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Phytal Marine Nematode Assemblage on *Sargassum confusum* Agardh, with Reference to the Structure and Seasonal Fluctuations¹⁾²⁾

By

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(With 6 Text-figures and 2 Tables)

Free-living nematodes are the major members of marine meiobenthic animals which play important roles in the secondary production and food webs (e.g. McIntyre, 1969; Gerlach, 1971, 1978), therefore a number of ecological studies on the nematode assemblages have been carried out in various marine habitats (see Nicholas, 1975). However, our quantitative knowledge concerning the seasonal variability in population density and species composition is poor, and most of it is given in sediment habitats (e.g. Tietjen, 1969; Warwick and Buchanan, 1970, 1971; Lorenzen, 1974; Juario, 1975). Although phytal marine nematode assemblages have been investigated mainly on the relation between their faunal characteristics and the morphology of seaweeds (Wieser, 1951, 1952, 1959a, b; Ott, 1967; Moore, 1971; Warwick, 1977), there were only a few data on seasonal change in population density (Mukai, 1971) and in species composition (Hopper and Meyers, 1967a; Warwick, 1977).

As a part of the ecological study on the phytal animals in the *Sargassum* region of Oshoro Bay, Hokkaido, northern Japan, the present paper deals with the free-living nematodes quantitatively and describes their seasonal changes in species composition, abundance, affinity, diversity, and distribution of physiognomic characters of nematodes. This study was based on the collections taken from among the thalli of a brown alga, *Sargassum confusum* Agardh, in the subtidal zone. In this *Sargassum* community nematodes were the second abundant group, next to harpacticoid copepods, averaging 32.1% of the total non-sessile phytal animals throughout the year: see my previous reports on the general account of whole phytal animals (1975), on the phenology of harpacticoid copepods (1977a), and on the taxonomy of nematodes (1976, 1977b, 1978, 1981).

1) Biology of phytal animals in the *Sargassum confusum* region in Oshoro Bay, III.

2) Studies on the free-living marine nematodes from Hokkaido, V.

Materials and Methods

A detailed account of the study area, variation in environmental factors (water temperature, specific gravity, and growth condition of *S. confusum*), and sampling techniques were given in Kito (1975).

Periodical sampling was carried out from August 1973 to July 1974 and duplicate seaweed samples were monthly collected with a mesh bag (0.094 mm mesh diameter). In the laboratory, they were preserved in 5% neutralized formalin-seawater solution and then were shaken enough to dislodge the animals. After the preliminary estimation of all the meiofaunal animals (Kito, 1975), another series of subsamples for the present detailed study of nematodes was prepared by the plankton sample divider (after Motoda, 1959). The number of nematodes per sample was computed by sorting the subsamples, of which size was adequately determined from among 1/64, 1/32, 1/16, 1/8, and whole sample according to the preliminary estimation. Nematode densities are given as the number of individuals per gram algae or per 10 cm² bottom: the latter index is calculated from the mean nematode density per gram algae and standing crop of *S. confusum* (Appendix 2 in Kito, 1975). All the nematodes sorted were identified and counted under the phasecontrast microscope after mounted in glycerine: to analyze their age distribution, they were classified into four cohorts, i.e. gravid females, non-gravid females, males, and juveniles (see Juario, 1975).

The degree of accumulation of detritus has an important effect on species composition of nematodes (e.g. Dahl, 1948; Wieser, 1954, 1959a). In this study, therefore, the amount of detritus on the *Sargassum* thalli was measured according to the method employed by Dahl (1948), as an important environmental factor besides water temperature and standing crop of *Sargassum* (Fig. 1). After removing the animals and coarser particles (algal fragments, mucilaginous residue, etc.) in the sample as much as possible, detritus was allowed to settle in a graduated glass and the volume of detritus was measured. The amount of detritus, mean value for the two samples every month, ranged from about 2 ml/l algae in January to 249 ml/l algae in September. After the gradual increase between the spring and summer, the amount increased steeply in September.

Species composition of nematode fauna was examined by two indices for each species: Dominance=total number of specimens of a species/total number of nematodes in the total collections, Frequency=number of samples in which species occurred/total number of samples.

For analysis of structural changes in this nematode assemblage, the following indices were measured on monthly collection. Species richness was represented by the number of species, and other two diversity indices were calculated on the basis of individual number per 1 m² bottom (from figures in Table 1): Shannon-Weaver function, $H' = -\sum P_i \log_2 P_i$, and Pielou's evenness index, $J' = H'/H_{\max} = H'/\log_2 S$ (after Pielou, 1969). Faunal affinity was examined by the trellis diagram method (see Wieser, 1960; Sanders, 1960).

