

On the Importance of Marine Meiofauna for Benthos Communities

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Received November 11, 1970

Summary. 1. In sublittoral sediments of silty sand live about 55000–1300000 meiofauna animals, which is a minimum figure because methods are not absolutely efficient.

2. Meiofauna biomass ranges from 0.2 to 2.0 g wet weight in sublittoral silty sand, that is about 3% of macrofauna biomass.

3. A higher percentage of meiofauna biomass is recorded from brackish water regions, intertidal beaches and from the deep sea, where meiofauna and macrofauna biomass are of the same magnitude.

4. Oxygen consumption in meiofauna animals is between 200 and 2000, in small macrofauna between 200 and 500, and in larger macrofauna between 10 and 100 mm³ O₂/h/g wet weight.

5. The assumption is forwarded that in general meiofauna has a metabolism five times more active than that of macrofauna.

6. Generation time in meiofauna lasts from a few days as was observed in cultures, to one or a few years, as was observed in natural populations. For a generalization the guess is forwarded that three generations per year would be an average meiofauna value.

7. Life cycle turnover rate as calculated from life cycle models of two nematodes is 2.2–3. Multiplied by three annual generations results in an average annual turnover rate of about 9 for meiobenthos, which is about five times more than that in macrobenthos.

8. If one compares meiobenthos and macrobenthos, meiobenthos importance in terms of food consumed and in terms of biomass provided for the food chain is 15% in a community like sublittoral silty sand, although meiobenthos in terms of standing stock is just 3% of macrobenthos.

Introduction

Meiofauna is present not only in the interstices of sand but also in soft bottom sediments which contain macrofauna in abundance, and which provide the food for commercially exploited fish and shrimp. For a better understanding of benthos productivity and benthic food chains, it is important, therefore, to evaluate the importance of meiobenthos in relation to macrobenthos. In this respect, one has to distinguish between the importance in terms of food consumed and the importance in terms of food provided for the food chain.

The following argumentation is based on data published by a great number of authors and on the reviews given by Thorson (1966) and McIntyre (1969).

Discussion and Conclusions

Standing Stock of Meiofauna

According to Wieser (1960b) and McIntyre (1969), sublittoral benthic communities down to a depth of 100 m are populated by 55000 to 1000000 specimens of meiofauna per m². This coincides with countings from various communities in Helgoland Bay, where the highest figures are in silty sand and sandy silt, the lowest, in clean sand (Stripp, 1969; see Table 1). The calculations of wet weight biomass range from 0,2 to 2,0 g per m², representing an average of 3% (1—4%) of the corresponding macrofauna biomass.

These figures of Stripp and other authors have to be evaluated with some precautions because they refer to just one fraction of the entire meiofauna. Only those animals are considered which

- a) pass through 500—1000 μ m meshes,
- b) endure a washing procedure,

Table 1. *Macrobenthos and meiobenthos in Helgoland Bay (from Stripp, 1969)*

	Macrobenthos per m ²		Meiobenthos per m ²		Biomass ratio macrobenthos/ meiobenthos
	number	wet weight (g)	number in 1000	wet weight (g)	
<i>Macoma balthica</i> -Comm.					
silty sand	4110	99	1181	1.8	54:1
fine sand	370	16	349	0.5	31:1
mixed sand	310	9	136	0.2	37:1
<i>Abra alba</i> -Community					
(silt)	1615	43	750	1.3	33:1
central area	1615	43	750	1.3	33:1
eastern area	985	34	694	1.1	34:1
southern area	1895	48	1311	2.0	24:1
<i>Echinocardium</i> - <i>Amphiura</i> -Community					
(silty sand)					
main area	4240	61	833	1.3	47:1
northern area	1565	39	596	0.9	42:1
<i>Venus gallina</i> -Community					
medium sand	690	16	173	0.3	53:1
coarse sand	315	18	81	0.2	90:1

- c) a subsequent filtration on 70—100 μm meshes and
 d) preservation in formalin.

Very small animals get lost; fragile animals like Turbellaria and Gastrotricha get destroyed. The method is applicable therefore to soft bottom sediments only where nematodes and Crustacea represent the majority of the meiofauna; the method gives much too low values for clean sand where Turbellaria etc. occur in considerable numbers.

