhode River, a small subestuary of Chesapeake Bay. Since Heinle (1966) has extensively analyzed copepod production in the larger Patuxent River estuary, and Williams et al. (1968) suggested that copepod standing crops correlate positively with embayment depth, our data are compared to those for the Patuxent to determine whether a similar relationship exists for production. We describe the composition of the zooplankton community as it varies seasonally and spatially towards its junction with Chesapeake Bay, and estimate the standing crops and biomass production for the two dominant copepods Acartia tonsa and Eurytemora affinis. Finally, we discuss the contention of Williams et al. (1968) that shallow embayments have low standing crops of zooplankton.

Methods

The Rhode River is a small tributary estuary entering western Chesapeake Bay approximately 8 km south of Annapolis. It is less than 5-km long and generally less than 1-km wide, with a total surface area of 5.9 × 10⁶ m² and volume of 11.47 × 10⁶ m³. Depths range between 1 and 3 m and average 1.94 m (Pritchard and Han 1972; Seliger and Loftus 1974). The Rhode River is subject to strong vertical and lateral mixing due to wind and tidal currents and is essentially isohaline in character. The annual salinity cycle normally reaches a peak of 12 to 16% about October and a low of 4 to 8% in June (Seliger and Loftus 1974).

Four sampling stations (Fig. 1) were selected from the mouth of Muddy Creek to the opening of the Rhode River to Chesapeake Bay. Station 9 is at the mouth of Muddy Creek, station 11 is midway between Big and High Islands, station 12 is located in midchannel off locust Point, and station 13 is

located between Cheston and Dutchman Points at the mouth of Rhode River. These stations form a transect 0, 1.1, 2.3 and 4.5 km from the mouth of Muddy Creek.

ZOOPLANKTON SAMPLING

Samples were collected with a #20 (80 $m\mu$) Wisconsin net from July 1973 to July 1974 at about mid-day and include various phases of the tidal cycle. At each station, 10 or 20 vertical hauls were made along a transect line 30-m long, resulting in a combined volume of water sampled of approximately 500 liters per station. The exact volume was recorded at each sampling. Samples were passed through a 2-mm sieve to remove ctenophores and preserved in 8% formalin. Depending on zooplankton densities, a 5 or 10% subsample was later removed for analysis. All copepods were identified to species and counted in the following categories: nauplii, copepodids and adults. The first 200 individuals in each sample were measured for total body length.

BIOMASS AND PRODUCTION ESTIMATES

Biomass and production for Acartia tonsa and Eurytemora affinis were estimated by the method of Heinle (1966, 1969). The instantaneous death rate for nauplii is given as:

$$-d_n = (1n C - 1n N)/t_n$$
 (1)

where d_n is the instantaneous death rate, C is the total number of copepodids and N the

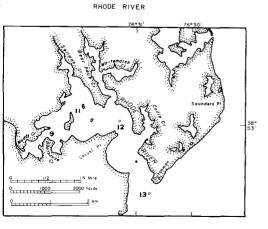


Fig. 1. Location of stations in Rhode River.

total number of nauplii at a point in time, and t_n is the temperature-dependent developmental time from nauplius to copepodid. Similarly

$$-d_c = (\ln A - \ln C)/t_c$$
 (2)

where A is the total number of adults and the subscript c in d_c and t_c refers to copepodids.

We computed finite death rates from:

$$D_n = 1 - e^{-d_n}$$

$$D_c = 1 - e^{-d_c}$$
 (3)

and turnover times from:

$$T_n = 1/D_n$$

$$T_c = 1/D_c \tag{4}$$

Since production may be estimated as biomass/turnover time it is necessary to estimate the standing crop biomass. The number in each naupliar stage was estimated by assuming that the constant exponential death rate (d_n) applied to each naupliar stage and that the time (t) per stage was constant (Heinle 1966). Then

$$N_{1} = \frac{N(\text{total})}{1 + e^{-dt} + e^{-2dt} + e^{-3dt} + e^{-4dt} + e^{-5dt}}$$

$$N_{2} = N_{1}e^{-dt}$$
(5)

where N_1 is the number of naupliar state 1, N_2 the number of naupliar stage 2, and so on. Similarly, the number in each copepodid stage was estimated by apportioning total copepods observed according to a constant exponential death rate. Our counts included copepodid stage V with adults as any individual with a well-developed fifth leg was scored in the adult category. We corrected for this by apportioning those individuals recorded as copepodids into four stages and those recorded as adults into two stages, using equation (5) modified for the appropriate number of stages. Then we determined a new estimate of total copepodids which included all five stages, and a new estimate of total adults. These estimates were used in biomass and production calculations.

