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THE MEIOFAUNA OFF THE COAST OF NORTHUMBERLAND

II. SEASONAL STABILITY OF THE NEMATODE POPULATION

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(Text-fig. 1)

Seasonal fluctuations in density, biomass, species composition and reproductive activity of an offshore nematode population have been investigated. The species composition is shown to remain relatively stable. The majority of species breeds throughout the entire year, and the age structure remains constant from month to month. By the methods employed, no significant change in population density throughout the year can be detected. The statistical variance between monthly samples taken throughout the year was found to be not significantly different from a series of replicate samples taken on a single day. The total dry weight of nematodes averages 393 mg/m^2.

INTRODUCTION

In an earlier paper (Warwick & Buchanan, 1970) the structure of the nematode communities at three stations off the Northumberland coast was compared. It was shown that the offshore mud community at station 'C' was faunistically the most homogenous. This station has been selected for a more intensive investigation of meiofaunal production since it provides the simplest situation for study, and furthermore the type of nematode community found here is thought to be of common occurrence in similar sediments round Northern Britain.

The meiofauna of littoral and shallow water sediments is known to fluctuate widely from month to month both in species composition and overall population density (Smidt, 1951; Perkins, 1958; Wieser & Kanwisher, 1961; Muus, 1967; Hopper & Meyers, 1967; Jansson, 1968; Tietjen, 1969). These fluctuations are associated with seasonal cycles of reproduction, at least in the Copepoda and Ostracoda (see review by McIntyre, 1969, pp. 272–3). For the Nematoda published information is scant. Wieser & Kanwisher (1960) have shown that the large nematode *Enoplus communis* Bastian has an annual cycle of reproduction, spawning taking place in spring and maturity being reached in autumn or early winter. However, Hopper & Meyers (1966) have suggested that another large enoploid, *Metoncholaimus scissus* Wieser & Hopper, has a cycle shorter than one year, and information from laboratory cultures suggests that a considerable number of smaller nematodes have cycles of about one month (Chitwood & Murphy, 1964; Hopper & Meyers, 1966*a*; Tietjen, 1967).

Little information is available on the fluctuations of offshore meiofaunal populations. McIntyre (1964) in his study of the Fladen and Loch Nevis grounds off the Scottish coast failed to reveal statistically significant differences in nematode and copepod counts between surveys, although the temporary meiobenthos was much more numerous in late autumn and winter. Stripp (1969) reports that the meiofauna of sand, silt and mixed sediments at depths of 16–49 m in Helgoland Bay is numerically 1·6 times greater in the summer than the winter, but here again a temporary fauna of young molluscs and polychaets has been included in the estimates. The only clue we have as to the seasonal reproductive activity of offshore nematode populations is the observation by McIntyre (1964) that '...juvenile nematodes...were present in most surveys'.

Seasonal fluctuations in offshore meiofaunal populations are clearly in need of investigation. Continuing our study of meiofaunal production off the Northumberland coast we here describe the seasonal stability in numbers and biomass, species composition and reproductive activity of the nematode population.

METHODS

The sampling station is situated 11 miles east of Blyth, Northumberland, at a depth of 80 m. The sediment here consists of fine silt with a median particle diameter of 0·056 mm. More precise details of the location and sediment composition are given in our earlier paper (Warwick & Buchanan, 1970). Bottom temperatures at this station vary between 5·3 °C in early April and 10·7 °C in late September, a difference between maxima and minima of only 5·4 °C. Two sets of four cores, each covering an area of 0·78 cm^2, have been taken each month, the method of collection and treatment of samples being exactly as described in the above-mentioned paper. Collections were made in October and December 1968, and January, March, May, July, August and September 1969. The station was relocated each month by means of 'Decca' navigator, and at best is only accurate to within 100 m radius of the station.

Dry weights were determined by washing samples of 200 and 500 nematodes through a preweighed membrane filter with a pore size of 0·45 μ. These samples were representative of all the size groups and all the species present. The filters were then vacuum dried over P_2O_5 for 48 h, reweighed on a microbalance and compared with the change in weight of a control filter which had been treated in the same manner.