A further error could result from neglecting the deeper strata of the sediment. Even if the majority of the meiofauna concentrates in the upper centimeter, meiofauna may penetrate far down, especially in sand. In medium coarse calcareous sand 40 m deep in Mururoa Atoll Salvat and Renaud Mornant (1969) found 360 000 meiofauna specimens in a stratum 15 cm below the sediment-water-interface, against 1300 000 specimens in an equal quantity of sediment from the superficial stratum. Many meiofauna investigations are confined to just the top layer of the sediment and their quantitative results may be too low.

Another addition will come from Foraminifera which quite often are neglected in meiobenthos studies because special methods are necessary to distinguish living from dead animals. Wet weight biomass of Foraminifera can be much higher than biomass of other meiofauna. For example, Andren *et al.* (1968) found in three sublittoral zones off Göteborg the following biomass (wet weight/m²):

	Inner zone	Medium zone	Outer zone
Macrofauna	—	76.8 g	160.5 g
Meiofauna	0.94 g	0.64 g	0.33 g
Foraminifera	0.43 g	1.31 g	4.91 g

Considering these values, one has to remember, however, that due to the high content of calcareous or sand skeletons the organic substance of Foraminifera is only about 4% of the total weight.

Open for further research is the question how many Ciliata occur in sublittoral benthos communities. Fenchel (1969) counted in 10 m deep fine sand from the Öresund 15 000 000 Ciliates per m², comparable to 1.4 g biomass.

Calculations published in various papers, therefore, must be considered as minimum figures, and it is obvious that in sand the traditional procedure of washing and sieving the sediment gives just a fraction of the meiofauna, probably well below 50%. On the other hand in soft bottom sediments nematodes and Crustacea dominate and the numbers of Turbellaria, Gastrotricha and (?) Ciliata are relatively small, so that counted animals and their actual numbers should not differ very much. There is some hope that a combination of washing and the Uhlig method

(seewater-ice) could extract most of the meiofauna from the sediment, and that this method can be applied even to silty sediments (Uhlig, 1968).

Guille and Soyer (1969) reported a very high relative meiobenthos biomass (8–30%) from the Mediterranean. Partially this can be explained by the relatively low macrofauna densities and small size of macrofauna animals in the Mediterranean (macrobenthos dry weight 1.3–6.7 g/m²), partially by the fact, that nematodes are less represented (50–70% of meiofauna numbers, 4–7% of meiofauna biomass) and larger copepods dominate. A confirmation of these results would be of interest. From the brackish Cochin Backwater in South India Desay and Kutty (1967) reported meiobenthos biomasses sometimes exceeding macrobenthos biomass, but macrobenthos is scarce and sometimes nearly absent. In intertidal beach communities, too, macrofauna is often poorly represented, resulting in a high percentage of meiofauna biomass (Renaud-Debyser and Salvat, 1963; McIntyre, 1968). Finally, deep sea sediments apparently yield as much meiobenthos as macrobenthos biomass. Thiel (1966) counted in deep sea sediment from the Indian Ocean (3000–5000 m) between 20000 and 110000 meiofauna individuals per m². If one assumes a wet weight of only 1 µg per individual, then there should be 0.02–0.11 g meiofauna biomass per m²; but 1 µg is the weight of a very small meiofauna animal, so probably one has to duplicate or triplicate this figure. Anyway deep sea macrobenthos generally occurs in the same order of magnitude from 0.02 to 0.2 g biomass per m² (Zenkevich, Barsanova and Beljaev, 1960; Frankenberg and Menzies, 1968). In Norwegian Sea samples taken between 1500 and 1800 m deep nematodes alone have about 2 g wet weight per m² (Thiel, 1971), while on the Atlantic slope of the Iceland-Faeroes-Ridge between 1500 and 2500 m 0.4–1.2 g meiobenthos per m² were calculated.

Metabolic Rate of Meiofauna

Small animals have a larger metabolism per unit weight than larger animals. This is a fact well known for about a century, and this statement is valid for marine benthic animals too. A meiofauna population, therefore, would have an ecological importance much higher than an aliquot of macrofauna biomass.

Pütter (1909) postulated for aquatic invertebrates a metabolic rate (metabolism per unit weight) ten times bigger if the individuals have a body weight of 0.001 instead of 1.0. This argumentation was adopted even in modern textbooks (Florey, 1966) and was used i.e. by Fenchel (1969) to calculate the metabolic rate of Ciliata and meiobenthos in relation to macrobenthos. As a consequence, a meiofauna population consisting of animals with 1 µg wet weight should have a metabolic rate 100 times bigger than a macrofauna population of animals weighing 1 g each.

