Population studies on benthic nematodes within a subtropical seagrass community*

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Abstract

Examination of the benthic nematode fauna of the soft surface sediments of a turtle grass (*Thalassia testudinum* König) bed in Biscayne Bay (Miami, Florida) has revealed a high degree of homogeneity exemplified by the dominance of four species out of approximately 100 nematode taxa from the area. The dominant species, *Metoncholaimus scissus, Theristus fistulatus, Spirinia parasitifera* and *Gomphionema typica*, regularly comprised between 87 and 95% of the total number of nematodes present in samples collected during the winter and spring of 1966. *T. fistulatus* showed an abundance of 56% over the course of the study, i.e., 160 samples collected over a period of 14 months. Maximal peaks in population densities were noted and correlated with physiographic alterations in the environment. The *M. scissus* population declined concurrent with changes in the community; at the same time, with accumulation of sediment, the *Terschellingia longicaudata* population increased. Ratios of species, and especially shifts in the dominant forms present, with repeated collections, are extremely useful indicators of important biological and physical changes in a particular environment. Analysis of distributional data on dominant species in 64 samples from eight closely approximated positions showed that observed temporal and spatial variations were not significant statistically at the 5% level. It is concluded that erroneous observations can be made from ecological studies based on field data derived without proper replication or consideration of seasonal factors. The latter as well as intrinsic variability within the particular locality itself contribute to the basic faunistic composition of benthic communities.

Introduction

In recent years, we have seen a gradual shift in marine nematology from studies primarily taxonomic to those in which greater emphasis has been placed on the activities of nematodes in their natural environment. In comparison with the extensive literature available on nematode taxonomy and systematics, ecological information is relatively scant. In the main, the latter data have been gleaned from papers concerned with systematics of the nematode fauna. Frequently, such observations were based only on single collections per area, sometimes without accurate characterization of the particular habitat(s).

While other investigators of marine nematode activity have provided information on density, biomass, vertical distribution and distribution along transects, we are unaware of any publications that provide specific data on temporal as well as spatial distribution, especially within a single well defined habitat. In the

few reports that provide detailed analysis of the faunal population, the data are deficient since information is not given over a valid period, or sample replication is lacking. It is apparent that undetected seasonal fluctuations may materially affect concentrations of varied or specific taxa. Unless these variable factors are known, subsequent analyses will give an erroneous picture of the basic faunistic composition. While these aforementioned considerations may be of little taxonomic importance, their ecologic significance is great.

The ecologically-oriented studies of Wieser (1959, 1960) are notable exceptions to the aforementioned approaches and have provided valuable information on benthic marine nematode populations. Particular note should be made of investigations in Buzzards Bay, Massachusetts, in which Wieser (1960) speculated on the fragmentation of an apparently uniform habitat into distinct niches ... a "mosaic type" environment. Implications of such heterogeneity within 'superficially homogeneous' communities are further discussed here.

The current work is a continuation of our efforts to discern patterns of nematological activity in subtropical marine waters, with particular emphasis on turtle grass (*Thalassia testudinum* König) communities in Biscayne Bay (Miami, Florida). Earlier investigations (Hopper and Meyers, 1966 a,b, 1967; Meyers and Hopper, 1966) have included characterization of the foliicolous nematode fauna on *Thalassia*, and examination of the bionomics of the large omnivorous benthic species, *Metoncholaimus scissus* Wieser and Hopper, 1967. Correlated investigations have dealt with aspects of possible interrelationships between various marine nematodes and degradation of cellulosic substrates, incited in part by fungal activity (Meyers and Hopper, 1967), and ancillary data on life cycle development of nematodes colonizing fungal-infested substrates (Hopper and Meyers, 1966 b).

Methods and Materials

Collection area

Sediments were taken within a well delineated turtle grass flat off the western shore of Key Biscayne in Biscayne Bay (Miami, Florida) (Fig. 1). This area was reported as "Site C" in Hopper and Meyers (1967) and is herein similarly designated. It is shallow and fairly sheltered, with a soft "ooze-like" bottom of a fine, loose, sandy silt with large quantities of small shells. The sedimentation rate of *Thalassia* particles and other detrital material is extensive. Approximately two feet of water covers the site at low tide.

A gradual, although steady, decline of the sea grass occurred during the course of the study. Initially there was a luxuriant and extensive plant community with a large number of algal epiphytes; currently the locale is greatly reduced in size with large barren patches and very little new vegetative growth. This condition, which appeared to be associated with an increasingly heavy rate of sediment deposition, is discussed subsequently in terms of qualitative and quantitative changes in the nematode biota.

Fig. 1. Location of collection site (Site C) in Biscayne Bay (Miami) Florida

Collection procedure

A quadrant was established within the collection area to examine and quantify the variability of the benthic nematode population. This quadrant (Fig. 2) consisted of a central wooden stake with four stakes at right angles, each three feet distant from the center position. The stakes were connected by monofilament line with stainless steel sleeves attached at a distance of one foot from each of the stakes. This permitted us to locate accurately, and without difficulty, specific positions at each sampling period.

Collections were made at low tide, when possible, using a face mask and snorkel. The collector (S.P.M.) floated over the site during sampling to avoid excessive disturbance of the sediment.

Twenty-four separate collections were taken from November 26, 1965, to December 14, 1966 (Table 1).

