AN ECOPHYSIOLOGICAL STUDY OF THE MEIOFAUNA OF THE SWARTKOPS ESTUARY

3. PARTITION OF BENTHIC OXYGEN CONSUMPTION AND THE RELATIVE IMPORTANCE OF THE MEIOFAUNA

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ABSTRACT

Benthic oxygen demand was measured by dark and light bottle technique at two beaches in the Swartkops estuary, near Port Elizabeth. Respiration of nematodes was measured by polarographic micro-respirometer technique. Secondary production was 82 g C/m^2/y in sandy areas and 863 g C/m^2/y in muddy areas rich in the prawn *Callianassa kraussi*. Meiofauna production was 1,72 g C/m^2/y in sand and 0,24 g C/m^2/y in mud. The meiofaunal contribution to secondary production was 2,1% and 0,03% for these two areas respectively. The largest proportion of secondary production was due to micro-organisms: 92% in sand and 75,5% in mud. Macrofauna accounted for 5,75% and 24,4%. It is concluded that meiofauna in these exposed sand and mud flat areas is not quantitatively important, but the qualitative importance may be considerable.

INTRODUCTION

This paper presents the concluding phase of a study of the meiofauna at two sites in the Swartkops estuary near Port Elizabeth. This phase was aimed at determining the relative importance of the meiofauna in the system. In order to do this it is necessary to know (a) the total benthic oxygen consumption and (b) the oxygen consumption of the meiofauna community. There are two basic approaches to the study of meiofauna respiration. Individual respiration rates under various conditions may be determined using sensitive manometric techniques such as the Cartesian diver method. Such a method can have a sensitivity of 2,5 — 5,0 $\times$ 10^{-5} µl O_2 (Zeuthen 1950) and is generally used when the respiratory physiology of a particular species is under investigation. However, due to individual variation many replicates must be done to get reliable results. Wieser & Kanwisher (1961) determined that the nematode *Theristus setosus* consumed 410–1 100 µl O_2/g wet mass/h at 20°C, a variation of 268%. Recent findings indicate that such individual respiration determinations are also affected by both the method of extraction of animals and by the absence of a substrate in the respiration chamber (Vernberg *et al.* 1977). Gerlach (1971) reviewed results obtained by such methods.

The aims of the present study did not justify investigation of individual respiration rates, because of the variation mentioned and partly because the taxonomy of the meiofauna will require some time to complete. Thus a method permitting the determination of the

respiration of a number of organisms was used. Since nematodes were dominant in both areas (Dye & Furstenberg 1978) this taxon was chosen. A polarographic micro-respirometer method was used. This is a well known and convenient technique which has been used in various forms for a number of years (Macfayden 1961). It has also been adapted for use on single organisms (Atkinson & Smith 1973). One possible criticism is that the animals are in continuous motion, mainly due to the proximity of other animals, and a high level of metabolic activity is thus measured. However, even in substrate samples which have been allowed to stand undisturbed for some time, many species are still very active. This method may well approximate natural conditions more closely than other techniques.

The measurement of benthic metabolism has been the subject of much study, particularly since the development of ecosystem dynamics, and, consequently, a great deal of data is available. The methods involve variations on the light and dark bottle technique but there are two basic approaches, the measurement of oxygen exchange *in situ* (Pamatmat 1968; Biggs & Flemmer 1972; Smith *et al.* 1972) and laboratory measurement of intact cores (Hayes & Macaulay 1959; Knowles *et al.* 1962; Carey 1967; Hargrave 1969; Riznyk & Phinney 1972). Most of the *in situ* methods, however, have failed to eliminate the possible exchange of materials with surrounding areas and this problem is dealt with below.

METHODS

Meiofauna collected from the sampling sites was extracted from the sand by the decanting technique (Cobb 1918). The animals were trapped on a 45 μm sieve, transferred to beakers and acclimated to the experimental temperature for 16 hours. They were maintained at the salinity from which they were collected, 35‰ for Station A and 27‰ for Station B. The oxygen monitoring equipment consisted of a Radiometer-Copenhagen Acid-Base analyser PHM 71 to which a Clark-type electrode was connected (E 5042). A special glass water-jacket was fitted to the electrode to facilitate temperature control and to allow the membrane to be inserted into the respirometer chamber (Figure 1A). The latter consisted of a stainless steel housing holding a container for the animals (Figure 1B). Excess water was allowed to escape via two outlet tubes. The volume of the chamber was adjusted to 120 μl by inserting stainless steel discs below the container. During the experiment the chamber was immersed in a water bath adjusted to the experimental temperature. Temperature control and circulation was achieved by means of a Radiometer thermostat unit in opposition to a Fryka DLK 300 cooling unit. The degree of temperature control was ± 0,2°C.