Metabolism in relation to body weight is expressed by the formula

$$M = k \cdot W^b \quad \text{or} \quad M/W = k \cdot W^{b-1}.$$

M = metabolism, M/W = metabolic rate, W = body weight.

While Pütter and others postulated the exponent b to be 0.66 later publications (see Zeuthen, 1947) gave reason to correct this to $b = 0.75$, and to restrict this statement to marine invertebrates above 40 mg wet weight. In very small metazoa between 1 μg and 40 mg there is just a small increase in metabolic rates with decreasing body weight, resulting in $b = 0.95$ (Zeuthen, 1953). Since 1960 when Hemmingsen discussed the problem, a number of experiments have been conducted with meiofauna animals between 1 μg and 1 mg wet weight (Table 2).

Some authors refer to oxygen consumption per wet weight, others to oxygen consumption per dry weight. In order to facilitate a comparison values in Table 2 have partially been recalculated with the assumption of a dry weight—wet weight ratio of 1:4. Coull and Vernberg (1970) were mistaken in their statement that the metabolic rates determined by Wieser and Kanwisher (1961) refer to dry weight; actually Wieser and Kanwisher determined wet weight by measuring the length and width of nematodes. Contrary to the opinion of Coull and Vernberg harpacticoid copepods have a metabolism more or less of the same magnitude like nematodes.

I would not dare to decide whether these results correct or confirm the statements of Zeuthen (see Fig. 1). At least it is evident that active, fast moving meiofauna animals (some copepods, some nematodes like *Axonolaimus*, Oncholaimidae, *Tripyloides*) have a metabolism twice or three times larger than sluggish species of the same size (ostracods, halacarids, nematodes like *Spirinia*, *Terschellingia*, *Paracanthochnus*). An accurate estimation of the relative metabolism of meiobenthos and macrobenthos should be based therefore on much more knowledge about the life history and habits of the meiofauna animals. Anyhow it is obvious that an 1 μg animal has a metabolic rate not much more or even less than 10 times that of a 1 g animal.

Presently one can just state that meiobenthos animals have a metabolic rate between 200 and 2000 $\text{mm}^3 \text{O}_2/\text{h/g}$ wet weight, that small macrobenthos animals in the milligram range have a metabolic rate of 200–500 $\text{mm}^3 \text{O}_2/\text{h/g}$ wet weight and that larger macrobenthos animals consume 10–100 $\text{mm}^3 \text{O}_2/\text{h/g}$ wet weight. If one wants to generalize one could say that the metabolic rate of meiobenthos biomass is about 5 times larger than that of macrobenthos biomass, or that an equivalent meiofauna biomass consumes five times more food than the respective macrofauna biomass does.

Generation Time of Meiobenthos

McIntyre (1964) and Fenchel (1968) based calculations about the relative importance of meiobenthos and macrobenthos on experiments

Table 2. Experiments on the metabolic rate of meiobenthos animals. Average values