Samples were taken from the uppermost 1—2 centimeters of substrate using small plastic petri dishes of a diameter of 5.35 cm. The procedure consisted of inversion of the bottom of the dish over the sediment and sliding the cover into position under the inverted bottom to obtain a relatively undisturbed sample. Observations of a limited number of core samples failed to disclose significant numbers of nematodes below 2 centimeters. Material was processed and preserved within 12 to 24 hours of collection.
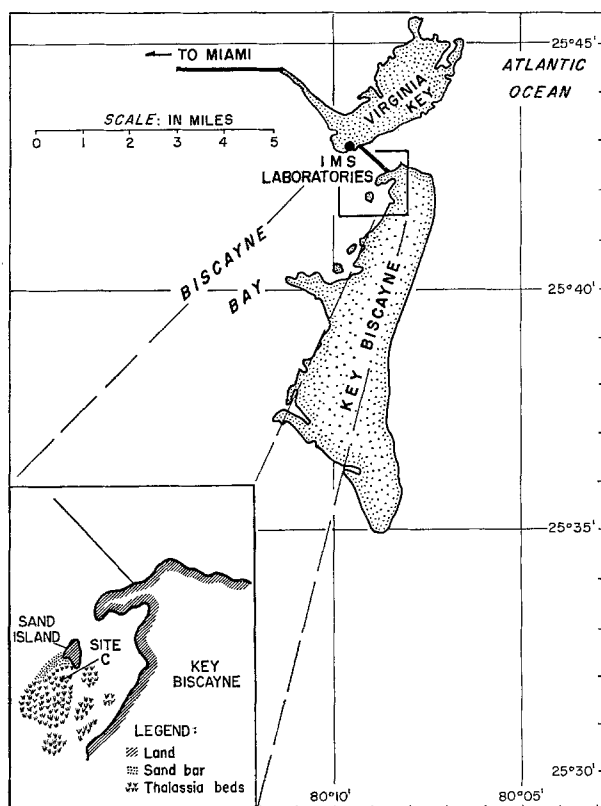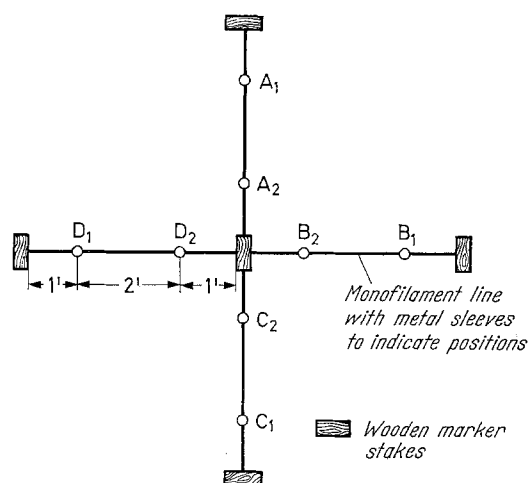

Fig. 2. Quadrant for establishment of sampling positions at Site C

Table 1. *Summary of collection data*

Collection		No. samples per collection	Total amount of sediment per collection (in ml)	No. of specimens	
Accession No.	Date			in $1/5$ aliquot	per 100 ml of sediment
652	11/23/65	6	186	1415	3777
654	11/26/65	8	193	2242	5808
655	11/30/65	8	264	3248	6151
656	12/ 3/65	3	83	1390	8373
657	12/ 6/65	8	207	1566	3783
658	12/14/65	11	194	2209	5693
663	1/25/66	5	189	927	2452
664	2/ 1/66	10	386	3160	4093
665	2/ 4/66	7	321	1617	2519
666	2/11/66	8	278	1177	2117
667	2/15/66	3	107	793	3706
668	2/17/66	3	104	1014	4875
669	2/24/66	9	360	2388	3317
670	3/ 1/66	5	211	1425	3377
671	3/ 4/66	2	63	962	7635
672	3/11/66	4	161	1026	3186
673	3/17/66	10	350	3778	5397
674	4/27/66	10	382	1705	2232
676	5/11/66	2	79	237	1500
679	7/28/66	8	316	1274	2016
686	9/ 1/66	8	329	1160	1761
688	9/19/66	6	199	1318	3312
695	11/ 3/66	8	306	2528	4131
704	12/14/66	8	351	2997	4269

Nematodes were extracted from the sediment by a modification of the Karo flotation method of TEAL (1960). The modification consisted of several decantations through a course (350 μ) and a fine sieve (44 μ) subsequent to volumetric determinations. This procedure effectually divided the sample into three components, viz.: a course fraction of sand and shells, a detrital fraction on the course sieve, and third, that portion of the sample retained on the fine sieve. Repeated examination showed the course fraction was free of specimens. This fraction was routinely discarded although periodical checks were made. The detrital material, with the larger specimens, viz.: *Metoncholaimus scissus*, *Meyersia minor*, *Comesoma* sp., etc., was saved and hand sorted. The material on the fine sieve was concentrated and transferred to 50 ml centrifuge tubes. These were filled with a 1:1 sea-water/Karo solution and shaken to disperse the sediment and specimens. The sample was then centrifuged for approximately two minutes at 1800—2000 rpm. Each sample was centrifuged twice to effect maximal numbers. While some nematodes may still have been lost despite this double procedure, in all likelihood, these constituted an insignificant part of the total population.

Characterization of the nematode fauna

The majority of the quantitative determinations were based on 1:5 aliquots of the sample except where large concentrations of animals necessitated greater dilutions. The remainder was examined for rarer species which failed to occur in the aliquot. Such species were arbitrarily assigned a value of one. The volume of sediment (13—53 ml, average 35 ml) in each sample was measured and recorded. Samples subjected to computer analysis were equated on a 25 ml volume basis to permit accurate comparisons.

Data analyses, involving standard deviation and T-test determinations, were run on a 1401 IBM computer at the Institute of Marine Science. The T-test involved a comparison of means based on *random* samples. The mean of a single species at a single location was compared with the mean of that species at subsequent locations as:

$$\text{Mean}_{(N,J)} : \text{Mean}_{(N+K,J)}.$$

Treatment was on an increment basis where K + N (location) was ≤ 8, N goes from 1 to 7, and J (species) goes from 1 to 4. We appreciate the invaluable assistance of Mr. DAVID L. SHAFFER of the Computer Section of IMS for his programming of these data and for his cooperation in the subsequent analyses.

Only the initial eight quadrant samples (654—674), for the period November 26, 1965, to May 27, 1966, were included in the computer analysis study. Supporting data were based on collections made from May 27, 1966, to December 14, 1966. Comparison of data from the initial collections with that from samples taken near the middle and the termination of our study allowed evalution of the quantitative and qualitative

aspects of the nematode population associated with the decline of the turtle grass community.

