Secondary Production of the Estuarine, Meiobenthic Copepod *Microarthridion littorale**

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ABSTRACT: Secondary production of *Microarthridion littorale*, an estuarine meiobenthic copepod, was determined in a South Carolina (USA) salt marsh by the use of size-frequency distributions and age specific growth rates. For all individuals production was highest in 1976 during late summer, with a daily production rate of $1.2 \mu g \ 10 cm^{-2} \ d^{-1}$. In 1978–1979, production for adults was much lower, less than half of the 1976 adult values. An annual production of $0.14 g \ m^{-2}$ dry weight is estimated, yielding a production/biomass ratio of $18.0 \ yr^{-1}$ in 1976.

INTRODUCTION

Empirically derived values of secondary production are helpful in understanding the functional dynamics of ecosystems. Production estimates of the ubiquitous marine meiofauna are particularly important in elucidating their role and energetic importance (Banse and Mosher, 1980). Measurements of production can yield an estimate of the potential meiofaunal calories that may be passed either to higher trophic levels or the decomposer food chain, and aid in determining how meiofaunal production is partitioned from the total energy assimilation of the benthos. Functionally, meiofauna may serve as food for higher trophic levels, as nutrient regenerators and as an aid an facilitating detritus transfer to macrofauna (Coull and Bell, 1979).

Perhaps the ideal way to determine production for a species is to identify a cohort and follow, over time, changes in density and biomass for that cohort. Some meiofauna species do produce only 1 or 2 generations per year (Barnett, 1970; Feller, 1980) making cohort recognition possible. However, in many other species, especially in warm water habitats, generations widely overlap making cohort identification unlikely. Gerlach (1971) estimates that the average meiofauna species produces 9 generations each year. When cohorts can-

not be followed from field collections, estimation of production requires painstaking analysis of population sizes and recruitment gathered over short time intervals, coupled with the use of size specific growth rates obtained from laboratory cultures (Mann, 1976; Warwick, 1980). Laboratory rearing of meiofauna has proven difficult (Palmer and Coull, 1980). Consequently, the only published account of empirically derived meiofauna production values is the report by Banse and Mosher (1980) of Feller's (1977) work with the meiobenthic harpacticoid *Huntemannia jadensis* in Puget Sound, USA.

We report here on production estimates of another meiobenthic copepod *Microarthridion littorale* (Poppe), which is world-wide distributed, being especially common in salt marshes of the southeastern US and Gulf of Mexico (Hiegel, 1969; Coull et al., 1979). *Microarthridion littorale* comprises from 10–38% of the copepod fauna of South Carolina intertidal marshes (Bell, 1979; Fleeger, 1980), being the dominant mud-dwelling estuarine copepod. As many as 12 overlapping generations per year with prolonged reproductive activity occur intertidally (Fleeger, 1979; Palmer, 1980). Because of its dominance among mud-dwelling copepods in marsh habitats, where copepods typically are the second most abundant meiofaunal taxon after nematodes, and because of its widespread distribution, *M. littorale* is an appropriate and representative meiobenthic species for production studies.

MATERIALS AND METHODS

The *Microarthridion littorale* population in a low marsh intertidal site in North Inlet Estuary, South Carolina (USA) was studied during 1976 by Fleeger, and 1978–1979 by Palmer. The site is characterized by soft, fine sediment (80 % silt and clay) and by the presence of numerous culms of healthy *Spartina alterniflora*. Consult Fleeger (1979) and Palmer (1980) for more complete details of the sampling site, sampling techniques, and original census data.

Quantitative collections were made by hand coring at low tide with 2.54 cm diameter core tubes. A total of 20 collections from 1976 were utilized in calculations of production. Total body length, excluding rostrum and candal rami, was measured from each collection on at least 200 individuals including nauplii, copepodites, and adults. Collections from 1976 were not equally spaced over time, but were concentrated during early spring, mid-summer, and early late fall so that short interval sampling (5–10 d) could be made when populations were growing or changing rapidly. A total of 25 collections were made at approximately 15 d intervals in 1978–1979. In 1978–1979, only the lengths of adult *Microarthridion littorale* were measured. Production values are reported here for the entire population for parts of 1976, but only for the adults in 1978–1979.