	Wet weight per individual (μg)	mm^3 $\text{O}_2/\text{h/g}$ wet weight	Author and experimental temperature ($^{\circ}\text{C}$)
<i>Enoplus communis</i> juv. (Nem.)	1	1600	Wieser and Kanwisher, 1960 (20 $^{\circ}$)
<i>Axonolaimus spinosus</i> (Nem.)	2	1800	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Marionina</i> (Oligochaeta)	3	3000	Lasserre, 1970 (19 $^{\circ}$)
<i>Monoposthia</i> (Nem.)	3	590	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Terschellingia</i> (Nem.)	3	450	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Paracanthochus caecus</i> (Nem.)	4	560	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Odontophora</i> (Nem.)	4	730	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Enhydrosoma propinquus</i> (Cop.)	4	720	Coull and Vernberg, 1970 (25 $^{\circ}\text{C}$)
<i>Asellopsis intermedia</i> (Cop.)	5	320	Lasker and Wells, 1970 (6 $^{\circ}$)
<i>Asellopsis intermedia</i> (Cop.)	5	400	Lasker and Wells, 1970 (10 $^{\circ}$)
<i>Asellopsis intermedia</i> (Cop.)	5	480	Lasker and Wells, 1970 (15 $^{\circ}$)
<i>Asellopsis intermedia</i> (Cop.)	5	950	Lasker and Wells, 1970 (20 $^{\circ}$)
<i>Bathylaimus</i> (Nem.)	5	1300	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
Ostracoda	5	560	Zeuthen, 1947 (15 $^{\circ}$)
<i>Oncholaimus paralangrunensis</i> (Nem.)	6	1400	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Tripyloides marinus</i> (Nem.)	6	1300	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Theristus setosus</i> (Nem.)	6	740	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Spirinia parasitifera</i> (Nem.)	6	370	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Sabatieria</i> (Nem.)	7	600	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Anticoma litoralis</i> (Nem.)	8	490	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Enoplus communis</i> juv. (Nem.)	10	700	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Mytilus</i> (Mollusca) juv.	10	400	Zeuthen, 1947 (15 $^{\circ}$)
Copepoda	15	800	Zeuthen, 1947 (15 $^{\circ}$)
<i>Oncholaimus campylocercoides</i> (Nem.)	16	1100	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Rhombognathides seahami</i> (Acari.)	20	250	Wieser and Kanwisher, 1959 (20 $^{\circ}$)
<i>Longipedia helgolandica</i> (Cop.)	20	2440	Coull and Vernberg, 1970 (25 $^{\circ}$)
<i>Metoncholaimus pristiurus</i> (Nem.)	21	920	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
<i>Bolbella tenuidens</i> (Nem.)	21	650	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
Nematoda	25	440	Zeuthen, 1947 (15 $^{\circ}$)
<i>Marionina</i> (Oligochaeta)	30	1000	Lasserre, 1970 (19 $^{\circ}$)
<i>Halichoanolaimus longicauda</i> (Nem.)	37	350	Wieser and Kanwisher, 1961 (20 $^{\circ}$)
Ostracoda	40	200	Zeuthen, 1947 (15 $^{\circ}$)
<i>Hirschmannia viridis</i> (Ostr.)	?	340	Hagerman, 1969a (20 $^{\circ}$)
<i>Capitella</i> (Polychaeta)	50	440	Zeuthen, 1947 (15 $^{\circ}$)
<i>Enoplus communis</i> (Nem.)	100	400	Wieser and Kanwisher, 1959, 1961 (20 $^{\circ}$)
div. Isopoda	100	650	Zeuthen, 1947 (15 $^{\circ}$)
<i>Mytilus</i> juv. (Mollusca)	200	300	Zeuthen, 1947 (15 $^{\circ}$)
<i>Halacarus basteri</i> (Acari.)	200	250	Wieser and Kanwisher, 1959 (20 $^{\circ}$)
<i>Fabricia</i> (Polychaeta)	350	300	Zeuthen, 1947 (15 $^{\circ}$)
<i>Pontonema vulgare</i> (Nem.)	350	200	Overgaard Nielsen, 1949 (16 $^{\circ}$)