SPECIES COMPOSITION

Several new and interesting nematode species have been encountered during this investigation, some of which have already been described (Warwick, 1969, 1970, 1970*a*), whilst others still await description. In studying the fluctuations in species composition from month to month only the ten numerically commonest species have been considered, since fluctuations in the rarer species are likely to have little significance. These ten species have been ranked in order of abundance each month (Table 1). It will be seen from this table that the percentage dominance of each species varies slightly from month to month, but it is clear that there is no seasonal pattern of variation. The coefficient of concordance (W) of the ranking has been calculated at 0·71, which is very high, and this concordance was found to be highly significant ($P > 0{\cdot}1\,\%$) when tested by the F-distribution. Thus there is a considerable degree of stability in the relative proportions of species present throughout the year.

TABLE 1. THE COMMONER NEMATODE SPECIES RANKED IN ORDER OF ABUNDANCE

Figures in parentheses express dominance as a percentage of the total population.

	Mean Rank	Oct.	Dec.	Jan.	Mar.	May	July	Aug.	Sept.
Dorylaimopsis punctatus Ditlevsen	1	1 (13·5)	1 (15·3)	2 (10·6)	1 (9·7)	1 (8·3)	3 (7·6)	2 (10·0)	3 (5·8)
Sabatieria cupida Bresslau & Stekhoven	2	2 (13·0)	3 (10·9)	1 (11·7)	2 (6·9)	3 (6·7)	1 (13·7)	3 (8·4)	2 (8·5)
Leptolaimus elegans (Stekhoven & De Coninck)	3	4 (8·7)	2 (11·2)	4 (6·9)	3 (6·2)	4 (5·2)	4 (5·0)	1 (11·5)	1 (11·5)
Sabatieria ornata Ditlevsen	4	3 (10·4)	4 (6·1)	4 (6·9)	4 (5·4)	2 (8·0)	8 (3·2)	5 (5·1)	7 (3·9)
Terschellingia longicaudata de Man	4	5 (6·0)	5 (4·8)	3 (8·8)	5 (4·2)	5 (3·9)	2 (9·5)	8 (3·5)	4 (4·4)
Pomponema multipapillata (Filipjev)	6	7 (2·5)	7 (1·8)	8 (1·9)	5 (4·2)	8 (3·7)	6 (4·4)	4 (5·3)	6 (4·0)
Axonolaimus spinosus (Bütschli)	7	8 (1·7)	6 (2·0)	9 (1·1)	7 (3·0)	10 (2·3)	5 (4·6)	7 (3·8)	4 (4·4)
Longicyatholaimus sp.	8	6 (3·5)	8 (1·5)	9 (1·1)	7 (3·0)	7 (4·6)	9 (2·6)	9 (3·3)	9 (3·4)
Actinonema pachydermatum Cobb	9	9 (0)	10 (0·7)	6 (2·7)	10 (1·2)	5 (3·9)	10 (2·0)	6 (4·0)	10 (3·2)
Microlaimus sp. 2	10	9 (0)	9 (1·1)	6 (2·7)	9 (1·7)	9 (2·8)	7 (3·4)	10 (1·3)	8 (3·5)

TABLE 2. THE AGE STRUCTURE OF THE TOTAL POPULATION

First figures are the actual numbers counted, and those in parentheses indicate the percentage of the identified total.

	Oct.	Dec.	Jan.	Mar.	May	July	Aug.	Sept.
Males	51 (13·7)	79 (21·1)	79 (26·6)	92 (26·7)	126 (20·8)	92 (21·9)	108 (29·0)	171 (22·5)
Gravid Females	16 (4·3)	15 (4·0)	5 (1·7)	9 (2·6)	17 (2·8)	17 (4·0)	15 (4·0)	36 (4·7)
Non-gravid females	59 (15·9)	85 (22·7)	44 (14·8)	55 (15·9)	87 (14·3)	63 (15·0)	53 (14·2)	103 (13·5)
Juveniles	246 (66·1)	196 (52·2)	169 (56·9)	189 (54·8)	377 (62·1)	249 (59·1)	197 (52·8)	451 (59·3)

TABLE 3. AGE STRUCTURE OF THE FIVE COMMONEST SPECIES

First figures are the actual numbers counted, and those in parentheses indicate the percentage frequency.