A length weight relationship of copepodite and adult *Microarthridion littorale* was determined with the aid of a Cahn Electrobalance. Frozen specimens of *M. littorale* were sorted in various size groups and placed into small, preweighed aluminum pans. Pans, each containing from 15–70 individuals, were dried to constant weight at 95°C, and re-weighed. One group of 75 nauplii averaging 180 μm in length was also weighed, however, nauplii values were not used in the length weight regression. An attempt was made to weigh smaller nauplii as well; however, too few were available to provide adequate numbers for accurate measurement.

Crisp's (1971) method 3A, production for stocks with recruitment, age classes not separable, was used for production calculations. Specifically,

$$P = \Sigma\Sigma \, f_i \, G_i \, \overline{w}_i \, \Delta t$$

where P = production; f_i = number of individuals per unit surface area of Size group i present during Period Δt; G_i = specific growth rate of the size group; $\overline{w}_i$ = mean weight of the size group. Growth rates (G_i) were determined independent of field sampling (see below). Six size classes were established, 3 approximating the 6 naupliar stages and 3 approximating the 5 copepodite stages and the adult. Weights of individuals were determined from their lengths by the use of the length

weight regression for *Microarthridion littorale*, and the size class mean weights $(\overline{w}_i)$ and variances for each collection were calculated. Population density estimates from field collections were averaged between each collection yielding a value of f_i for each size class. Egg weights of gravid females were not estimated at any time.

The growth data of Palmer and Coull (1980), who determined time from egg to adult stage of *Microarthridion littorale* at different temperatures, were used to calculate size specific growth rates. To calculate a growth rate, growth by the Bertalanffy equation was assumed:

$$l_t = L_\infty - (L_\infty - L_0)e^{-Kt}$$

where L_0 and L_∞ = constants representing length at zero age and maximum age respectively; l = length at time t; K = a constant. K was estimated graphically by the method of Ricklefs (1967) for each temperature of Palmer and Coull's (1980) data. This growth constant was then regressed with temperature, and a predicted K at each average South Carolina field temperature was calculated. Crisp (1971, pp. 241–243) has shown that the weight specific growth rate (G) may be given by

$$G = bK(L_\infty - l)/l$$

where b = weight/length regression coefficient and l = mean length for a size class under consideration. Growth rates (G) were determined for each size class at each collection interval by this method.

Confidence limits for the estimates of production were determined for 1976 by the methods of Chapman (1967). This method uses estimates of the variation in f_i, w_i, and G_i to find the variation of the product of these terms. Several sources of error are included in the production variability estimates. These include variance in estimates of density, $V(N)$, for a size group on a collection date (determined by calculation of variance among replicate samples), variance in mean weight (measured as variance among all individual weights of a size class on a sampling date) and variance in growth rate determination (measured as variance in individual growth; see Palmer and Coull, 1980). Confidence limits for 1978–1979 production values were not determined because density estimate variability among replicate samples was not available from those data.

RESULTS AND DISCUSSION

The length weight regression for *Microarthridion littorale* (Fig. 1) was determined by weighing individuals of mean lengths of from 220 μm (Stage 1 and