The dry weights of the twelve developmental stages N_1 through adult were determined from body length data and Heinle's (1969) length-weight relation for A. tonsa and

E. affinis. Standing crop biomass (B) for nauplii, copepodids and adults was determined from the product of numbers and average weight of each stage. Production was estimated as:

$$P = B_n / T_n + B_c / T_c + B_A / T_A$$
 (6)

where P is production in mg/m³·day, and we assume equal turnover times for copepodids and adults.

Results

ABUNDANCES

The predominant copepods were Acartia tonsa, Eurytemora affinis and Scottolana canadensis, which together usually comprised more than 90% of the copepods (Fig. 2). In addition, we observed low densities of Acartia clausi, Eugrasilus caeruleus, Hemicyclops americanus, Oithona brevicornis, Pseudodiaptomus coronatus. Only A. clausi reached moderate densities, as high as 20,000/m³ in February 1974. Total numbers of copepods showed a well-defined peak in February and March of 1974, with the peak occurring first at station 9 near the main fresh-water input and last at station 13 at the mouth of the estuary (Fig. 3). Maximum densities were of similar magnitude at the four stations, ranging from 10^5 to 3.6×10^5 per cubic meter. A second, less pronounced peak occurred in August of each year. A graph of relative abundances reveals that A. tonsa predominated during most of annual cycle with S. canadensis occasionally abun-

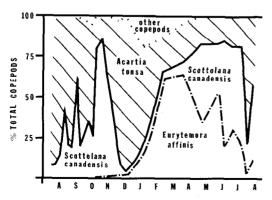


Fig. 2. The relative abundances of predominant species of copepods, averaged over all four stations, in the Rhode River, 1973-74.

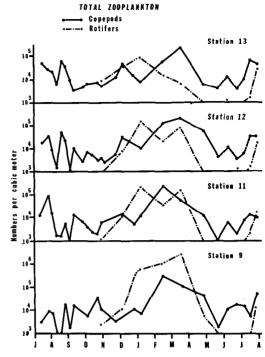


Fig. 3. Total numbers of copepods and rotifers collected at each of four sampling stations in the Rhode River, 1973-74.

dant in the fall and spring and E. affinis most abundant during the spring peak (Fig. 2).

Although rotifers were not identified to species, *Brachionus plicatilis* was observed to be the predominant species in our samples throughout the year. For most stations and sites rotifers were of a similar mean density as copepods, and also reached peaks in spring and late summer. However, during the spring bloom at station 9 rotifers were a full order of magnitude more abundant, reaching a peak density of approximately 2.5×10^6 per cubic meter.

PRODUCTION

We estimated instantaneous death rates and turnover times for A. tonsa and E. affinis using Heinle's (1969) estimates of developmental time and Rhode River temperature data provided by the Chesapeake Bay Center for Environmental Studies. Results for A. tonsa were determined from samples collected between 18 July and 9 October 1973 (Table 1). Production estimates for the four

stations were extremely similar as densities were roughly the same at each station. Consequently we used average densities from all four stations in estimating production. Mean population statistics for the period 18 July to 9 October 1973 were calculated based on the average population over this time period. Subsequent dates were not included because of the presence of A. clausi nauplii which could not be distinguished from the nauplii of A. tonsa. Turnover times for the mean population were 2.26 days for the nauplii and 1.80 days for the copepodids. Individual sample estimates were all fairly close to this mean and represent the range of natural variation.

Results for *E. affinis* were determined from samples collected between 20 November 1973 and 31 July 1974, and for the mean population during the period when *E. affinis* was abundant (8 January to 22 May 1974) (Table 2). A greater range of values was obtained, reflecting the wide range of temperatures and hence developmental times from winter to late spring. Turnover times for the mean population were 14.20 days for nauplii and 11.96 days for copepodids.

The standing crop biomasses were calculated for all sample dates. A. tonsa standing crop was greatest in mid-summer and in December-January (Table 3). The winter estimates presumably are biased upwards by the lumping of A. clausi and A. tonsa nauplii in our counts. E. affinis standing crop was greatest in February (Table 4). Although Acartia was present in substantial numbers in

TABLE 1. Instantaneous death rates (d) and turnover times (T) of *Acartia tonsa* nauplii and copepodids averaged over four stations in the Rhode River subestuary. Time units are days.

Date	d _n	$d_{\rm c}$	T_n	$T_{\rm c}$
July 18, 1973	.50	1.1	2.54	1.5
27	.46	.66	2.71	2.06
Aug. 1, 1973	.38	1.12	3.16	1.48
8	1.17	03	1.45	
16	.51	1.17	2.51	1.45
22	.97	.65	1.61	2.10
Sept. 4, 1973	.98	.01	1.80	87.65
11	. 7 7	.93	1.87	1.65
25	1.05	1.07	1.54	1.52
Oct. 2, 1973	.55	01	2.38	_
9	.44	.45	2.81	2.75
mean population, 18	July 197	3-9 Oct.	1973	
	.59	.81	2.26	1.80

TABLE 2. Instantaneous death rates (d) and turnover times (T) of *Eurytemora affinis* nauplii and copepodids averaged over four stations in the Rhode River subestuary. Time units are days.