	Oct.	Dec.	Jan	Mar.	May	July	Aug.	Sept.
Dorylaimopsis punctatus								
Males	7 (10·8)	9 (12·9)	4 (10·0)	11 (28·2)	5 (8·1)	4 (10·5)	7 (15·6)	9 (16·1)
Gravid females	3 (4·6)	5 (7·1)	1 (2·5)	1 (2·6)	3 (4·8)	5 (13·2)	2 (4·4)	2 (3·6)
Non-gravid females	8 (12·3)	5 (7·1)	4 (10·0)	2 (5·1)	4 (6·5)	5 (13·2)	7 (15·6)	7 (12·5)
Juveniles	47 (72·3)	51 (72·9)	31 (77·5)	25 (64·1)	50 (80·6)	24 (63·2)	29 (64·4)	38 (67·9)
Sabatieria cupida								
Males	7 (11·1)	7 (14·0)	10 (22·7)	3 (10·7)	8 (16·0)	16 (23·5)	11 (28·9)	12 (14·8)
Gravid females	1 (1·6)	0 (0·0)	1 (2·3)	1 (3·6)	1 (2·0)	2 (2·9)	1 (2·6)	1 (1·2)
Non-gravid females	4 (6·3)	6 (12·0)	2 (4·5)	2 (7·1)	2 (4·0)	11 (16·2)	3 (7·9)	2 (2·5)
Juveniles	51 (81·0)	37 (74·0)	31 (70·5)	22 (78·6)	39 (78·0)	39 (57·4)	23 (60·5)	66 (81·5)
Leptolaimus elegans								
Males	7 (16·7)	7 (13·7)	7 (26·9)	9 (36·0)	5 (12·8)	3 (12·0)	8 (15·4)	36 (32·7)
Gravid females	3 (7·1)	1 (2·0)	0 (0·0)	0 (0·0)	1 (2·6)	0 (0·0)	4 (7·7)	7 (6·4)
Non-gravid females	11 (26·2)	18 (35·3)	2 (7·7)	2 (8·0)	10 (25·6)	2 (8·0)	6 (11·5)	16 (14·5)
Juveniles	21 (50·0)	25 (49·0)	17 (65·4)	14 (56·0)	23 (59·0)	20 (80·0)	34 (65·4)	51 (46·4)
Sabatieria ornata								
Males	2 (4·0)	12 (42·9)	10 (38·5)	5 (22·7)	11 (18·3)	5 (31·3)	6 (26·1)	9 (24·3)
Gravid females	6 (12·0)	2 (7·1)	1 (3·8)	4 (18·2)	3 (5·0)	3 (18·8)	0 (0·0)	5 (13·5)
Non-gravid females	5 (10·0)	2 (7·1)	2 (7·7)	1 (4·5)	5 (8·3)	1 (6·3)	4 (17·4)	5 (13·5)
Juveniles	37 (74·0)	12 (42·9)	13 (50·0)	12 (54·5)	41 (68·3)	7 (43·8)	13 (56·5)	18 (48·6)
Terschellingia longicaudata								
Males	3 (10·3)	5 (22·7)	5 (15·2)	1 (5·9)	6 (20·7)	9 (19·1)	5 (31·3)	10 (23·8)
Gravid females	3 (10·3)	1 (4·5)	1 (3·0)	0 (0·0)	0 (0·0)	0 (0·0)	0 (0·0)	2 (4·8)
Non-gravid females	8 (27·6)	7 (31·8)	5 (15·2)	1 (5·9)	7 (24·1)	14 (29·8)	5 (31·3)	2 (4·8)
Juveniles	15 (51·7)	9 (40·9)	22 (66·7)	15 (88·2)	16 (55·2)	24 (51·1)	6 (37·5)	28 (66·7)