Results and Discussion

Enumeration of Species

Complete species analyses were made on samples from the initial two quadrant collections and for five others selected near the mid and terminal portions of the study. These data, summarized for each collection, are presented in Table 2. Certain species had high frequency values, i.e., occurred in one-half or more of all samples, and these may be further divided into two groups based on percentage abundance. One group of four species, *Metoncholaimus scissus*, *Theristus fistulatus*, *Spirinia parasitifera*, and *Gomphionema typica*, discussed subsequently, had abundance values that ranged from 8.3 to 56.6% and occurred in 63 to 100% of samples. These taxa were regarded as the dominant forms in the sediment community and provided a reference point with which subsequent samples were compared. The remainder of the nematodes were identified either to species or to a convenient generic, or family group. The second group consisted of *Comesoma* sp., *Hypodontolaimus* sp., *Longicyatholaimus* spp., *Graphonema* sp., and *Metachromadora* spp. These had low percentage abundance values, 0.3 to 1.2%, and occurred in 50 to 85% of the samples. While other species had abundance and frequency values that would warrant their placement in this group, analysis of the data indicated that these were either more common initially, i.e., *Prochromadorella* spp., or toward the termination of the study, i.e., *Terschellingia longicaudata*, *Parodontophora brevamphida*. A number of species present in low numbers and of infrequent occurrence, were recognized as normal inhabitants of the epiphytic algae on *Thalassia* in this area (HOPPER and MEYERS, 1967), viz.: *Oncholaimus dujardinii*, *Chromadora macrolaimoides*, *Paracanthonchus platypus*, *Chromadorina epidemos*. *Acanthonchus cobbi* also has been found in close association with algal substrates in Biscayne Bay (unpublished data). In all likelihood, these specimens were fortuitously introduced from the overlying foliicolous habitat and do not constitute regular components of the benthic community. It was interesting to note that certain taxa, i.e., *O. dujardinii*, *A. cobbi*, *P. platypus*, were found only when the site contained portions of the original turtle grass growth. Their absence in later samples may be attributed to the disappearance of the *Thalassia* and its associated epiphytes.

The relationship of number of taxa found to number of samples taken is presented in Fig. 3. Based on the extrapolated terminal portion of the curve, a total of approximately 80 taxa would be expected. In view of the evolving nature of Site C, undoubtedly the fauna is also in a state of transition. Thus, the observed terminal portion of the curve may indicate new individuals entering the area or an increase in the endemic

Table 2. *Abundance and frequency of nematode taxa from seven sediment collections at site C.* * = Less than 0.1%

Collection No. Identification	654 % abund.	654 Freq No./8	655 % abund.	655 Freq No./8	673 % abund.	673 Freq No./8	674 % abund.	674 Freq No./8	679 % abund.	679 Freq No./8	686 % abund.	686 Freq No./8	688 % abund.	688 Freq No./6	Total % abund.	Total Freq No./54	Total Freq abund.
Metoncholaimus scissus WIESER and HOPPER	35.5	8	10.0	7	9.0	6	7.8	7	0.4	3	0.3	1	0.5	2	11.1	34	63
Theristus fistulatus WIESER and HOPPER	41.8	8	58.3	8	70.1	8	46.9	8	53.1	8	51.2	8	65.6	6	56.6	54	100
Spirinia parasitifera (BASTIAN) sensu, WIESER and HOPPER	7.5	8	17.0	8	12.6	8	18.8	8	6.0	8	4.4	7	1.4	4	11.0	51	94
Gomphionema typica WIESER and HOPPER	5.6	8	4.0	8	3.9	8	13.1	8	16.6	8	19.4	8	9.0	6	8.3	54	100
Graphonema sp.	0.8	6	0.7	6	0.1	2	1.0	6	0.2	4	0.3	2	0.5	2	0.6	28	52
Comesoma sp.	0.6	7	0.6	8	0.8	8	1.0	6	0.7	6	1.0	5	2.0	6	0.9	46	85
Neotonchus spp. (3)	0.1	3	*	1	*	1	0.1	2	*	2	0.5	5	0.6	4	0.2	18	33
Prochromadorella spp. (2)	1.2	7	1.4	7	*	1	0.4	4	0.7	4	0.6	5	*	1	0.8	31	57
Mesonchium porijerum COBB	0.4	4	0.1	4	0.2	3	0.4	5	0.4	5	0.2	3	0.2	2	0.3	24	44
Desmodoridae spp. (?—3)	0.6	6	0.7	6	0.2	3	0.5	3		5	0.3	3	0.4	1	0.5	24	44
Hypodontolaimus sp.	1.1	6	0.5	7	0.1	3	1.0	3	4.3	6	2.0	8	1.7	5	1.2	43	80
Meyersia minor HOPPER	*	1	0.1	4											0.3	20	37
Cheironchus spp.	0.1	3	*	3	0.1	2	0.2	2	1.2	3	0.3	3	0.4	4	0.2	20	37
Phanodermopsis spp. (2)	*	2			*	1	0.2	1	0.1	3	0.3	4	0.2	3	0.1	13	24
Oncholaimus dujardinii DE MAN	0.1	3	0.1	2	*	1	0.2	1	0.1	1			0.1	2	*	5	9.3
Paramonohystera canicula WIESER and HOPPER	0.3	5	0.1	4	0.1	3	0.2	4	*	1	0.2	3	*	1	0.2	21	39
Acanthonchus cobbi CHITWOOD	0.3	5	0.8	4	*	1									0.3	9	17
Terschellingia longicaudata DE MAN	0.1	3	*	1	*		0.7	6	2.9	6	5.3	8	5.5	6	1.4	33	61
Spilophorella paradoxa (DE MAN)	0.8	2	0.8	4			*	1	0.7	1	0.8	5	0.6	4	0.6	20	37
Longicyatholaimus spp. (2)	0.1	3	0.4	8	0.4	6	0.8	5	0.2	5	0.4	4	0.8	6	0.5	34	63
Metoncholaimus pelor HOPPER	0.2	1	*	2	0.1	2	*	6	0.7	1	0.4	4			*	5	9.3
Unidentified	0.4	5	0.5	7	0.1	2	0.2	2	*	3	1.7	7	1.2	6	0.5	28	54
Leptolaimus sp.	*	2	0.3	5			0.2	2	0.4	4	0.2	3	0.3	3	0.2	19	35
Halalaimus longisetosus HOPPER	0.2	3	0.4	3			0.4	3	1.5	5	*	1	0.3	2	0.3	18	33
Microlaimus spp. (4)	*	2	0.1	3			0.3	4	0.3	3	1.8	7	0.8	3	0.5	24	44
Halalaimus spp. (2)	0.2	4	*	4	0.2	2	0.6	6			0.1	2			0.2	18	33
Didelta maculata COBB	*	1		1											*	1	1.9
Chromadorella spp. (2)	*	1	*	1	0.2	2		2							*	2	3.7