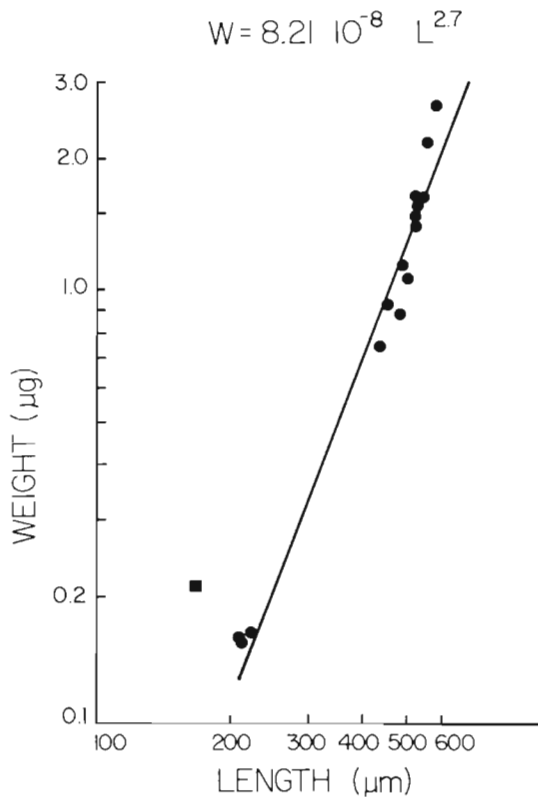$$W = 8.21 \cdot 10^{-8} \cdot L^{2.7}$$

Fig. 1 *Microarthridion littorale*. Length weight relationship for adults and copepodites. Each circle represents the average length and weight of at least 15 individuals. Square: 1 determination for nauplii

Stage 2 copepodites) to 540 μm (sexually mature individuals). The calculated least squares expression, excluding nauplii, is in the form of the allometric equation, and is $W = 8.21 \cdot 10^{-8} \cdot L^{2.7}$, where W = weight in μg dry weight; L = body length in μm. The standard error of b, the regression slope, is 0.137; the regression is significantly different from 0 at the 0.001 level. The values found for *M. littorale* agree closely with the linear length weight regression for several harpacticoid species found by Goodman (1980).

Larger nauplii were approximately equal to, or slightly heavier than, the smallest copepodites (Fig. 1). Similar results were obtained in the few instances where length weight relationships for nauplii, as well as copepodites and adults, were calculated (Durbin and Durbin, 1978; Landry, 1978). In fact, the length weight relationship for nauplii should differ from adults due to the major changes in body shape which occur in the molt from the rounded nauplii to the more elongate copepodite. Due to the difficulty in weighing smaller nauplii, the copepodite adult regression was extrapolated for nauplii weight determinations. Therefore, the use of this regression will underestimate naupliar weights because the nauplii are shorter per

unit of body weight. Thus, biomass values for all naupliar weights are conservative estimates.

In 1976, dry weight production for all individuals was determined for 3 time periods; 15 February – 21 March, 13 July – 10 August and 7 September – 30 November (Table 1). Total production for the entire 143 d under investigation amounted to 97.8 μg 10cm^{-2}. Production on a daily basis was lowest during the early spring, 0.068 μg 10 cm^{-2} d^{-1}, when population densities and recruitment were low. Production was much higher in the late summer and early fall (1.2 μg $10\text{ cm}^{-2} d^{-1}$), and reached peak at 2.0 μg $\cdot$ $10\text{ cm}^{-2} d^{-1}$ during early September when densities were also at a maximum. Weekly production rates declined through the fall as temperatures and densities declined. Variability was highest during July – August when 95 % confidence limits exceeded 100 % of the production estimate (Table 1). Generally, more confidence could be placed in production estimates during the fall months when density estimates were most reliable (Fleeger, 1979). Production trends for adults mirrored trends for the entire population.

Generally, production of *Microarthridion littorale* correlated well with population density. Given the 1976 seasonal pattern of *M. littorale* abundance (winter and spring low densities, $< 100\text{ cm}^{-2}$, to sustained high densities from July – October, > 300 10 cm^{-2}), the intensive collections during 13 July – 10 August and 7 September – 30 November measured a large portion of the annual production in 1976. An estimate of the total annual production would be of great interest. To estimate annual production, we derived empirical values of daily P/$\overline{\text{B}}$ (production to biomass) ratio for the intensive collections of February – March, July – August and September – November by the use of the production data of Table 1 and from field derived average biomass values for the same time periods. P/$\overline{\text{B}}$ d^{-1} were 0.045, 0.103 and 0.058 for February – March, July – August and September – November, respectively. We used these values to estimate production between intensive collections. Production was correlated with density, and densities of *M. littorale* changed gradually through much of the year; thus change in P/$\overline{\text{B}}$ ratios were probably not abrupt but gradual between intensive collections. The P/$\overline{\text{B}}$ d^{-1} value of 0.045 (calculated from February – March) was used for the 22 March – 12 July interval, and a value of 0.081 (interpolated between July – August and September – November) was used for the 11 August – 6 September interval. Production during the winter months of December and 1 January – 14 February was assumed to be nil. The P/$\overline{\text{B}}$ d^{-1} ratio for each interval was multiplied by the average biomass and the number of days to arrive at a production value for the interval.