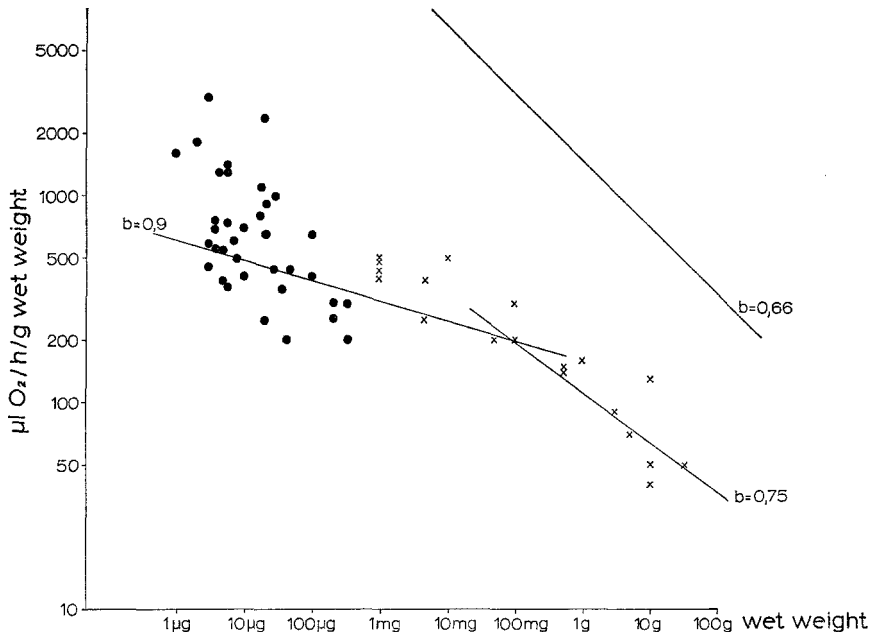


Fig. 1. Metabolic rate and wet weight in marine benthic invertebrates. This diagram contains all data referring to meiofauna experiments (Table 2) together with some data on macrofauna experiments published by Zeuthen (1947): 1 mg *Balanus*, *Gammarus*, *Idothea*, *Polydora*; 5 mg *Nereis*, *Lepidonotus*; 10 mg *Balanus*, average from various Crustacea; 50 mg average from various Mollusca; 100 mg *Mytilus*, average from various Crustacea; 500 mg *Nereis*, average from various Mollusca; 1 g average from various Crustacea; 3 g *Nereis virens*. 10 g *Mytilus*, *Asterias*, average from various Crustacea; 30 g *Sipunculus*. The lines representing $b = 0.66$, $b = 0.75$ and $b = 0.9$ have been inserted just for didactic purposes; they are not a result of the data demonstrated. Data are not reduced to standard temperature

which indicated three to six weeks for one meiofauna life cycle. As can be seen from Table 3 it is true that quite a number of copepods, nematodes, ostracods and acoelous Turbellaria in culture experiments showed such short periods between two generations, but there are other experiments too which strongly argue against generalizing towards the statement that meiobenthos reproduces at 6–15 generations per year:

a) There are species with a much longer generation time; they yield just 2–3 generations per year, like some nematodes and ostracods, or just one generation per year, like the nematode *Enoplus communis*, halacarids, some ostracods, Foraminifera and Turbellaria. There are even species known which need 2 or 3 years for development. Presently it is

not known whether species with short development of species with long development dominate under natural conditions.

b) Even in species which develop from egg to adult in a short period it is not a general rule that one generation follows the other instantaneously. Several ostracods have hibernating eggs (Theisen, 1966), probably the same is true for Turbellaria of the genus *Paromastomum*, according to Pawlak (1969). Eggs of the nematode *Halichoanolaimus robustus* have been observed in cultures at 7° C to hatch after an egg period of more than 150 days (unpublished observation by M. Schrage). The harpacticoid copepod *Asellopsis intermedia* mates in August, but the nauplia do not hatch from the egg masses before May next year, and there is just one generation per year in this species (Lasker and Wells, 1970). A similar life cycle with just one or two generations per year has been observed in the harpacticoid copepod *Platychelipus* (Barnett, 1970). Other species reproduce with preference in winter, like the acoelous Turbellaria *Pseudohaplogonaria vacua* and *Convoluta convoluta* (Apelt, 1969), some nematodes (Skoolmun and Gerlach, 1971) and some Oligochaeta (v. Bülow, 1967).

c) Culture experiments are normally conducted under favourable conditions and at high temperatures. Their results cannot without precautions be interpreted. Between 20° and 7° C generation time of the nematode *Monhystera disjuncta* is from 12 to 20 days. At 1° C generation time is about 80 days, at about 0° C 135 days (Gerlach and Schrage, 1971). *Archaphanostoma agile*, an acoelous Turbellaria, has at 16–18° C a generation time of 21–47 days. In cultures at 5–6° C generation time is prolonged to 104 days, at 3–4° C eggs hatch, but juveniles do not grow; at 0° C adults do not produce eggs (Apelt, 1969). In winter there are only few or no generations of many meiofauna animals.

On the other hand, there are some meiofauna animals with a life span which exceeds generation time. In contrast to the results of Chitwood and Murphy (1964) and v. Thun (1968) we found that the females of the nematode species *Monhystera disjuncta* live for about 60 days, and lay eggs over a period of 20 days. In this experiment the development from egg to egg did not last more than 12 days (Gerlach and Schrage, 1971). In *Archaphanostoma agile* (Turbellaria Acoela) Apelt (1969) recorded a life span of more than 19 months and a continuous production of 12 eggs within every ten days.

If one summarizes these results, one can just state that life histories of different meiobenthos species are very diversified, probably not less than in different macrobenthos animals. Before one could calculate an average meiobenthos generation time, one should know more on life cycles of really dominant species. A guess would be three generations per year.