Date	d_n	$\mathbf{d_c}$	T_n	$T_{\rm c}$
Nov. 20, 1973	.38	_	3.15	
Dec. 4, 1973	.33	_	3.59	_
26	.11	.04	9.51	27.82
Jan. 8, 1974	.20	_	5.58	_
Feb. 14, 1974	.05	.05	23.3	21.55
Mar. 22, 1974	.12	.24	9.22	4.65
April 26, 1974	.76		1.87	
May 22, 1974	.28	.46	4.12	2.69
June 5, 1974	1.08	_	1.51	_
19	.66	.78	2.07	1.85
July 3, 1974	1.61	_	1.25	
17	1.41	_	1.32	_
31	1.24	.69	1.41	2.0
mean population, 8	Jan. 1974	–22 M a	ay 1974	
/	.073	.087	14.20	11.96

the spring peak (Fig. 2), most were nauplii; and in terms of biomass, the peak was almost entirely E. affinis. Maximum biomasses were 16.3 mg/m³ for A. tonsa en 27 July 1973, and 218.6 mg/m³ for E. affinis on 14 February 1974.

Production, estimated as biomass/turnover time, was 2.70 mg/m³·day for the mean summer population of A. tonsa, and a maximum of 7.47 mg/m³·day. Production of the mean E. affinis population was only slightly higher, 3.82 mg/m³·day, but the maximum was much greater, at 20.47 mg'm³·day. Thus in the Rhode River copepod production was substantially greater during the February-March peak than during the secondary August peak.

Discussion

Estimates of copepod abundances present notorious difficulties owing to their net avoidance ability (Fleminger and Clutter 1965). The likely result is to underestimate total numbers, particularly of older stages. In turn, death rates will be overestimated and biomass underestimated. However, production estimates may not be affected substantially (Heinle 1966). Our method of adjusting the raw data to account for the inclusion of C-V copepodids with adults raised death rates and lowered biomasses relative to uncorrected data but did not change production substan-

TABLE 3. Biomass and production of Acartia tonsa averaged over four stations in the Rhode River subestuary.

	Nauplii		Adults	Total	Production (mg/m³·day)
Date		Copepodids			
July 18, 1973	2.33	3.77	1.00	7.10	4.10
27	3.78	8.09	4.43	16.30	7.47
Aug. 1	1.11	2.30	.59	4.00	2.30
81	0.19	.07	.21	.47	.13
16	2.63	4.09	.97	7.69	4.54
22	1.80	1.32	.74	3.86	2.10
Sept. 4	.13	.09	.19	.41	0.08
11 ~	1.00	.99	.35	2.34	1.35
25	1.11	.56	.17	1.84	1.20
Oct. 21	.46	.49	1.16	2.11	.19
9	.26	.29	.14	0.69	.25
16²	.19	.16	.08	.43	-
23	.23	.03	.16	.42	
Nov. 20	.72	.41	1.22	2.35	
Dec. 4	3.16	3.24	6.85	13.25	
26	.88	3.34	10.82	15.04	_
Jan. 8, 1974	.47	1.75	11,17	13.39	_
Mar. 22	1.12	.25	1.85	3.22	_
June 19	.19	.05	0	.24	_
July 3	.16	.01	0	.17	_
17	2.41	.69	.07	3.17	_
31	1.32	.12	.06	1.50	. —
Iean population, 18 Jui	ly 1973-9 Oct. 19				
	1.46	2.38	1.31	5.15	2.70

¹ Based on production of naupliar stages only.

TABLE 4. Biomass and production of Eurytemora affinis averaged over four stations in the Rhode River subestuary.

Date	Nauplii	Copepodids	Adults	Total	Production (mg/m³·day)
Nov. 20, 1973	.04	0	0	.04	.01
Dec. 4	.13	0	0	.13	.04
26	.54	.36	.31	1.21	.08
Jan. 8, 1974 ¹	.45	0	1.71	2.16	.08
Feb. 14	38.57	104.71	75.34	218.62	10.01
Mar. 22	26.45	73.1	8.59	108.1	20,47
April 26	.33	0	0	.33	.17
May 22	.38	.38	.09	.85	.27
June 5	.31	0	0	.31	.20
19	.55	.11	0	.66	.32
July 3	.35	0	0	.35	.28
17	.12	0	0	.12	.09
31	.91	.04	0	.95	.67
n population, 8 Jan.	1974-22 May 19	974			
, ,	12.33	20.66	14.63	47.62	3.83

¹ Based on production of naupliar stages only.

tially, underscoring Heinle's (1966) point above.