The experimental procedure was as follows: 50 nematodes of mean mass 0,43 μg, were randomly selected from acclimated samples and placed in a drop of artificial sea water in the respirometer; artificial sea water was used to reduce bacterial action and to achieve a constant composition. The recipe was that of Van der Horst (1975). The oxygen probe was then inserted into the chamber to form an air-tight seal. A ten-minute equilibration period was allowed in order to let the probe stabilize. Thereafter readings were taken at ten-minute intervals for one hour at 10 and 20° C. At 30° C a slightly different procedure was followed due to the activity of the electrode. Since all oxygen electrodes are consumptive, blank runs

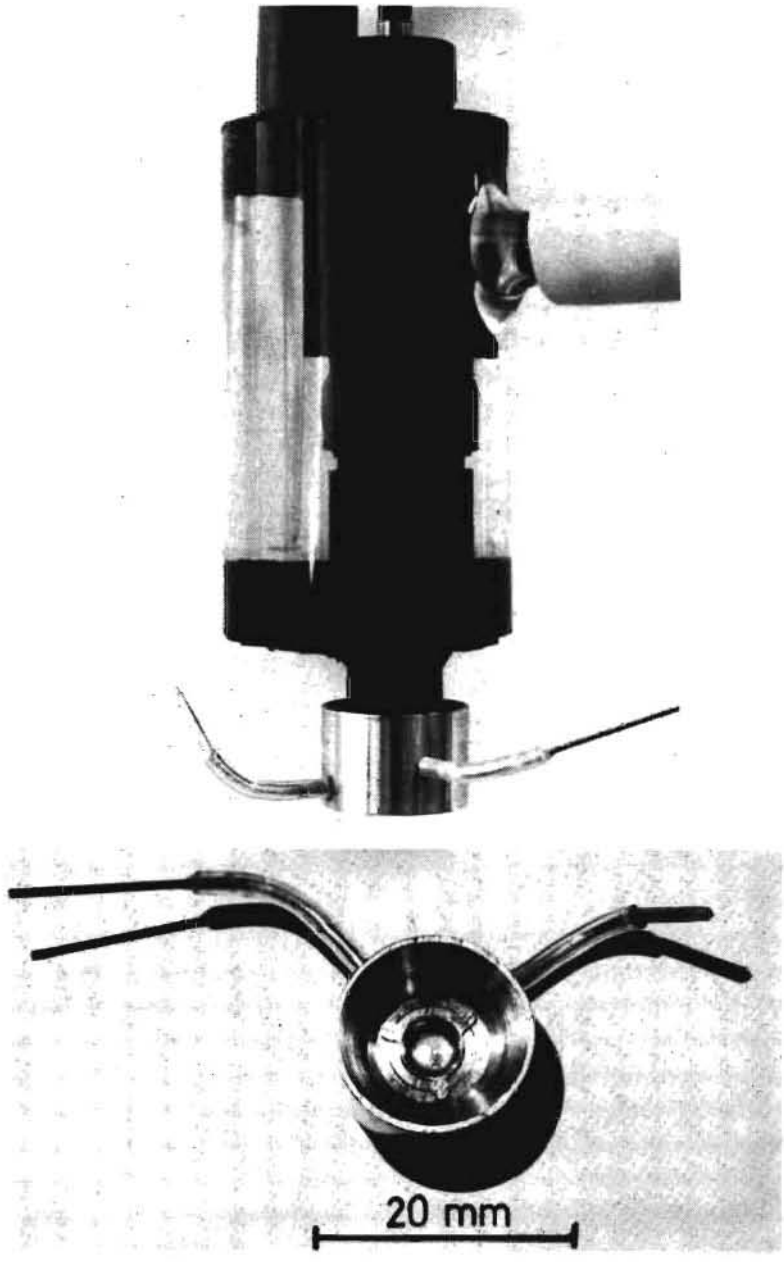

FIGURE 1

A (Above). Temperature-controlled water jacket for the electrode used in the oxygen consumption study. The respirometer chamber is shown in the operating position.