Table 3. Duration of development and number of annual generations in marine meiobenthos. Development: mostly from hatching to adult stage. Generation time: from a certain stage to the same stage of the next generation

	Duration	Gene-	Life-	Gene-	Author and method
	of devel- opment	ration time	span (days)	rations per year	C = culture 18-25° C N = natural conditions
	(days)	(days)	(days)		
<i>Cytherura gibba</i> (Ostr.)	11			3	Theisen, 1966 (C)
<i>Elofsonia baltica</i> (Ostr.)	14			1-2	Theisen, 1966 (C)
<i>Elofsonia baltica</i> (Ostr.)	30				Theisen, 1966 (N)
<i>Cytherois fischeri</i> (Ostr.)	20			3	Theisen, 1966 (C)
<i>Cytherois fischeri</i> (Ostr.)	25				Theisen, 1966 (N)
<i>Tisbe furcata</i> (Cop.)	19-24		40-50		Johnson and Olson, 1948, cit. Thorson, 1966
<i>Monhystera disjuncta</i> (Nem.)		18-28	33		v. Thun, 1968 (C)
<i>Monhystera disjuncta</i> (Nem.)		30			Chitwood and Murphy, 1964 (C)
<i>Chromadorita tenuis</i> (Nem.)		19-34	43		v. Thun, 1968 (C)
<i>Patellina corrugata</i> (Foram.)	21				Myers, 1942, cit. Thorson, 1966 (C)
<i>Loxocoelha elliptica</i> (Ostr.)	22			3	Theisen, 1966
<i>Cytherois arenicola</i> (Ostr.)	22			3	Theisen, 1966 (N)
<i>Archaphanostoma agile</i> (Turb.)	21-47		570		Apelt, 1969 (C) (16-18° C)
<i>Diplolaimella ocellata</i> (Nem.)		22-39	56		v. Thun, 1968 (C)
<i>Diplolaimelloides oscheri</i> (Nem.)		23-35	54		v. Thun, 1968 (C)
<i>Monhystera filicaudata</i> (Nem.)		24-35			Tietjen, 1967 (C)
<i>Leptocythere lacertosa</i> (Ostr.)	25			3	Theisen, 1966 (C)
<i>Leptocythere lacertosa</i> (Ostr.)	45				Theisen, 1966 (N)
<i>Acanthonichus indica</i> (Cop.)	25-30				Chandrasekhara, 1967 (C)
<i>Acanthonichus cobbi</i> (Nem.)		29			Hopper and Meyers, 1966 (C)
<i>Monhystera paretentata</i> (Nem.)		30			Hopper and Meyers, 1966 (C)
<i>Euchromadora gaulica</i> (Nem.)		30-40			Hopper and Meyers, 1966 (C)
<i>Diplolaimelloides islandica</i> (Nem.)		31-39	50		v. Thun, 1968 (C)
<i>Diplolaimella schneideri</i> (Nem.)		40			Chitwood and Murphy, 1964 (C)
<i>Theristus setosus</i> (Nem.)				3	Skoolmun and Gerlach, 1971 (N)
<i>Enoploides spiculohamatus</i> (Nem.)				2-3	Skoolmun and Gerlach, 1971 (N)
<i>Axonolaimus demani</i> (Nem.)				2-3	Schütz, 1966 (N)
<i>Adoncholaimus thalassophygas</i> (Nem.)	48-58	55-72	78		v. Thun, 1968 (C)