Table 1. *Microarthridion littorale*. Production (P) by size class for periods of 1976. 95 % confidence limits expressed as a % of production estimate

| Time period | Size class (μm) | | | | | |
	64–86	87–128	128–179	180–280	281–440	> 440
15 Feb – 22 Feb	0.008	0.023	0.001	0.007	0.008	0.060
22 Feb – 29 Feb	0.041	0.084	0.043	0.014	0.028	0.115
29 Feb – 7 Mar	0.056	0.132	0.078	0.037	0.098	0.141
7 Mar – 14 Mar	0.024	0.125	0.106	0.064	0.163	0.146
14 Mar – 21 Mar	0.022	0.104	0.126	0.107	0.179	0.165
Total by size class	0.151	0.468	0.354	0.228	0.476	0.627
Variance (P)	0.059	0.134	0.100	0.066	0.248	0.213
Total production for entire time period	2.3 μg 10 cm^{-2}					
95 % Confidence limit	87.4 %					
13 Jul – 20 Jul	0.395	1.246	0.804	0.552	1.320	1.883
20 Jul – 29 Jul	0.820	2.224	4.806	1.010	2.282	3.325
29 Jul – 10 Aug	1.017	2.578	1.577	1.643	3.011	3.862
Total by size class	2.232	6.048	7.187	3.205	6.613	9.070
Variance (P)	0.484	1.450	0.860	0.802	1.936	3.946
Total production for entire time period	34.4 μg 10 cm^{-2}					
95 % Confidence limit	128.8 %					
7 Sep – 16 Sep	1.610	4.139	2.321	2.703	2.619	4.166
16 Sep – 21 Sep	0.806	1.363	0.550	1.340	2.126	2.559
21 Sep – 28 Sep	0.756	0.875	0.183	1.042	2.715	3.006
28 Sep – 7 Oct	0.701	0.845	0.277	0.483	1.942	3.516
7 Oct – 16 Oct	0.597	0.715	0.330	0.662	1.667	2.721
16 Oct – 30 Oct	0.384	0.526	0.262	0.581	2.128	3.000
30 Oct – 9 Nov	0.139	0.177	0.096	0.063	0.668	1.300
9 Nov – 21 Nov	0.101	0.177	0.082	0.012	0.454	0.707
21 Nov – 30 Nov	0.019	0.095	0.027	0.078	0.266	0.380
Total by size class	5.113	8.912	4.128	6.964	14.585	21.355
Variance (P)	1.340	4.450	1.100	2.250	5.290	17.067
Total production for entire time period	61.1 μg 10 cm^{-2}					
95 % Confidence limit	65.4 %					

These calculations yield a production value of 11 μg 10 cm^{-2} from 22 March – 12 July and a value of 33 μg 10 cm^{-2} from 11 August – 6 September. When these values are summed with the empirical estimates of Table 1, total annual production for *Microarthridion littorale* was 0.14 g m^{-2}, yielding an annual P/$\overline{B}$ ratio of 18.0 y^{-1}.

Production for adult *Microarthridion littorale* (> 440 μm) for the year beginning in July, 1978, was lower than the adult 1976 value (Tables 1 and 2). When comparing years, adult production on a weekly basis was quite similar during the spring months, however, production during the fall of 1978 was not sustained at as high a rate for as long compared to 1976. The sustained peak in population density and biomass observerd in 1976 did not occur in 1978. Total population densities averaged 423 10 cm^{-2} during July – September, 1976, compared to 130 10 cm^{-2} during the same time in 1978 (Fleeger, 1979; Palmer, 1980). Production of adults for the year beginning in July, 1978, totalled only 14.4 μg 10 cm^{-2}, compared to 31.0 μg

10 cm^{-2} in the 143 d under investigation in 1976. Thus, *M. littorale* displayed high variation in production between the 2 years under investigation with adult production in 1976 more than double that for adults in 1978–1979. Large variability from year to year in meiofauna density is not uncommon (Coull and Fleeger, 1977), and has been reported specifically for *M. littorale* by Bell (1979). The cause of this variation is unknown; further quantification of temporal and spatial variation of meiofauna production is certainly worthy of future investigation, and necessary to help evaluate the ecological role of meiofauna. Ratios of production to biomass may vary greatly over space and time.