Table 2 (continued)

Collection No. Identification	654 Percentage abundance	654 Frequency No./8	655 Percentage abundance	655 Frequency No./8	673 Percentage abundance	673 Frequency No./8	674 Percentage abundance	674 Frequency No./8	679 Percentage abundance	679 Frequency No./8	686 Percentage abundance	686 Frequency No./8	688 Percentage abundance	688 Frequency No./6	Total Percentage abundance	Frequency No./54	Frequency abundance
Chromaspirina sp.	*	1	*				*						0.1	2	*	4	7.4
Eubostrichus spp. (2)	0.2	4	0.1	2	0.1	2	0.3	4	0.2	2	0.3	1	0.1	2	0.2	15	28
Linhomoeidae spp.	*	2		3		2	0.2	4	0.3	4	0.6	4	0.5	4	0.2	23	43
Anticyathus spp. (2)	*	1	*	2											*	5	9.3
Euchromadora meadi WIESER and HOPPER	*	2	0.1	4			*	1	0.2	2	0.4	3			*	9	17
Sphaerolaimus sp.	*	2	*	2		2			0.3	3			0.3	2	0.2	16	30
Chromadora macrolaimoides STEINER	0.1	1	0.2	3			*		*	1	0.4	3		3	0.1	8	15
Paracanthonchus platypus WIESER and HOPPER	*	1	*						*	1					*	1	1.9
Paracomesoma sp.	0.1	2	*	2	*	1	*		0.3	3	*				*	9	17
Chromadorina epidemos HOPPER and MEYERS			*	2	*						0.2	3			*	7	13
Metachromadora spp. (2)	*	2	*	2	0.2	4	1.0	6	0.4	6	0.2	2	0.4	3	0.3	27	50
Parodontophora brevamphida TIMM	*	1	*	2	0.1	3	0.2	2	1.8	8	0.8	6	0.5	4	0.4	26	48
Viscosia macramphida CHITWOOD	*	1	0.2	5	*	2	0.1	2	0.3	3	0.6	5	0.3	3	0.2	20	37
Ironella (?) sp.			*	1		1	*	1							*	1	1.9
Ilium sp.			*	1	*										*	2	3.7
Neochromadora sp.			0.1	5	*	1	*	1					*	1	*	6	11
Pareurystomina spp. (2)			0.1	4	0.2	4	*	1	0.3	3	*	1			0.2	14	26
Pontonema problematicum CHITWOOD			*	1							*		*	1	*	1	2
Enchelidiidae sp.			*	1					0.1	2	*	1	*	1	*	4	7.4
Epacanthion sp.			*	2							*				*	2	3.7
Didontolaimus sabulosus SOUTHERN			*	1									*	1	*	2	3.7
Monoposthia mirabilis SCHULZ			*	1	*	1	0.5	5	0.2	3	*		*	1	0.1	11	20
Phanoderma sp.			*	1							*				*	1	1.9
Atrochromadora denticulata WIESER and HOPPER			*	1							0.2	2			*	8	15
Pseudolella sp.							0.2	2	0.5	5	0.2	2	0.3	4	0.1	11	20
Filoncholaimus prolatus HOPPER			*				*	1	0.2	2	*				*	4	7.4
Richtersia sp.					*	2					*	1			*	1	1.9
Cyatholaimidae sp.					*	1					*	1			*	2	3.7
Paramonohystera sp. (2)					*	2					*				*	2	3.7
Anticoma sp.					*	1					*	1			*	1	1.9
Terschellingia sp.					0.1	4					*	1			*	5	9.3

Table 2 (continued)

Collection No / Identification	654 % abund.	654 Freq No./8	655 % abund.	655 Freq No./8	673 % abund.	673 Freq No./8	674 % abund.	674 Freq No./8	679 % abund.	679 Freq No./8	686 % abund.	686 Freq No./8	688 % abund.	688 Freq No./6	Total % abund.	Total Freq No./54	Total Freq abund.
Laimella longicauda COBB					*	1									*	1	1.9
Theristus floridens WIESER and HOPPER					*	1	0.2	1	1.0	5	0.3	2			0.2	9	17
Oncholaimellus sp.					*	1			0.3	4			*	1	*	6	11
Spirinia sp.					*	1									*	1	1.9
Paracyatholaimus sp.							*	1							*	1	1.9
Oncholaimoides sp.							*	1							*	1	1.9
Calyptronema sp.							*	1							*	1	1.9
Siphonolaimus sp.							*	1							*	1	1.9
Prooncholaimus hastatus WIESER and HOPPER									*	1	0.1	2	0.2	3	*	6	11
Theristus ostenator WIESER and HOPPER									0.1	2					*	2	3.7
Tripyloides gracilis (DITLEVSEN)											*	1			*	1	1.9
"Cobbia-like" sp.											1.1	6	0.3	3	0.1	9	17
Theristus sp. 3							*	2			0.5	2	1.0	3	0.2	7	13
Theristus xyaliformis WIESER and HOPPER											0.1	1	*	1	*	2	3.7
Oxystomina sp.											*	1			*	1	1.9
Antomicron sp.											*	1			*	1	1.9
Monhystera paerelegantula DE CONINCK									*	1					*	1	1.9
Desmolaimus sp.													*	1	*	1	1.9
Epsilonematidae sp.													*	1	*	1	1.9
Theristus sp. 4											0.2	1	0.5	4	*	5	9.3
Siphonolaimidae sp.											0.1	1	0.7	5	*	1	1.9
Monhysteridae sp.											*	1	0.1	1	*	6	11
Sabatheria sp.													*	1	*	1	1.9
Theristus sp.													*	1	*	1	1.9
Leptolaimus sp.													*	1	*	1	1.9

[1] Species present in collections other than the above seven are: *Pomponema* sp. (Col. 650), *Symonchiella* sp. (Col. 652) *Euchromadora pectinata* WIESER and HOPPER (Col. 652).