B (Below). View of the assembled respirometer chamber.

were made to correct for probe activity. At 30° C the probe used oxygen rapidly and to ensure at least a 50% oxygen saturation by the end of a run, the time was reduced to 30 minutes with readings at five-minute intervals. This was necessary since it is well known that nematodes compensate for low oxygen tensions by reducing their metabolism (Atkinson & Smith 1973). The radiometer readings in partial pressure of oxygen were converted to volumes by use of the following formula (Dye 1977):

$$V_{O_2} = \frac{3{,}5886 \times 10^{-2} \cdot C \cdot \Delta P}{} \mu l\ O_2/mg/h.$$

where V_{O_2} is the oxygen consumption per mg ash-free dry mass, C is the maximum concentration of oxygen in water of temperature T°C and salinity S‰ (obtained from standard tables) and ΔP is the change in partial pressure of oxygen during the experiment.

In addition, sensitivity tests were carried out with 25, 50, 75 and 100 nematodes at a time, at 20° C.

Benthic metabolism, that is production by epibenthic algae and total oxygen consumption, was measured twice during the study, once in spring and once in autumn, by means of dark and light bottle respirometers. The light bottle consisted of a standard 500 ml clear glass bottle, with the bottom removed, fitted to an aluminium tube, 7,8 cm in diameter and 22 cm long. The tube was attached to the bottle by means of an aluminium ring and epoxy resin (Figure 2). The ring was fitted with two handles to facilitate insertion into the substrate. The dark bottle was identical except that it was made from a solid piece of aluminium reamed out to the same internal dimensions as the light bottle. Both units were fitted with rubber stoppers provided with two glass capillary tubes, one 5 cm and the other 12 cm long. Samples were taken from both and the mean used to correct for oxygen gradients. The capillary tubes were fitted with cannula tubing to which standard 10 ml glass syringes could be attached. At the start of a run the respirometers were pushed 22 cm into the substrate. When filled with surrounding water the units were sealed and remained filled even when exposed during low tide. When the start of a run coincided with low tide and no head of water was available for filling and sealing the units, a 10 *l* rectangular tank with a rubber-lined hole in the bottom was placed on the area to be studied and the respirometer pushed through this hole to the required depth. The tank was then filled with water and the units were filled and sealed as before.

To correct for the metabolism of organisms in the water itself two 250 ml glass bottles, one dark and one light, were filled with sea water and left lying on the substrate in the vicinity of the respirometers. At the start of each run water samples were taken for oxygen analysis as above. At the end of the experiment duplicate samples were taken from each respirometer and analysed for oxygen in the same way. Each run was started at first light and ran for six hours ensuring that the units were subjected to conditions from zero to maximum insolation and thus a true "half day" measured. The weather was clear and sunny during the determinations, carried out in duplicate, and the mean temperature was 18°C.

The partial pressure readings were converted to volumes in litres of oxygen per m^2 per hour by means of the following formulae (Dye 1977);

O_2 production: $V_{O_2} = 2{,}9142 \times P$ (Station A)

O_2 production: $V_{O_2} = 3{,}0841 \times P$ (Station B)

O_2 consumption: $V_{O_2} = 5{,}8296 \times P$ (Station A)

O_2 consumption: $V_{O_2} = 6{,}1693 \times P$ (Station B)

where P is the change in partial pressure of oxygen after correction for the controls.

In order to partition the benthic oxygen consumption the results of the respiration experiments were converted to $l\,O_2/m^2/y$. Since nematodes were dominant their respiration was used, which resulted in the expression:

$$V_{O_2} = 9{,}7455 \times 10^{-7} \times M \times R\, l\,O_2/m^2/y$$

where M is the standing crop of meiofauna (nos/m^2) and R is the respiration rate at 18°C.