The nematode assemblage was also examined on distribution of the five physiognomic characters after Wieser (1953, 1959a), i.e. body length, body setal length (cephalic and somatic setae including cervical setae), structure of buccal cavity (feeding type), visual mechanism, and cuticular structure. In this study the body length and the body setal length were presented by the average of some adult specimens, but those of the species in which whole adult was absent were given from some larger juveniles. Four feeding types were deduced from the structure of buccal cavity: 1A, selective deposit feeders; 1B, non-selective deposit feeders; 2A, epigrowth feeders; 2B, predators and omnivores.

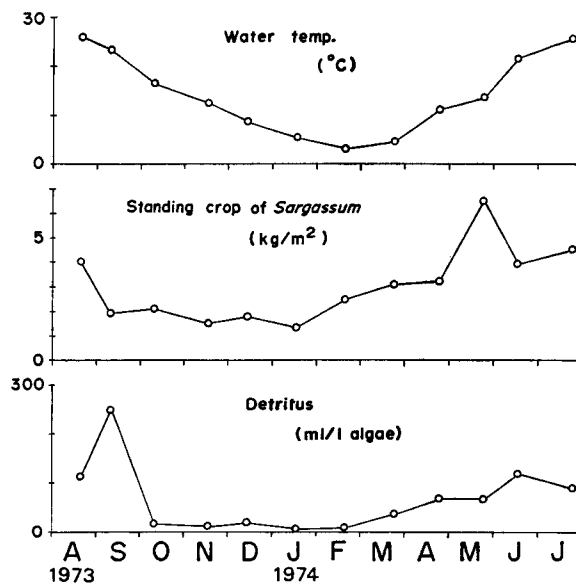


Fig. 1. Seasonal changes in water temperature, standing crop of *Sargassum confusum*, and amount of detritus.

Results

Species Composition

A total of 49 species were recognized in 17 families and 39 genera from 12530 nematodes subsampled (Table 1). The family Monhysteridae was numerically most important and its six species occupied 60.24% of the total nematode fauna. The subdominant family was the Chromadoridae (26.23%) which taxonomically showed the highest diversity, comprising 12 species in nine genera. There were only two other families constituting more than 1% of the total fauna, the Axonolaimidae (9.48%) and the Cyatholaimidae (2.13%). These four families formed about 98% of the total nematodes.