[2] Number in parenthesis refers to species present.

nematode population to a detectable size. The nematode taxa from the initial eight samples comprised over 50% the theoretical total, and those from 25 samples yielded nearly 80%. Eighteen of the taxa were repre-
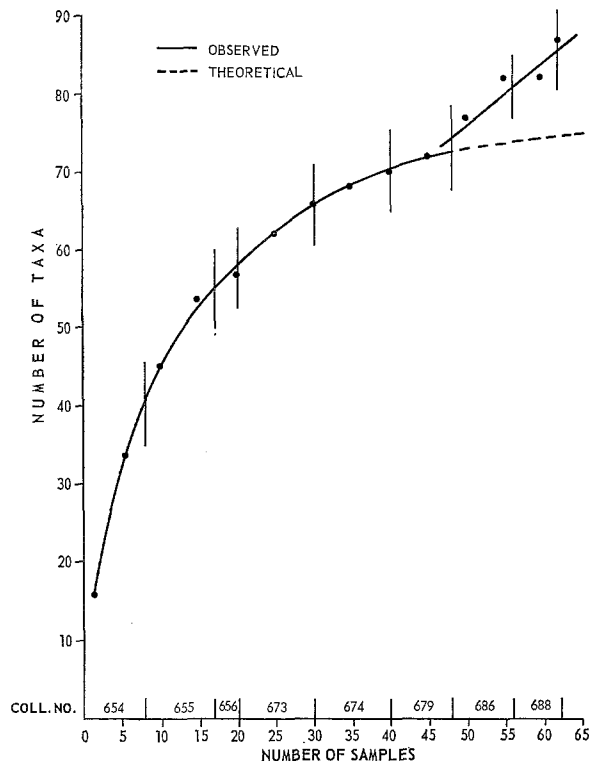
Fig. 3. Relationship of number of taxa found to number of samples examined
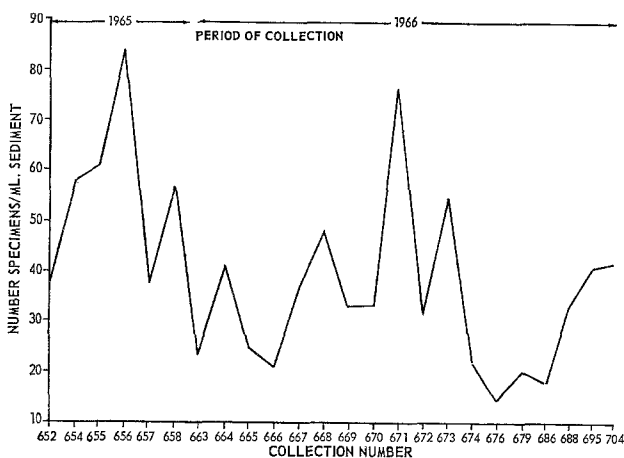
Fig. 4. Population density or number of specimens over the entire collection period

sented by single specimens and, as has been suggested (SCHUURMANS STEKHOVEN, 1935), such species can be considered foreign to the habitat in which they are found. These singular specimens probably were transported to Site C by tidal current.

The population densities recorded for collections taken over the entire study are given in Fig. 4. It is recognized that interpretation of the data is difficult since of the 24 collections, 17 were made within a five-month period, while the remaining nine months were represented by only seven. Thus, while the graph initially is well documented, the latter portion is deficient. Nevertheless, it appears that the nematode population at Site C attained two peaks, one in November-December, 1965, and another in February-March, 1966. The former peak was repeated, to a lesser degree, in the November-December samples of 1966. While this latter peak was reduced (possibly due to the changing habitat), it appears that, regardless of habitat conditions, the nematode population tends to be larger at this time of the year. The higher densities during these periods were consonant with previous observations on the foliicolous fauna (HOPPER and MEYERS, 1967). In

Table 3. *Population data on four dominant benthic nematode species at eight sampling sites over eight collection periods*

Sampling site	Nematode species			
	Theristus fistulatus	*Metoncholaimus scissus*	*Spirinia parasitifera*	*Gomphionema typica*
A₁	829 ± 472*	62 ± 89	129 ± 114	58 ± 28
A₂	551 ± 385	187 ± 378	61 ± 36	46 ± 37
B₁	748 ± 561	363 ± 492	302 ± 215	60 ± 34
B₂	515 ± 387	35 ± 47	190 ± 126	48 ± 26
C₁	414 ± 259	94 ± 208	204 ± 169	45 ± 26
C₂	541 ± 452	45 ± 89	191 ± 238	45 ± 26
D₁	507 ± 243	108 ± 153	90 ± 47	52 ± 27
D₂	673 ± 644	166 ± 229	92 ± 68	80 ± 55

* *Medial average* number of animals and standard deviation.

these studies, nematode populations were found to be highest during the period October-March. The causes of these seasonal fluctuations are still unknown, although there does appear to be an inverse correlation with water temperature, i.e., with maximal numbers present during periods of lowest temperatures.

Quantitative data on the dominant species over the first eight collections facilitated statistical analysis of population variability and the general uniformity in abundance within and between closely situated sites. The divergent stomatal morphology of these species, illustrated in Fig. 5, suggests that each may represent a different trophic level.

Spirinia parasitifera (BASTIAN, 1865) GERLACH, 1963. Examination of a limited number of specimens failed to reveal any recognizable material within the intestinal lumen. The species is presumed to feed primarily on bacteria (perhaps also minute algae).

Theristus fistulatus WIESER and HOPPER, 1967. This species appears to feed quite selectively on diatoms. The intestine is often packed with the tests of *Diplones* and *Nitzschia*, although a large number of taxa may be utilized as foodstuffs.

Gomphionema typica WIESER and HOPPER, 1966. Green pigmentation within the intestine is presumptive evidence that this species feeds on chlorophyll-containing cells. The absence of definite form would indicate that higher algae were the source of the coloration.