Prawn respiration was estimated from Hill (1967) to be 90µl/prawn/h at 18°C and 50% oxygen saturation (the average for the areas studied). The oxygen consumption of the

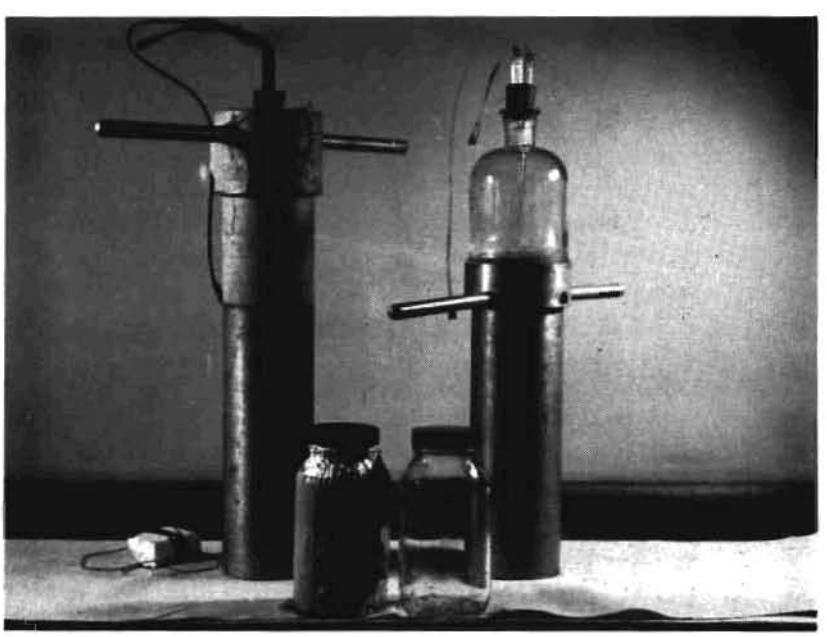

FIGURE 2

The dark and light respirometer units used in the benthic metabolism study. Also shown are the bottles used to correct for water column activity.

prawns is thus given by:

$$V_{O_2} = 7{,}8840 \times 10^{-1} N / O_2/m^2/y$$

where N is the prawn population.

In the case of the other macrofauna, *Psammotellina capensis* and *Diogenes brevirostris*, which occurred in very low numbers, the expression is:

$$V_{O_2} = 2{,}9784 \times 10^{-2} N' / O_2/m^2/y$$

where N' is the population density. This expression assumes a respiratory rate of 3,4 µl/individual/h at 18°C (Smith 1973).

Finally, the carbon equivalent of the oxygen consumed was calculated by assuming an RQ of 0,85 (Hargrave 1969). In the case of meiofauna the turnover method of production estimation was used by way of comparison. In this method the standing crop, expressed as g/m^2 (dry mass) is multiplied by the turnover (McIntyre 1964, 1969; Gerlach 1971) and converted to carbon by assuming a 50% carbon content (Hargrave 1969).

RESULTS

The oxygen consumption rates of nematodes from the two stations are shown in Figure 3. The metabolic activity increases with temperature but this is more pronounced at Station B, particulary between 20 and 30°C. The metabolic rate increased from 1,39 to 3,03 µl O_2/mg ash-free dry mass/h between 10 and 30°C for Station A individuals and from 1,53 to 7,47 µl O_2/mg ash-free dry mass/h over this temperature range for Station B individuals. This gave averages of 1,48 and 2,48 µl O_2/mg ash-free dry mass/h for these groups respectively. Table 1 gives the statistical analysis of the oxygen consumption at each temperature. The sensitivity tests revealed no significant changes in individual respiration rate with changes in animal numbers from 25 to 100 individuals ($p \leqslant 0{,}10$).

Table 2 gives the results of the benthic oxygen consumption study and its partition into macro-, meio- and microfauna in terms of carbon produced per m^2 per year. Also shown is a comparison of the RQ and P/B methods of production estimation for meiofauna assuming a turnover of eight per year (see Discussion). Secondary production accounts for 82,48 and 863,02 g $C/m^2/y$ at Station A and B respectively. At Station A the meiofauna production is 1,72 and at B 0,24 g $C/m^2/y$. Macrofauna accounted for 4,74 g $C/m^2/y$ at A and 196,02 at B. The micro-component, obtained by difference, accounted for 76,02 and 666,77 g $C/m^2/y$ at Stations A and B respectively.