Table 1. Monthly abundance (ind./10 cm²), dominance (D,%) and

	1973					Jan.
	Aug.	Sep.	Oct.	Nov.	Dec.	
<i>Monhystera refringens</i>	36.79	222.17	1.01	0.25	5.78	3.41
<i>Chromadora nudicapitata</i>	61.84	190.69	6.23	0.60	6.85	4.37
<i>Chromadora heterostomata</i>	—	—	—	0.17	1.43	3.74
<i>Araeolaimus elegans</i>	56.39	151.90	6.64	0.60	2.31	3.27
<i>Theristus acer</i>	1.79	2.45	0.11	—	—	0.53
<i>Acanthonchus tridentatus</i>	18.85	56.48	1.21	0.05	0.29	0.33
<i>Euchromadora ezoensis</i>	15.01	28.53	0.50	—	—	—
<i>Steineridora borealis</i>	—	0.97	0.11	0.03	—	0.36
<i>Neochromadora bilineata</i>	2.12	3.82	0.43	—	0.12	0.27
<i>Monhystera disjuncta</i>	1.52	6.48	1.08	0.10	2.28	0.17
<i>Oncholaimus dujardinii</i>	4.05	7.42	0.91	0.07	0.38	0.07
<i>Enoplus anisospiculus</i>	—	—	—	—	0.29	1.29
<i>Eurystomina</i> sp.	3.19	1.23	—	—	—	—
<i>Rhabditis marina</i>	2.12	2.80	0.11	—	—	—
<i>Spilophorella tollenifera</i>	1.13	2.94	0.13	—	0.12	0.07
<i>Eurystomina ophthalmophora</i>	1.46	1.27	0.17	0.03	—	0.10
<i>Graphonema metuliferum</i>	—	2.14	—	—	0.35	—
<i>Onchium minutum</i>	0.73	0.92	—	—	0.12	0.07
<i>Dichromadroa amphidiscoides</i>	0.73	0.31	—	—	—	—
<i>Convexolaimus</i> sp.	—	—	—	—	0.12	0.17
<i>Neochromadora oshoroana</i>	0.79	—	—	0.02	—	—
Monhysterinae sp.	—	1.98	—	0.07	—	—
<i>Phanoderma</i> sp.	0.73	—	—	—	—	—
<i>Leptolaimus</i> sp.	0.33	1.32	—	0.02	—	—
<i>Pseudaraeolaimus ocellatus</i>	0.79	—	0.06	—	—	—
<i>Paramonohystera pellucida</i>	0.33	0.71	—	—	—	—
<i>Monoposthia costata</i>	—	—	—	—	0.09	—
<i>Nemanema</i> sp.	0.33	0.61	—	—	—	—
<i>Viscosia</i> sp.	0.33	0.66	—	—	—	—
<i>Theristus</i> sp.	—	0.31	—	—	—	—
<i>Innocuonema</i> sp.	—	0.31	0.06	—	—	—
<i>Paracanthonchus kamui</i>	0.40	0.35	—	—	—	—
<i>Paracanthonchus macrodon</i>	0.40	—	—	—	—	—
<i>Halenchus</i> sp.	—	—	—	—	0.12	—
<i>Diplopeltinae</i> sp.	0.33	0.35	0.06	—	—	—
<i>Paracanthonchus perspicuus</i>	—	0.61	—	—	—	—
<i>Microilaimus</i> sp.	—	0.35	—	—	—	—
<i>Polygastrophora</i> sp.	—	—	—	0.02	—	—
<i>Anticoma</i> sp.	—	0.35	—	—	—	0.07
<i>Eleutherolaimus</i> sp.	0.40	—	—	—	—	—
<i>Camacolaimus</i> sp.	—	0.35	—	—	—	—
<i>Chromadorita</i> sp.	—	—	—	—	0.35	—
<i>Symplocostoma</i> sp.	—	0.31	—	0.02	—	—
<i>Desmodora</i> sp.	0.33	—	—	—	—	—
<i>Calyptronema</i> sp.	0.33	—	—	—	—	—
<i>Halichoanolaimus</i> sp.	0.33	—	—	—	—	—
<i>Pontonema</i> sp.	—	—	—	—	—	—
<i>Spilophorella</i> sp.	—	—	—	—	—	—
<i>Pelagonema</i> sp.	—	—	0.11	—	—	—
Indet.	—	4.52	—	—	—	0.17
Total	213.87	695.61	18.93	2.05	21.00	18.46

frequency (F, %) of the phytoplankton nematode fauna.

1974						Total	D	F
Feb.	Mar.	Apr.	May	Jun.	Jul.			
5.48	55.65	67.65	757.35	1075.08	8.96	2239.58	57.52	100
4.49	12.00	7.66	102.80	102.62	20.65	520.80	13.38	100
4.69	12.99	70.24	280.72	8.13	0.28	382.39	9.82	71
3.40	6.66	6.96	50.30	51.77	26.54	366.74	9.47	100
0.11	2.54	9.42	63.80	0.92	0.84	82.51	2.12	67
—	0.46	0.12	0.69	0.92	1.40	80.80	2.08	79
—	0.25	0.19	3.62	1.83	3.48	53.41	1.37	58
1.05	0.50	1.38	12.75	6.28	1.83	25.26	0.65	71
1.73	2.54	1.49	4.38	5.49	1.64	24.03	0.62	79
0.46	3.25	0.42	1.09	1.37	0.47	18.69	0.48	100
—	0.25	—	0.29	—	0.28	13.72	0.35	58
0.99	1.17	1.83	2.43	4.68	0.83	13.48	0.35	67
—	—	0.12	0.29	1.37	1.03	7.23	0.19	29
—	—	—	0.29	1.15	—	6.47	0.17	29
—	0.71	—	0.29	0.34	0.28	6.01	0.15	50
—	—	—	—	1.02	0.24	4.29	0.11	46
0.06	—	—	—	0.34	—	2.89	0.07	17
0.10	—	—	—	0.57	0.24	2.75	0.07	29
—	—	—	0.29	0.57	0.80	2.70	0.07	29
1.02	0.71	0.46	—	—	—	2.48	0.06	33
—	—	—	—	1.26	0.24	2.31	0.06	21
—	—	—	—	—	—	2.05	0.05	13
—	—	—	—	—	1.27	2.00	0.05	17
—	—	—	—	—	—	1.67	0.04	17
—	—	—	0.29	—	0.52	1.66	0.04	21
—	—	—	—	0.34	0.28	1.66	0.04	17
0.41	—	—	0.87	—	—	1.37	0.04	17
—	—	—	0.29	—	—	1.23	0.03	13
—	—	—	—	—	—	0.99	0.03	13
—	—	—	0.29	0.34	—	0.94	0.02	13
—	—	—	—	0.57	—	0.94	0.02	4
—	—	0.12	—	—	—	0.87	0.02	13
—	—	—	0.40	—	—	0.80	0.02	8
0.10	0.25	—	0.29	—	—	0.76	0.02	17
—	—	—	—	—	—	0.74	0.02	13
—	—	—	—	—	—	0.61	0.02	4
—	—	—	—	—	0.24	0.59	0.02	8
—	—	—	—	0.57	—	0.59	0.02	8
0.10	—	—	—	—	—	0.52	0.01	13
—	—	—	—	—	—	0.40	0.01	4
—	—	—	—	—	—	0.35	0.01	4
—	—	—	—	—	—	0.35	0.01	4
—	—	—	—	—	—	0.33	0.01	8
—	—	—	—	—	—	0.33	0.01	4
—	—	—	—	—	—	0.33	0.01	4
—	—	—	—	—	—	0.33	0.01	4
—	—	—	0.29	—	—	0.29	0.01	4
—	—	—	—	—	0.24	0.24	0.01	4
—	—	—	—	—	—	0.11	0.003	4
—	1.63	0.24	3.67	0.92	0.52	11.67	0.30	
24.19	101.56	168.30	1287.77	1268.45	73.07	3893.26		