REPRODUCTION

The only field data available concerning the reproductive cycles of marine nematodes is that of Wieser & Kanwisher (1960) on *Enoplus communis*. These authors were able to measure a sample of the worms at various times of the year, and the distribution of size groups throughout the year lead to the postulation that this species had a single annual cycle of reproduction. However, neither body weight nor measurements provided a good basis for distinction between the five instars, since there is continuous growth between moults. In view of the large number of species encountered in the present samples individual measurements were not practicable. For the purposes of this study, therefore, only four cohorts have been counted; mature males, mature gravid females, mature non-gravid females and juveniles. Table 2 shows the variation in the proportions of these cohorts throughout the year for the total of the identified population. It will be noted that juveniles dominate the population throughout the year, and that gravid females are present in all seasons. Calculation of the variance ratio within samples (between the two sets of four cores) and between samples (between months) indicates that the fluctuations in the proportions of the four cohorts are not significant. Turning to individual species, information on the commonest five species is presented in Table 3, and it will be seen that the same trend is evident. We are therefore forced to the conclusion that at least the majority of nematode species is breeding throughout the year, and that there is complete asynchrony in the reproductive cycles. Observations on *Dorylaimopsis punctatus*, the dominant species, indicate that both very small and very large juveniles are present in all months.

POPULATION DENSITY AND WEIGHT

The monthly mean numbers for total population density are given in Table 4. In no month was there a statistically significant difference in population density between the two duplicate sets of four monthly cores, and the values from both sets have been combined to give a monthly mean. It will be seen that there are considerable fluctuations in the mean population density from month to month throughout the year, but their significance as representing true seasonal fluctuations is open to question. The fluctuations may well be due to the variance inherent in the population as a whole and reflect the relationship between the dispersion pattern and the size and number of samples taken. For comparison, a series of eight replicate sets of four cores were taken from the station on a single day in July 1970. The population counts for these samples are presented in Table 4. When the two sets of monthly cores are compared with the replicates taken in July, it is found that although the within sample variances of the three sets of cores are approximately equal, the between sample variance is in fact higher in the July replicates than in either of the monthly sets of samples. Thus the fluctuations in the mean population density from month to month throughout the year are well within the limits of the fluctuation to be expected in any one month. Within the limits of the number and size of samples taken it has not therefore been possible to demonstrate a significant seasonal fluctuation. An increased number of monthly cores would no doubt give a more refined population estimate, but both the number and the size of the cores have in fact been chosen as a compromise compatible with the time-consuming effort of sorting and identification. If, however, any seasonal fluctuation in population does occur, it is reasonable to suggest that it cannot be very marked, especially in view of the stability of age structure throughout the year.

TABLE 4. NEMATODE NUMBERS AND DRY WEIGHTS

	Numbers in monthly samples A	Numbers in monthly samples B	Monthly mean	Mean/10 cm²	Mean dry wt (g/m²)	Numbers in July replicates
Oct.	88	13	—	—	—	83
	72	91	60	774	0·347	33
	78	14	—	—	—	172
	64	63	—	—	—	116
Dec.	33	58	—	—	—	76
	67	86	57	732	0·328	47
	63	53	—	—	—	62
	31	66	—	—	—	102
Jan.	95	64	—	—	—	117
	22	33	47	604	0·271	71
	46	36	—	—	—	95
	46	35	—	—	—	90
Mar.	43	82	—	—	—	99
	44	41	51	647	0·290	154
	62	37	—	—	—	161
	32	63	—	—	—	119
May	98	67	—	—	—	136
	64	93	93	1197	0·536	65
	78	93	—	—	—	86
	184	70	—	—	—	55
July	77	34	—	—	—	13
	116	35	62	796	0·357	15
	50	83	—	—	—	11
	68	34	—	—	—	14
Aug.	24	33	—	—	—	132
	130	73	57	724	0·325	57
	38	46	—	—	—	74
	72	36	—	—	—	102
Sept.	145	87	—	—	—	131
	103	170	119	1535	0·688	23
	110	185	—	—	—	109
	74	84	—	—	—	141