Several authors have speculated on the average annual P/$\overline{B}$ ratio for meiofauna, with most estimates at 9–10 y^{-1} (McIntyre, 1964; Gerlach, 1971). Such values have achieved theoretical (Banse and Mosher, 1980) as well as practical importance. Annual P/$\overline{B}$ values are regularly used in collaboration with standing crop biomass to estimate meiofauna productivity in carbon

Table 2. *Microarthridion littorale*. Production of adults for 1978–1979

	Δt (d)	Average frequency (10 cm^{-2})	Average weight (μg)	Growth rate (d^{-1})	Production (μg 10 cm^{-2})
9 Jul –17 Jul	10	41.0	0.120	0.028	1.373
17 Jul –28 Jul	9	45.0	0.123	0.032	1.597
28 Jul – 3 Aug	6	34.5	0.125	0.033	0.852
3 Aug –18 Aug	15	8.0	0.125	0.030	0.450
18 Aug – 1 Sep	15	7.5	0.108	0.030	0.366
1 Sep –12 Sep	11	13.0	0.110	0.027	0.424
12 Sep –23 Sep	11	18.0	0.107	0.026	0.551
23 Sep –28 Sep	5	23.5	0.134	0.026	0.410
28 Sep –12 Oct	14	32.0	0.103	0.026	1.196
12 Oct –26 Oct	14	29.0	0.152	0.024	1.477
26 Oct –12 Nov	17	23.0	0.153	0.015	0.899
12 Nov –27 Nov	15	20.0	0.177	0.011	0.585
27 Nov –17 Dec	20	14.5	0.166	0.008	0.386
17 Dec – 2 Jan	16	10.0	0.159	0.005	0.127
2 Jan –18 Jan	16	10.5	0.158	0.005	0.133
18 Jan –14 Feb	27	10.5	0.151	0.005	0.214
14 Feb –11 Mar	25	6.0	0.178	0.010	0.267
11 Mar –28 Mar	17	5.5	0.184	0.013	0.224
28 Mar –16 Apr	19	5.5	0.180	0.016	0.301
16 Apr – 7 May	22	5.5	0.176	0.020	0.448
7 May –20 May	14	7.5	0.161	0.025	0.424
20 May –10 Jun	21	9.5	0.131	0.025	0.651
10 Jun – 1 Jul	21	15.5	0.119	0.028	1.083
					14.4

or energy models of marine ecosystems (Day et al., 1973; Rosenberg et al., 1977). The present study shows that, at least in warm waters, the annual P/$\overline{\text{B}}$ ratio of 9 yr^{-1} would underestimate production for *Microarthridion littorale*, and the possibility exists that meiofauna production is underestimated in various models. No comparative data exists for any warm water meiofauna species and certainly generalizations based on one species should be taken with caution. For example, we have already shown that temporal variability exists for production in *M. littorale*. A surface-dweller such as *M. littorale* in the upper few mm, may be under considerable predation pressure as shown by life history data (Fleeger, 1979) and field experimentation (Bell, 1980). Further interpretation of P/$\overline{\text{B}}$ ratios in meiofauna awaits the determination of temporal and spatial variation of production for a wider cross section of the meiofauna community.