Metoncholaimus scissus WIESER and HOPPER, 1967. Observations on the bionomics of *M. scissus* have been reported previously (HOPPER and MEYERS, 1966 a). While feeding observations substantiate the predatory capabilities of *M. scissus*, no conclusive evidence is available that establishes this animal as an obligate predator. The only specific material found within the intestine has been a solitary diatom and it

	THERISTUS FISTULATUS WIESER AND HOPPER, 1967	METONCHOLAIMUS SCISSUS WIESER AND HOPPER, 1967	SPIRINIA PARASITIFERA (BASTIAN, 1865) GERLACH, 1963	GOMPHIONEMA TYPICA WIESER AND HOPPER, 1966
BUCCAL CAVITY	UNARMED LIPS ROUND WITH SHORT SETOSE PAPILLAE	ARMED LONG TOOTH (35–38μ) SHORTER TEETH (25–28μ)	SMALL MINUTE TEETH	1 LARGE DORSAL TOOTH
LENGTH	0.86–1.04mm	4.0–5.2mm	1.57mm	1.24–153mm
DIAMETER	30–36μ	60–80μ	55μ	78–90μ

Fig. 5. Salient characteristics of the four dominant benthic nematode species

is not known whether this was ingested directly or as material within a prey animal (i.e., *Theristus fistulatus*). Certainly the predatory instincts of oncholaimids in general are not as well developed as they are in the parallel evolved mononchids of freshwater habitats. The latter animals, in water with other nematodes, frequently have been observed devouring certain species. In our earlier studies of *M. scissus*, such predatory activities were not observed.

Species characterization of the habitat

The area at Site C was unique among other Biscayne Bay localities studied (unpublished data), in that four species were dominant out of an estimated 100 species present. These four nematodes, *T. fistulatus*, *M. scissus*, *S. parasitifera*, and *G. typica*, regularly comprised between 87 and 95% of the total number found in samples collected during the winter and spring of 1966 (Table 4). Pilot investigations of the sediment at the sites of our earlier foliicolous study has shown a more diversified fauna without individual species assuming a dominant position. Rather, dominance at these sites was manifest at the family level, i.e., moderate numbers of species of low density within the same taxonomic hierarchy.

The fauna at Site C may be compared favorably with that recorded at Penzance Marsh, Woods Hole WIESER and KANWISHER, 1961), i.e., 3—4 species

constitute the dominant fauna. Two of the three species dominant in their first sample (Pen. —1) are very closely related to species dominant in our material, viz.: *Metoncholaimus pristiurus* vs. *M. scissus* and *Spirinia parasitifera* (BASTIAN) *sensu* (COBB, 1928) vs. *S. parasitifera* (BASTIAN) *sensu* WIESER and HOPPER, (1967).

WIESER (1960) has utilized the concept that the degree of homogeneity of a habitat can be determined by an analysis of the species composition of its fauna, as well as by the relative abundance of each species. This, he indicates, is an application of GAUSE'S (1934) principle of animal exclusion which states that two species with identical ecological requirements cannot occupy the same niche. As each species requires and occupies its own niche, the extent of specific diversity within a habitat (microhabitat) would be in direct proportion to the number of existing niches. Areas with a large number of niches are regarded as heterogeneous and are commonly rich in species of low density. Conversely, areas that lack a variety of ecological niches are termed homogeneous. These areas support a low number of species, often with certain of them numerically dominant (SCHUURMANS STEKHOVEN, 1935; WIESER, 1960).

Our data can be paralleled with WIESERS (1960) R-samples from Buzzards Bay (Massachusetts) (Fig. 6), which contained the largest clay-silt fraction (79.7%), the least number of species (63), and the numerical dominance of a single species, *Terschellingia longicaudata* (30.9% abundance) (Fig. 6b). His J- and P-samples had lower clay-silt fractions (30.0 and 11.8%) along with larger numbers of species (98 and 103), several of which were of similar and low numerical dominance (7.6—9.5 and 9.6—11.8% abundance) (WIESER, 1960, Table 5, p. 126, and Fig. 1, p. 128). Data from our investigation, summarized from Table 2, are presented in Fig. 6a. Two points are immediately apparent: a) the numerical dominance of a single species (*Theristus fistulatus*, 56.6%) throughout the study, and b) the large number of taxa present. The first is an expression of the habitat homogeneity, while the latter is due to the large number of samples examined (62).

Data summarized for collections taken near the beginning (No. 654) and end (No. 688) of our study are presented in Figs. 6c and d. Collection No. 654 reveals the presence of two species of nearly equal abundance, *T. fistulatus* (41.8%) and *M. scissus* (35.5%). Both of these exceed the percentage abundance value found by WIESER (1960) in his R-samples which were considered to be most homogeneous of the three areas he investigated. Collection No. 688 reflects the "disappearance"

of the *M. scissus* population. Possibly its position in the specific composition was filled by *T. fistulatus*. As the number of samples on which the data are based decreases (62 vs. 8 and 6), the number of taxa encountered decreases (101 vs. 40 and 47). Thus, while a

Table 4. *Percentage occurrence of four dominant benthic nematode species at eight sampling sites over eight collection periods**

| Sampling site | Nematodes Species | | | |
	Theristus fistulatus	*Metoncholaimus scissus*	*Spirinia parasitifera*	*Gomphionema typica*
A_1	50—72—95	0— 5—19	3—10—19	1— 5—11
A_2	39—63—81	0—10—46	1—13—31	0— 7—16
B_1	23—51—74	0—11—54	8—21—57	1— 5—16
B_2	29—54—79	0— 6—27	5—25—67	2— 6—18
C_1	35—56—86	0— 7—41	11—24—58	3— 7—19
C_2	30—57—82	0— 6—23	9—22—54	2— 8—30
D_1	49—64—80	0—13—38	4—12—18	3— 7—17
D_2	40—61—84	1—13—41	8— 9—20	0—11—27

* Compilation of data for eight collection periods. Based on minimal percent — *medial average percent* — maximal percent.

Fig. 6. Habitat homogeneity of Site C compared with R-sample from Buzzards Bay, Massachusetts (WIESER, 1960)

reduced number of samples may not materially influence the expression of numerical dominance, the number of taxa recorded (high numbers of which have been associated with heterogeneous habitats) is decreased.

While certain similarities exist between Figs. 6 c and d, incorrect faunistic interpretation would develop if only one of the two collections had been examined. At the present time, we do not know enough about

subtle changes in the environment to dismiss these facts: a) in one instance, two species coexist with nearly equal dominance while, b) in another situation, one species has become depressed, eliminated by unknown factors which seem to allow the other codominant species to attain an extreme position in the fauna.