Thirteen species showed high frequency values occurring in one-half or more of all the samples, and these may be further divided into two groups based on the dominance values. One group was composed of four species, *Monhystera refringens* Bresslau et S. Stekhoven, *Chromadora nudicapitata* Bastian, *Chromadora heterostomata* Kito, and *Araeolaimus elegans* De Man, represented by the range of the dominance and frequency values, 9.47 to 57.52% and 71 to 100%, respectively. The second group of nine species, *Theristus* (*Theristus*) *acer* Bastian, *Acanthonchus* (*Seuratiella*) *tridentatus* Kito, *Euchromadora ezoensis* Kito, *Steineridora borealis* Kito, *Neochromadora bilineata* Kito, *Monhystera disjuncta* Bastian, *Oncholaimus dujardinii* De Man, *Enoplus anisospiculus* Nelson et al., and *Spilophorella tollenifera* Wieser, showed rather low dominance values, 0.15 to 2.12% and frequency values, 50 to 100%. These common species except for *S. tollenifera* also occurred above the average 1% in relative abundance throughout the year; especially, the dominant four species, *M. refringens*, *C. nudicapitata*, *C. heterostomata*, and *A. elegans*, always fixed their position over the fifth rank and occupied together about 90 and 82% of the total and the average nematode population, respectively (the range in monthly abundance, 72.48% in August to 97.57% in June). The remaining nematode species showed infrequent occurrence and low dominance values, most of which appeared restrictedly in the warmer seasons: *Rhabditis marina* Bastian, *Eurystomina ophthalmophora* (Steiner), *Graphonema metuliferum* Kito, *Onchium minutum* Kito, *Dichromadora amphidiscoides* Kito, *Neochromadora oshoroana* Kito, *Pseudaraeolaimus ocellatus* Kito, *Paramonohystera* (*Leptogastrella*) *pellucida* (Cobb), *Monoposthia costata* (Bastian), *Paracanthonchus kamui* Kito, *Paracanthonchus macrodon* (Ditlevsen), *Paracanthonchus perspicuus* Kito, and the other indeterminable species.

Abundance and Age Distribution

Monthly fluctuation in abundance and age distribution of the nematode population over the year is illustrated in Fig. 2. The population density per 10 cm² and per gram algae significantly increased twice in the spring and early autumn, although the two indices showed each maximum value in a different period: 2.05 (November)-1287.77 individuals (May)/10 cm² and 1.4 (November)-368.9 individuals (September)/g algae. The mean density was about 330 individuals/10 cm² and 93 individuals/g algae. The gravid females occurred constantly throughout the year (mean 12%). The sex ratio, females to males, varied from 0.7 to 1.88 (mean 1.3).