LITERATURE CITED

Banse, K., Mosher, S. (1980). Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. 50: 355–379

Barnett, P. R. O. (1970). The life cycles of two species of *Platychelipus* Brady (Harpacticoida) on an intertidal mudflat. Int. Revue ges. Hydrobiol. 55: 169–195

Bell, S. S. (1979). Short- and long-term variation in a high marsh meiofauna community. Estuar. coast. mar. Sci. 9: 331–350

Bell, S. S. (1980). Meiofauna-macrofauna interactions in a high salt marsh habitat. Ecol. Monogr. 50: 487–505

Chapman, D. W. (1967). Production in fish populations. In: Gerking, S. D. (ed.) The biological basis of freshwater fish production. Wiley, New York, pp. 3–30

Coull, B. C., Bell, S. S. (1979). Perspectives in marine meiofauna ecology. In: Livingston, R. J. (ed.) Ecological processes in coastal marine ecosystems. Plenum, New York, pp. 189–216

Coull, B. C., Bell, S. S., Savory, A. M., Dudley, B. W. (1979). Zonation of meiobenthic copepods in a Southeastern United States salt marsh. Estuar. coast. mar. Sci. 9: 181–188

Coull, B. C., Fleeger, J. W. (1977). Long-term variation and community dynamics of meiobenthic copepods. Ecology 58: 1136–1143

Crisp, D. J. (1971). Energy flow measurements. In: Holme, N. A., McIntyre, A. D. (eds.) Methods for the study of marine benthos. IBP Handbook 16. Blackwell, Oxford, pp. 197–279

Day, J. W., Smith, W. G., Wagner, P. R., Stowe, W. C. (1973). Community structure and carbon budget of a salt marsh

and shallow bay estuarine system in Louisiana. Publ. No. LSU – SG – 73 – 04, Louisiana State, University

Durbin, E. G., Durbin, A. G. (1978). Length and weight relationships of *Acartia clausi* from Narragansett Bay, R.I. Limnol. Oceanogr. 23: 958–969

Feller, R. J. (1977). Life history and production of meiobenthic harpacticoid copepods in Puget Sound. Dissertation, University Washington, Seattle

Feller, R. J. (1980) Quantitative cohort analysis of a sand-dwelling meiobenthic harpaciticoid copepod. Estuar. coast. mar. Sci. 11: 459–476

Fleeger, J. W. (1979). Population dynamics of three estuarine meiobenthic harpacticoids (Copepoda) in South Carolina. Mar. Biol. 52: 147–156

Fleeger, J. W. (1980). Community structure of an estuarine meiobenthic copepod assemblage. Estuar. coast. mar. Sci. 10: 107–118

Gerlach, S. A. (1971). On the importance of marine meiofauna for benthos communities. Oecologia (Berl.) 6: 176–190

Goodman, K. S. (1980). The estimation of individual dry weight and standing crop of harpacticoid copepods. Hydrobiologica 72: 253–259

Hiegel, M. H. (1969). A survey of the bottom dwelling copepods of a Louisiana marsh lake. M.S. thesis, Louisiana State University, Baton Rouge

Landry, M. R. (1978). Population dynamics and production of a planktonic marine copepod, *Acartia clausii*, in a small temperate lagoon on San Juan Island. Washington. Int. Revue ges. Hydrobiol. 63: 77–119

Mann, K. H. (1976). Production on the bottom of the sea. In: Cushing, D. H., Walsh, J. J. (eds.) The ecology of the seas. Saunders, New York, pp. 225–250

McIntyre, A. D. (1964). Ecology of marine meiobenthos. Biol. Rev. 44: 245–190

Palmer, M. A. (1980). Variation in life history patterns between intertidal and subtidal populations of *Microarthridion littorale*. Mar. Biol. 60: 159–165

Palmer, M. A., Coull, B. C. (1980). The prediction of development rate and the effect of temperature for the meiobenthic copepod, *Microarthridion littorale* (Poppe). J. exp. mar. Biol. Ecol. 48: 73–83

Ricklefs, R. E. (1967). A graphical method of fitting equations to growth curves. Ecology 48: 978–983

Rosenberg, R., Olsson, I., Ölundh, E. (1977). Energy flow model of an oxygen deficient estuary on the Swedish west coast. Mar. Biol. 42: 99–107

Warwick, R. M. (1980). Population dynamics and secondary production of benthos. In: Tenore, K. R., Coull, B. C. (eds.) Marine benthic dynamics. University of South Carolina Press, Columbia, pp. 1–24