Analysis of occurrence and distribution of four dominant species

The numerical data on the dominant species has been analyzed to determine the significance of the observed variability. The variability in occurrence of the four species in a single collection (No. 654) of eight samples is given in Fig. 7. In Fig. 8, data are shown for position A_2, selected to illustrate this phenomenon at a particular position over the eight collection periods. The percentage frequency of occurrence of the species (Fig. 7) fluctuates considerably between positions, especially that of *T. fistulatus* and *M. scissus*. The inverse correlation for these two species, suggested by the data plotted in Fig. 7, was not evident in subse-
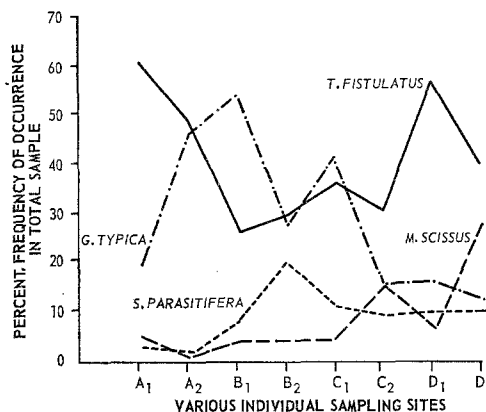

Fig. 7. Percentage frequency of occurrence of four species in the eight samples of collection 654

quent collections. Ratios of the species were irregular, and varied greatly between sampling positions within the same collection as well as between different collections.

Over the period of eight collections, the percentage frequency of occurrence of the species at position A_2 (Fig. 8) similarly varied greatly. The most obvious population change was the rapid decline of *M. scissus* wherein the species represented only a small percentage of the total population in collection 674. The observations were supported in subsequent samples, for *M. scissus* no longer could be detected from the specific collection sites, although it was found sporadically in portions of the adjacent *Thalassia* area. The data for the other seven sites are comparable to that given for position A_2, viz., decrease in *M. scissus*, variability in *T. fistulatus*, with a final reduction in percent frequency, and low fluctuating populations of *G. typica* and *S. parasitifera*. Concurrent with decline of the *M. scissus*

population, another heretofore undescribed oncholaimid, *Meyersia minor*, was isolated with increasing frequency. Rarely have the two species been found together in large numbers, suggesting either competition between these animals at a stage of their respective life cycles or actual different physical requirements. Further speculation along these lines are presented in a subsequent section.

Population data on the four species at the eight sampling sites for eight collection periods are given in Tables 3 and 4. The tremendous range in numbers of species showed that, at any one sampling position, the population varied over the period of analysis. The mean for *T. fistulatus* is rather uniform compared with that of *M. scissus*. At each position, except D_2, there were collections in which the latter species was absent. The abundance of *T. fistulatus* and overall population
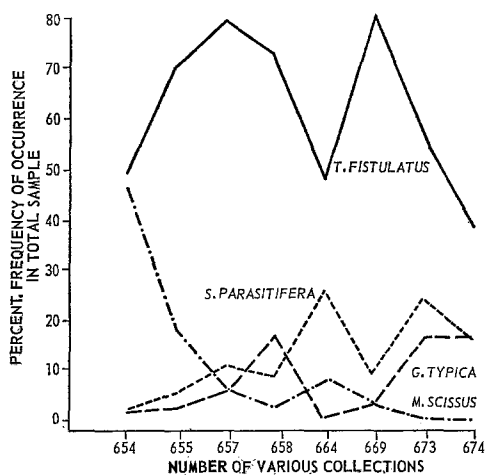
Fig. 8. Percentage frequency of occurrence of four species at position A_2

fluctuation can be seen in the data expressed as percentage occurrence in Table 4. Correlations between the minimal, average, or maximal means of the four animals could not be discerned.

Theristus fistulatus is the predominant species and shows minimal variability, i.e., 18—90%, with a mean of approximately 50%. *M. scissus* and the other two species vary from <1% to nearly 60%. Since the *T. fistulatus* population remained high throughout the year, it is apparent that conditions in the collection area were uniformly favorable to this species. The decline of the *Thalassia* had no noticeable effect on the *T. fistulatus* community. The high occurrence of this species is comparable to that noted in the sheltered littoral sand habitat on the Chilean coast (WIESER, 1959). However, while the Chilean sample had a high incidence of *Theristus (T. anteferans* WIESER, 1956), no other taxa were common to our fauna. Comparison of our sublittoral habitat with the Chilean environment may not be possible as the different species probably have different biological requirements.

Analysis of standard deviation (S.D.) suggests a random distribution with no tendency of the data to cluster around a point. The magnitude of the S.D. figures given in Table 3 reflects the tremendous variability between minimal and maximal populations. The T-test compared means of the four species and the various sites, and was not programmed to include a time factor, i.e., seasonal effects. Differences between the means were not statistically significant at the 5% level, although certain significant differences appear at the 10% level. This suggests that in one collection out of ten the results obtained would be due to mere chance, while differences observed in the remaining nine would be real. A greater level of significance might have appeared at the 5% level if other variables had been available for the program, i.e., site microcharacteristics, individual species bionomics, etc. Since the habitat is a continually evolving locale, wherein new variables are being introduced, a complete study, requiring a multi-variant analysis, was beyond the scope of the present investigation.

Temporal population fluctuations

Changes in the patterns of distribution of the nematode population, from initial to terminal collection, is given in Fig. 9. Abundance of taxa is expressed as a percentage of the total population. The "others" designation represents, collectively, all taxa other than the four dominant species. The various trends can be summarized: a) *M. scissus* exhibited a steady rapid decline from an initially large population; b) *T. fistulatus* was numerically superior and continued at a high fluctuating level throughout the collection period; c) *S. parasitifera* was represented by a low fluctuating population gradually decreasing to 5%; and d) *G. typica* was low with a slight increase in numbers during the spring and summer months. In general, the dominant species declined slowly in relative abundance, i.e., from 89 to 95% in collections 654—674 to 61% in collection 704. Of these species, only *G. typica* showed some response to seasonal influences. Decline of the *M. scissus* population, and to some extent, *S. parasitifera*, is related to the gradual change in the habitat. The remaining species, ("others") increased in percentage steadily, especially toward the latter portion of the study. The rise in this population may be correlated with the "observed terminal" portion of the curve given in Fig. 3. The increase in the "others" group is attributed to the increasing population of *Terschellingia longicaudata*, i.e., from initial concentrations of 3, 1, 1, 11, through 37, 62, 73, and 86, to a final collection of 416 specimens. Of the latter, 367 occurred in but one of the total of eight samples. Calculated on the average number of specimens in the seven remaining samples, the theoretical number of *T. longicaudata* would have been approximately 60. The practice of basing results on single samples thus can lead to ill-conceived concepts regarding faunistic composition. *T. longicaudata*, currently the third most abundant species, is a typical