<i>Adoncholaimus thalassophygas</i> (Nem.)	52		2-3	Schütz, 1966 (N)
<i>Monocelis fusca</i> (Turb.)	29			Giesa, 1966 (C)
<i>Monocelis lineata</i> (Turb.)	35			Giesa, 1966 (C)
<i>Viscoia viscosa</i> (Nem.)			1-2	Skoomum and Gerlach, 1971 (N)
<i>Anticoma limalis</i> (Nem.)			2	Schütz, 1966 (N)
<i>Oncholaimus brachycereus</i> (Nem.)			1-2	Skoomum and Gerlach, 1971 (N)
<i>Cytherura nigrescens</i> (Ostr.)	30-35			Elofson, 1942
<i>Loxocochna</i> (Ostr.)	40		1	Elofson, 1942
<i>Pseudaphanostoma</i> sp. (Turb.)	44			Apelt, 1969 (C) (16-18° C)
<i>Discorbis globularis</i> (Foram.)	52			Myers, 1942, cit. Thorson, 1966 (C)
<i>Xestoleberis aurantiä</i> (Ostr.)	60			Elofson, 1942
<i>Cythere lutes</i> (Ostr.)	60	365	1	Elofson, 1942
<i>Cyprideis torosa</i> (Ostr.)	63		1	Theisen, 1966 (C)
<i>Asellopsis intermedia</i> (Cop.)	90		1	Lasker and Wells, 1970
<i>Pseudohaplogonaria</i> sp. (Turb.)	90			Apelt, 1969 (C) (16-18° C)
	(years)	(years)	(years)	
<i>Nematoplana</i> and other Turb.	0.75		1	Ax, 1969 (N)
<i>Hirschmannia viridis</i> (Ostr.)	0.8	1	1	Elofson, 1942; Hagerman, 1969 b (N)
<i>Cythereis villosa</i> (Ostr.)	0.8-1		1	Elofson, 1942
<i>Parasterope pollex</i> (Ostr.)		1	1	Hullings, 1969 (N)
<i>Paromatostomum</i> sp. (Turb.)			1	Pawlak, 1969 (N)
<i>Enoplius communis</i> (Nem.)			1	Wieser and Kanwisher, 1960; McClosky, 1970 (N)
<i>Metarhombognathus armatus</i> (Acari.)			1	Straarup, 1968 (N)
<i>Rhombognathus seahami</i> (Acari.)			1	Straarup, 1968 (N)
<i>Halacarus basteri</i> (Acari.)			1	Kirchner, 1969 (N)
<i>Halacarus basteri</i> (Acari.)		1	1	Kirchner, 1969 (C) (9-120° C)
<i>Foraminifera</i> sp.			1	Myers, 1942, cit., Thorson, 1966; Boltovskoy and Lena, 1969
<i>Trubijex costatus</i> (Oligoch.)		2		Brinkhurst, 1964 (N)
<i>Cytheridea papillosa</i> (Ostr.)	2-3			Elofson, 1942
<i>Cythereis tuberculata</i> (Ostr.)	2-3			Elofson, 1942
<i>Philomedes globosus</i> (Ostr.)	3	4		Elofson, 1942
<i>Rhabdomakys ruber</i> (Holothuria)		3		Menker, 1970 (N)

Egg Number in Meiofauna

Data about the number of eggs produced by one female meiofauna animal are scarce. Some Turbellaria like *Archaphanostoma* are very productive, laying more than 600 eggs over a period of many months (Apelt, 1969). Generally, much smaller numbers are the rule in ostracods, copepods and nematodes. Lasker and Wells (1970) found 30–40 eggs to be the annual production of one female of the copepod *Asellopsis*, Elofson (1942) found the number of eggs in the brood-pouch of various ostracods to vary between 4 and 41, and v. Thun (1968) counted averages from 21 to 36 eggs per female in nematodes.

Turn over Rate of Meiobenthos

With the insufficient knowledge regarding the number of meiobenthos generations per year, it is difficult to calculate the annual turn over rate of meiofauna animals. It is easier, instead, to calculate the life cycle turn over rate or the relation between the average standing stock and the production of animals which succumbed to predators or died and got desintegrated, during one life cycle. I want to do this calculation for a typical representative of meiobenthos, i.e. the medium sized brackish water nematode *Chromadorita tenuis*. For this species v. Thun (1968) provided a number of facts from culture experiments at 20–22° C.

Adults are 800–1300 μm long and 40 μm large. Using the formula of Andrassy (1956) and assuming a specific weight of 1.1 the wet weight of adult *Chromadorita tenuis* varies between 0.8 and 1.3 μg . Eggs are globular with a diameter of about 34 μm . They have a wet weight of about 0.025 μg . Freshly hatched juveniles should have about the same weight.

According to v. Thun eggs are deposited singly during the course of 5–11 days; their number is 16–28 (average 20). Juveniles hatch after 4–5 days and develop within 12–15 more days to the adult stage. The total life cycle takes 26 days (average from 27 experiments). For a general scheme I dare the simplification that 20 eggs are deposited and develop simultaneously. The embryos should develop in five days, the adult stage should be reached on day 21, eggs deposited on day 26. I assume that growth is similar to that observed in the nematode *Enoplus communis* by Wieser and Kanwisher (1960). Wet weights of different stages can be derived from Fig. 2.