Figure 4 shows the relative importance of the various components of the benthos. At both stations the micro-component accounted for the greatest percentage of secondary production, i.e. 92,16% and 75,56% at A and B respectively. This is followed by the macrofauna which accounted for 5,75% at A and 24,41% at B. Finally the meiofauna contributed 2,1% at A and 0,03% at B.

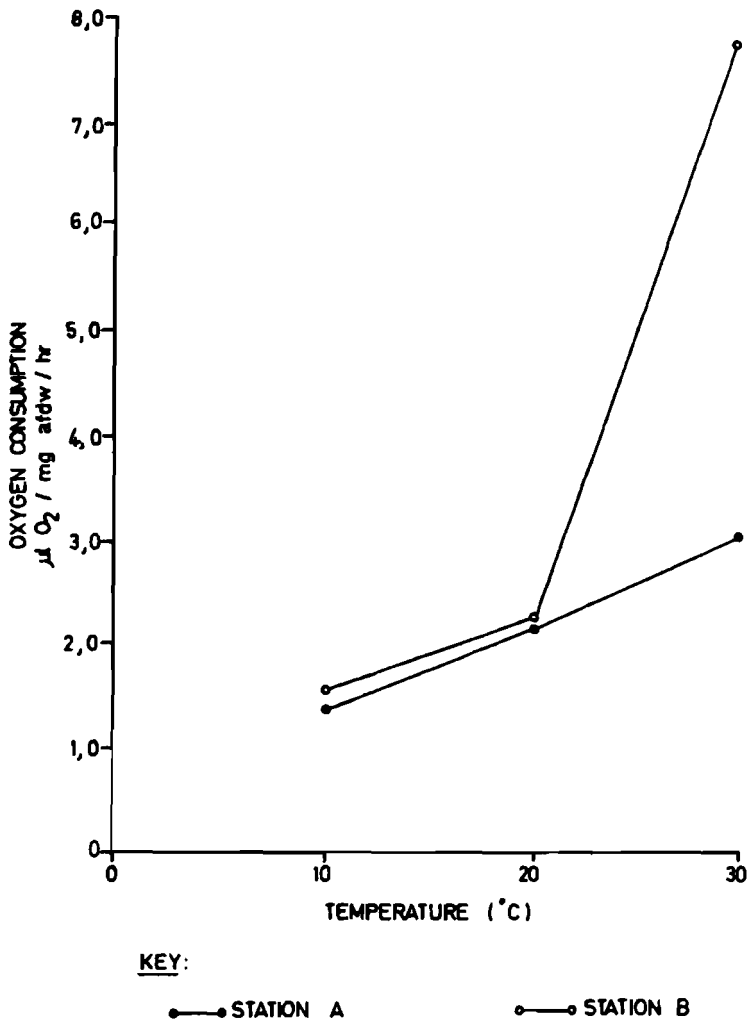

FIGURE 3

Oxygen consumption of nematodes from Station A (sand) and B (mud) as a function of temperature. afdm = ash-free dry mass.

TABLE 1.

Statistical analysis of the oxygen consumption data for nematodes from Stations A and B. Variances are for the 95% confidence level.

* mm Hg vs time, n = 7.

Station	Temperature °C	Regression coeff.*	O_2 consumption µl O_2/mg afdm/h
A	10,0	— 0,95	1,39 ± 0,08
	20,0	— 0,97	2,13 ± 0,09
	30,0	— 0,97	3,03 ± 0,10
B	10,0	— 0,98	1,53 ± 0,03
	20,0	— 0,95	2,20 ± 0,05
	30,0	— 0,99	7,74 ± 0,04

TABLE 2.

Annual secondary production in terms of g C/m^2/y at Stations A and B. Also given is a comparison of the RQ and P/B ratio methods of meiofauna production estimation.

* Assuming an annual turnover of 8.