In view of the stability in both species composition and age structure of the population it is valid to extrapolate weights from numbers directly throughout the year. The 200 and 500 formalin preserved nematodes from the study area were pooled from samples collected in March, November and December, and gave weights of 0·06 and 0·224 mg respectively. The sample of 500 probably gives the most reliable weight, and an average of 0·000448 mg for a single nematode has been used in the following calculations. These weighings agree quite closely with values obtained from other areas with a similar sediment composition, the R-stations in Buzzards Bay (Wieser, 1960) and the Fladen and Loch Nevis grounds off the Scottish coast (McIntyre, 1964). The number/weight relationship for these areas is illustrated in Fig. 1, and this could be used as an approximate conversion chart for other areas of similar sediment composition. It should be pointed out that data for Copepoda drawn from the same two sources produces a line about which there is much less scatter of points, and this provides a more accurate conversion chart.

The dry weights varied between 271 and 688 mg/m^2 with a mean of 393. These figures are quite comparable with the weights estimated in Buzzards Bay (Wieser, 1960) and from the two Scottish grounds (McIntyre, 1964). The figures in closest agreement are those from the Fladen ground, which varied from 263 to 643 mg/m^2, with a mean of 432. Lower estimates are recorded from Loch Nevis and the R-stations of Buzzards Bay, with means of 192 and 226 mg/m^2 respectively.

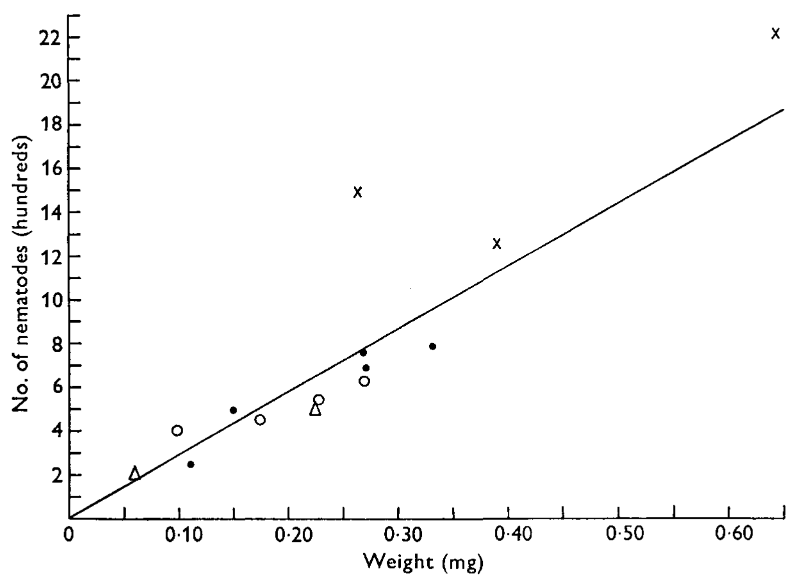

Fig. 1. Dry weight/numbers relationship for offshore nematode populations of silty sediments. Numbers represent hundreds of nematodes. ○, Loch Nevis (McIntyre, 1964); ×, Fladen (McIntyre, 1964); ●, Buzzards Bay R-stations (Wieser, 1960); △, present study.

DISCUSSION

Estimations of production in terms of g/m^2/year are hampered by the fact that the life cycles are asynchronous and that breeding is a continuous process. Thus generation times cannot be estimated from field data, and laboratory cultures will now have to be established to provide these estimates. Matters are further complicated by the fact that it is impossible to determine the number of eggs produced per individual. Egg deposition in marine nematodes may be of two types. The female may store a large number of eggs in her uteri, release them in a mass and subsequently die, or egg laying may be a continuous process where only one or two eggs per uterus mature at a time. In the former case it is easy to determine the number of eggs produced, but in the latter case this is more difficult. Unfortunately the continuous type of production is exhibited by the vast majority of the offshore species investigated in this study. This may be inferred from the low average number of eggs found in the uteri. Specimens of *Dorylaimopsis punctatus*, for example, have seldom been found with more than one egg per uterus, and a similar situation is found in the other common species. Inability to estimate recruitment, together with a lack of knowledge of the generation times, make the formulation of a life table for any species impossible at the present time.

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