Although we did not replicate sample at any station and cannot estimate sampling error directly, the fact that all four stations exhibit similar seasonal patterns of abundances suggests a high degree of sampling replicability.

We assumed that temperature-dependent development rates and length-weight relation-

² Production not estimated after this date due to presence of A. clausi.

ships determined in Heinle's (1969) study of Patuxent populations could be applied to our Rhode River populations. As the estuaries are separated by less than 100 km and subject to similar temperature and salinity regimes it seems reasonable to assume that samples from the two estuaries represent one population with identical development rates under similar environmental conditions.

Negative values for the instantaneous death rate (d_c) were obtained on two occasions (8 August and 2 October, Table 1) and an unrealistically small value on one other date (4 September). Clearly one assumption of the approach is not met; that is, individual sampling dates do not represent true steady state conditions (see Fager 1973 for a critique) and on several occasions adults from an earlier period of high abundance survived into a subsequent period of lower copepodid abundance. However, the negative values are small (respectively -.03, -.01), indicating that this assumption does not meet with extreme exceptions.

Comparison of our values to Heinle's (1966, 1969) indicate that copepod biomass and production are substantially less in the Rhode River then in the Patuxent estuary. In the Rhode River, biomass of A. tonsa is about 5% and of E. affinis about 50% of those observed in the Patuxent. Turnover times are fairly similar, hence total production varies to the same extent as does biomass.

Recent experiments by Mullin and Evans (1974) using an alga—copepod (Acartia tonsa and Paracalanus parvus)—ctenophore food chain in a 70-m³ tank resulted in copepod standing crop and biomass comparable to but higher than our values. Assuming g C=50% g dry weight, copepod standing crops in the study of Mullin and Evans generally ranged between 5 and 50 mg/m³ and were maintained in the presence of 22% daily harvesting which implies production ranged from 1 to 10 mg/m³ day.

Williams, Murdoch and Thomas (1968) suggested that shallow embayments have low standing crops, and that zooplankton may be less important than benthic organisms as the herbivore link in these shallow areas. Since the Patuxent is a considerably larger estuary than the Rhode River, this seems at first glance consistent with our observations of

lower standing crop and production in the Rhode River.

Unfortunately, Williams et al. (1968) made a critical error in their calculations. Standing crop per cubic meter was multiplied by average depth to determine total standing crop per square meter of surface area, and plotted against depth. If standing crop per cubic meter were independent of the depth of the embayment this would result in a slope of 1.00 (depth vs depth). Their calculated slope of 1.145, which was not significantly different from 1.00, reflects the fact that standing crop per cubic meter (their Table 3) shows a slight positive but not significant correlation with depth. Hence, their conclusion that shallow embayments have low standing crops of zooplankton is not valid on a per unit volume basis. Furthermore, their Fig. 4 which plots phytoplankton photosynthesis/zooplankton standing crop against depth is similarly suspect, since its shape is consistent with a plot of 1/depth versus depth. However, the data are not complete enough in the paper of Williams et al. for a careful re-computation of their Fig. 4.

We attempted to estimate upper and lower bounds on rotifer production in the Rhode River to compare with copepod production. As we do not have species-specific growth rates and biomass figures, these results are highly speculative. Nevertheless, using published data for Brachionus plicatilis (Theilacker and McMaster 1971; Walker 1973) we estimate that a pure Brachionus population comparable in total numbers per cubic meter to our total rotifer population would produce from 4 to 40 mg/m³ day, up to an order of magnitude above copepod production. If correct, this comparison would suggest that rotifers account for the bulk of zooplankton production in the Rhode River. Hence, zooplankton collections using relatively large nets (#10 in the case of Williams et al. [1968]) may underestimate the importance of plankton food chains because rotifers are not sampled accurately.

Finally, the difference between the Rhode and Patuxent rivers was greatest for the summer Acartia bloom in copepod production, and less for the spring Eurytemora bloom. The Eurytemora peak may be associated with marsh detritus since it occurs early

in the spring, is greatest at the mouth of Muddy Creek (February peak), and appears to proceed outwards toward the main bay (March peaks at stations 12 and 13). Heinle and Flemer (1975) calculated that the carbon demand of Patuxent E. affinis populations can only be met by substantial grazing on detrital carbon. Hence it may be that the smaller Rhode River is less productive than the Patuxent primarily with respect to summer phytoplankton and resulting Acartia tonsa populations, while the detritus food chain in the Rhode River may support substantial E. affinis populations.

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