	Station	Total production	Component Production			Meiofauna P/B*
			Macro	Meio	Micro	
A	HW	90,32	—	1,56	88,76	1,56
	MW	163,66	18,77	2,09	142,80	1,97
	LW	49,52	0,21	1,92	47,39	2,08
	UW	26,46	—	1,28	25,18	1,39
	Mean	82,48	4,74	1,72	76,02	1,75
B	HW	106,66	5,63	0,35	100,95	0,36
	MW	874,08	209,10	0,17	664,81	0,18
	LW	1409,26	321,67	0,24	1087,35	0,22
	UW	1062,08	247,95	0,18	813,95	0,18
	Mean	863,02	196,02	0,24	666,77	0,24

DISCUSSION

There is little information on the effect of temperature on nematode respiration since most studies have been concerned with species differences measured at a particular temperature (Gerlach 1971) or with the effect of body size on metabolism (Atkinson 1973). However, the data in Figure 3 follow the general pattern for poikilothermic organisms and the oxygen consumption rates at 20°C compare well with published results (Gerlach 1971). The differences in species composition which must occur between the two stations probably

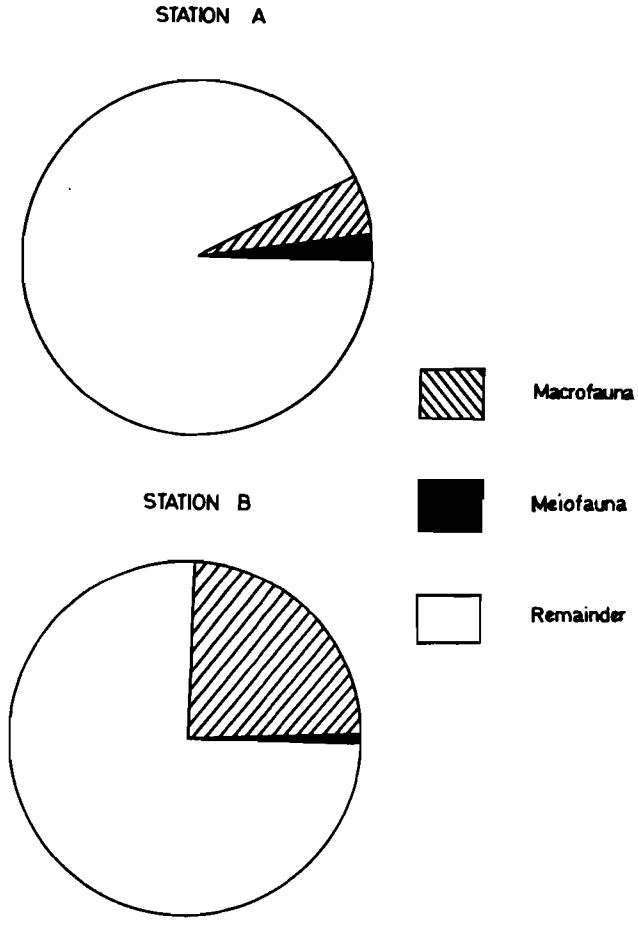

FIGURE 4

The percentage contribution of the various components of the benthos to total secondary production.

accounts for the difference in Q_{10} between Station A and Station B individuals. Wieser & Kanwisher (1961) reported a range of metabolic rates for a number of marine nematodes at 20°C. They found that the metabolic rate of *Axonolaimus spinosus* was 7,2 and that of *Halichoanolaimus longicauda* 1,38 µl O_2/mg dry mass/h. This represents a species-dependent range of 4,82 µl O_2/mg dry mass/h.

It was concluded by Wieser & Kanwisher (1961) that the nematode species they examined could not regulate their metabolism in the face of changing temperature. The present study, however, shows that this may only be the case for nematodes from fine substrates. The Q_{10} values of 1,48 for A and 2,48 for B indicate a lesser degree of metabolic control in the fine substrate organisms. It may be that the fine waterlogged substrate of Station B provides a degree of buffering against temperature fluctuation reducing the need for the nematodes to compensate. In coarser substrates where drainage is good and desiccation becomes significant, the meiofauna would be expected to have a greater degree of tolerance to fluctuating temperatures.

Little information is available on secondary production of sandy substrates. Smith *et al.* (1972) estimated a production of 171,6 g C/m^2/y in a sublittoral area off Bermuda, and Pamatmat (1968) estimated a production of 202 g C/m^2/y. The muddy areas have been studied more intensively and Table 3 gives a summary of available data. The mean production of 605 g C/m^2/y after correction for chemical oxygen demand of 30% (Hill 1976), found in the present study, lies in the upper half of the published range and is considerably higher than the average. This may be ascribed to a great contribution of approximately 200 g C/m^2/y made by the macrofauna.