Virtually nothing is known about the rate of mortality in free living nematodes or other members of the meiofauna under natural conditions. I assume a mortality of 10% per day during juvenile life even if this assumption is not based on facts. It is certainly wrong, of course, to assume no mortality in eggs and in reproductive adults before they die on days 33 and 36, but this helps to simplify the model.

From this simple model of one life cycle of *Chromadorita tenuis* (Fig. 2) results an average standing stock of 3.3 μg wet weight. During

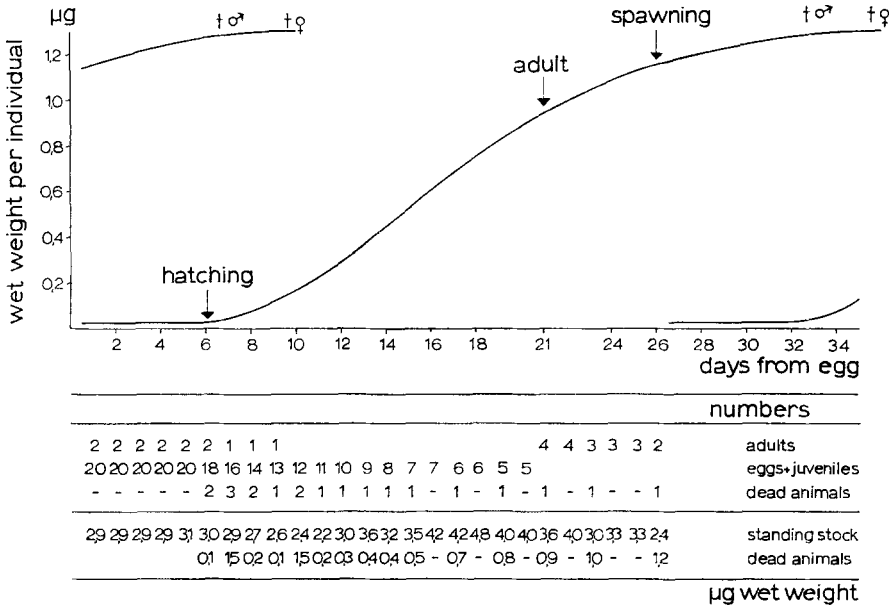


Fig. 2. Data for the calculation of the life cycle turnover rate in *Chromadorita tenuis* (Nematoda). See text. Top: wet weight of different stages of *Chromadorita tenuis* Bottom: Offspring of one couple of *Chromadorita tenuis* (numbers and wet weight), assuming a mortality of about 10% during juvenile life

this life cycle 20 animals weighing 9.8 µg are produced for the consumption of predators or scavengers. This gives a life cycle turnover rate of 3. I got a similar result, a life cycle turnover rate of 2.2, by calculating one life cycle of the nematode *Monhystera disjuncta*, simulating natural conditions more closely by assuming the production of 2-3 eggs per day over a period of 8 days, and by letting mortality work at random. In this model, the standing stock was 2.5 µg and the production of dead animals was 5.6 µg.

For freshwater invertebrates, Waters (1969) postulated life cycle turnover rates from 2.5 to 5. If one can dare to generalize calculations of nematode models, then meiofauna seems to fit into the lower range of these limits.

A multiplication of life cycle turnover rates with the number of annual generations gives the annual turnover range. In *Monhystera disjuncta* we calculated 12 generations per year (Gerlach and Schrage, 1971): this results in an annual turnover rate of 26. But as the majority of meiofauna animals probably has much fewer generations, it seems reasonable to multiply a life cycle turnover rate of 3 with three annual generations.

The result fits well with the annual meiobenthos turnover rate of ten, postulated by McIntyre (1964). If one takes twice the standing stock as the annual turnover rate of macrobenthos, then meiobenthos turnover is about five times greater. In relation to macrobenthos a meiobenthos standing stock of only 3% would contribute about 15% to the food chain, in terms of animals and spawn which are predated upon or are consumed by scavengers and decomposers.

One should point out, however, that data on macrobenthos turnover rates are contradictory (Sanders, 1965; Thorson, 1966), and that an overall generalization of macrobenthos turnover rates is presently not much better founded than that proposed for meiobenthos.

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