representative of a type of "climax" community, i.e., soft sediments with a large silt-clay fraction (WIESER, 1959, 1960; WIESER and HOPPER, 1967). WIESER and HOPPER (1967, Table 2) found this species to be the dominant form in the soft sediment in Florida Bay (Flamingo, Florida). The increasing incidence of *T. longicaudata* at Site C is indicative of a trend toward a mud habitat — the "Special muds" of WIESER (1959).

Particular attention should be given to the striking decrease in *Metoncholaimus scissus* wherein the species now occurs sporadically in samples from Site C and the adjacent *Thalassia* environs. Since our sampling method is adequate to detect small numbers of nematodes, the absence of *M. scissus* from both sediment samples and fungal-infested cellulose "traps" is all the more significant. Possibly *M. scissus* may have used portions of the *Thalassia* as a substratum for attach-
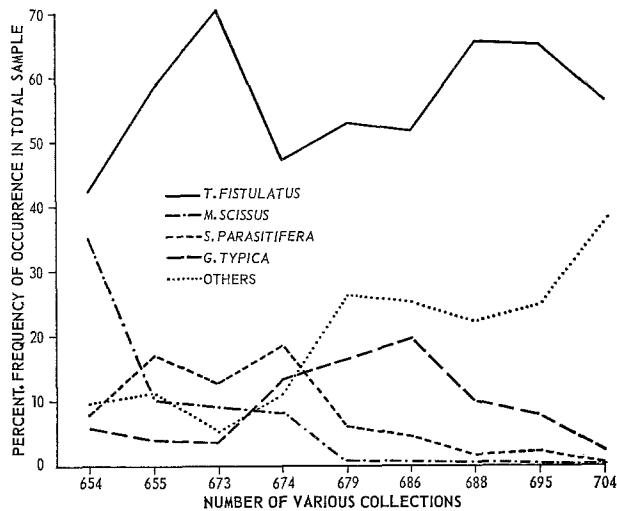
Fig. 9. Fluctuations of species from initial to terminal collections

ment of eggs. With decline of the plant community insufficient sites remained for egg deposition and maintenance of the species. Elsewhere, WIESER and KANWISHER (1961) mention the common occurrence of *Mentoncholaimus pristiurus* in November with its "disappearance" from the middle of December to June, and replacement by a closely related species, *Oncholaimus campylocercoides*. No mention was made of subsequent population studies of *M. pristiurus* during the following fall. The factors affecting distribution of *Metoncholaimus* are not immediately apparent. It is interesting that the closely related species, *Metoncholaimus pelor*, was rarely found, although individuals were isolated with the remains of as many as 25 young *M. scissus* within their intestines. Apparently, the factors which affected the drastic reduction of the *M. scissus* population also influenced *M. pelor*.

Observations on later samples suggested that other oncholaimid populations were increasing, i.e., *Meyersia minor, Filoncholaimus prolatus.* Rarely were *M. scissus*

and *M. minor* found together in large numbers. The incidence of *Meyersia* may be indicative of slight changes in sediment deposition within the environment. *Meyersia* was found in fairly large numbers in one collection (671), in the *Thalassia* area immediately south of Site C, whereas comparable collections made at Site C showed negligible concentrations. The former locale has a firmer bottom with notably less deposition of fine particulate material.

The benthic nematode fauna, i.e., *M. scissus*, is extremely variable, affected by a complexity of environmental factors. Although the general topography and floral characteristics in Site C appeared uniform, in all likelihood, micro-differences in physical and biological characteristics affected the concentration and movement of *M. scissus*, as well as the ratio of the sexes. Great irregularity occurred in numbers of this species at the various positions over the sampling period, with striking differences in numbers at individual positions within 24—48 hour periods.

These faunal fluctuations in the sediment community may be due to seasonal effects or to a decline of the habitat, or to a combination of both. However, regardless of the variability imposed upon the data by seasonal effects, there exists an intrinsic variability within the locality itself. Both of these facets contribute to the faunistic composition depending upon the time and the place that the data are collected. This intrinsic variability must be considered when reliable data on faunistic composition and seasonal population are to be evaluted.

Summary

1. The benthic nematode fauna of the soft surface sediments of a turtle grass (*Thalassia testudinum* KÖNIG) bed in Biscayne Bay (Miami, Florida) was examined quantitatively and qualitatively from 160 samples collected over a period of 14 months.

2. A high degree of homogeneity was exemplified by the dominance of four species out of an approximately 100 nematode taxa from the area. The dominant species, *Metoncholaimus scissus*, *Theristus fistulatus*, *Spirinia parasitifera* and *Gomphionema typica*, regularly comprised between 87 and 95% of the total number of nematodes present in samples collected during the winter and spring of 1966. *T. fistulatus* showed an abundance of 56% over the course of the study.

3. Population densities reached a maximal in November-December and again in February-March. The former peak was repeated, although to a lesser degree, the second year and probably was associated with the striking decline of the *Thalassia* community.

4. Physiographic alterations in the environment were reflected in the species composition. The *Metoncholaimus scissus* population declined concurrent with changes in the sea grass habitat. At the same time, with the accumulation of sediment, the *Terschellingia*

longicaudata population increased. These ratios of species, and especially shifts in dominant forms present, with successive collections, are extremly useful indicators of important biological and physical changes in a particular environment.

5. Analysis of distribution data on the dominant species in 64 samples, from eight closely approximated positions, showed that observed temporal and spatial variations were not statistically significant at the 5% level.

6. Erroneous conclusions can be attained from ecological studies based on field data derived without proper replication or consideration of seasonal factors. The latter as well as intrinsic variability within the particular locality itself contribute to the basic faunistic composition of benthic communities.

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