TABLE 3

Comparison of published data on secondary production of muddy areas. All the data have been recalculated in terms of g C/m^2/y.

Region	Area	Production g C/m^2/y	Author
Cold temperate	Sublittoral	56,9	Hargrave 1969
Cold temperate	Sublittoral	320,0	Hargrave 1973
Cool temperate	Sublittoral	476,0	Knowles *et al.* 1962
Cool temperate	Sublittoral	779,6	Edwards & Rolley 1965
Cool temperate	Sublittoral	210,2	Carey 1967
Cool temperate	Intertidal	271,5	Wieser & Kanwisher 1961
Warm temperate	Intertidal	604,1	Present study
Mean, excluding present study:		325,3	

There is great variation in the relative importance of the components of the benthos. McIntyre (1964) estimated the meiofauna contribution to be between 34 and 61% of secondary production, and McLachlan (1975) estimated a contribution of between 60 and 82%. Other authors have estimated meiofauna contribution to be 29% (Wieser & Kanwisher 1961), 15% (Marshall 1969; Gerlach 1971) and 1,65% (Smith *et al.* 1972). Estimates for the combined meio-/microfauna and flora contribution have ranged from 11% (Smith 1973) to 58% (Smith *et al.* 1973). Thus meiofauna appears to account for a mean of 15% of secondary production. In the present study the meiofauna accounts for only 1,07% on average and this may be ascribed to the relatively low populations as well as to the high macrofauna populations, particularly at Station B. It should be mentioned, however, that McIntyre (1964) and McLachlan (1975) considered only macro- and meiofauna and did not measure the micro-component. If this was done in the present case the meiofauna at Station A would account for 36% of secondary production and that at B for only 0,12%. However, since secondary production is defined as the "rate of storage at consumer levels" (Odum 1971) a true partition of secondary production can only be made by considering all the components. To ignore the microbial component is to grossly overestimate the relative importance, in terms of energy, of the meio- and macrofauna. A correction for chemical oxygen demand of 5% in sand (Smith 1973) and of even 30% in mud (Hill 1976) will not greatly affect the contribution of the various components of the benthos. If such a correction is made then the contribution of the macro-, meio- and microfauna at Station A are: 6,05%; 2,20%; and 91,76% respectively. For Station B the relative contributions are: 32,45%; 0,04% and 67,51% respectively.

Production estimates for meiofauna are usually made by multiplying the mean standing crop by a certain turnover. This is obtained from growth rate and life cycle studies (Gerlach 1971) and these have revealed great variations. Some nematodes reproduce in as little as five days under optimal laboratory conditions (Tietjen & Lee 1972) while some copepods require three months (Gerlach 1971). The marine nematode *Enoplus communis* requires a year to produce one generation and the eggs of the harpacticoid copepod *Asellopsis intermedia* require seven months to hatch (Gerlach 1971). Tietjen (1967) found that the life cycle of the nematode *Monhystera filicaudata* took between 24 and 25 days at 20° to 25°C. Similarly the life cycle of *M. disjuncta* and *Diplolaimella schneideri* took 40 days (Chitwood & Murphy 1964). Life cycles of approximately one month have been reported for such groups as monhysterids, chromadorids and oncholaimids (McIntyre 1969). These studies have, however, been done under laboratory conditions, which are usually optimal, and on the assumption that reproduction takes place immediately upon reaching sexual maturity (Gerlach 1971). These conditions are rarely met in nature and the life cycle turnover rate is expected to be somewhat lower than the estimates indicate. In his summary on the subject Gerlach (1971) estimated an annual turnover of 9. McIntyre (1964) estimated 10 and Arlt (1973) 5,7. The mean of these three is 8,23 and indicates a life cycle of approximately 44 days. When an estimate of eight per year was used to calculate meiofauna production, the results were strikingly similar to estimates obtained from the respiration experiments. However, since P/B ratios vary due to species composition, available food, temperature and oxygen,

etc., it is suggested that the RQ method of production estimation be applied wherever possible and that respiration should be determined on a number of individuals to reduce variation.

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