Among the 12 common species which showed each maximum density in either May-June or September, the dominant four species fluctuated significantly in abundance and age distribution (Fig. 2). *M. refringens* increased in the spring and autumn, and the former increase was greater than the latter: 0.25 (November)-1057.08 individuals (June)/10 cm² and 0.2 (November)-279.7 individuals (June)/g algae. The gravid females were present throughout the year, and the juveniles abundantly occurred on the way to the spring population expansion: the sex

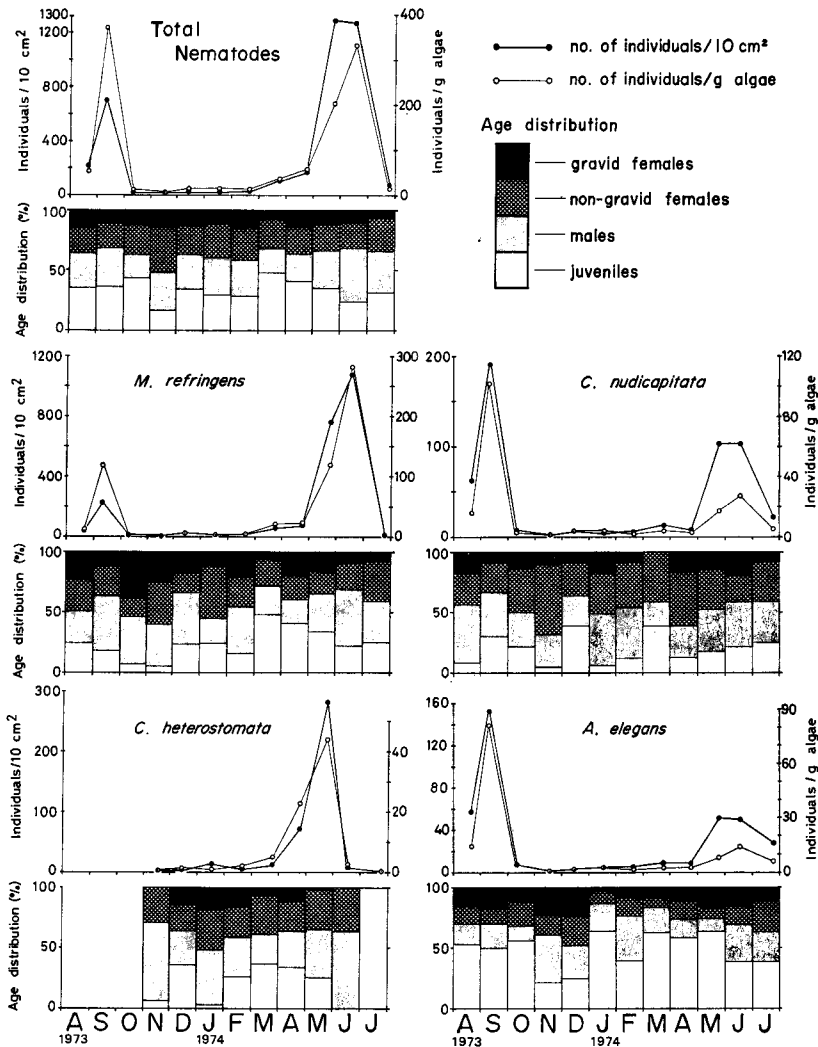


Fig. 2. Seasonal variation in abundance and age distribution of the total nematodes and the 4 dominant species, *Monhystera refringens*, *Chromadora nudicapitata*, *Chromadora heterostomata*, and *Araeolaimus elegans*.

ratio, 0.7–2.6 (mean 1.4). *C. nudicapitata* also showed two peaks of the abundance, and the autumnal density increase was higher than the spring one: 0.60 (November)–190.69 individuals (September)/10 cm² and 0.4 (November)–101.1 individuals (September)/g algae. The gravid females occurred every month except for March: the sex ratio, 0.7–2.6 (mean 1.5). *C. heterostomata* occurred from November

to July and showed the maximum density in May, 280.72 individuals/10 cm² and 43.8 individuals/g algae. The gravid females were present from December to May: the sex ratio, 0.4–1.6. *A. elegans* varied seasonally in density, following a similar trend to that of *C. nudicapitata*, although the second peak was not so conspicuous as that of *C. nudicapitata*: 0.60 (November)–151.90 individuals (September)/10 cm² and 0.4 (November)–80.6 individuals (September)/g algae. The gravid females were observed over the year: the sex ratio, 0.6–2.6 (mean 1.4). Of the above species, *M. refringens*, *C. nudicapitata*, and *A. elegans*, seem to belong to Juario's (1975) Group II, of which the reproduction is not restricted to any particular season, for the reason of the simultaneous presence of the gravid females and juveniles in every month. Occurrence of the gravid females in *C. heterostomata* was, contrary, restricted in a definite period as his Group I, of which the reproduction is restricted to particular seasons, but the number of generations per year could not be determined from this field study.

Diversity

Monthly change of the number of species (Fig. 3) showed clearly a seasonal trend that after the maximum value in September the number of species dropped sharply to the low level in October–April, but it increased again from May. Consequently, species richness of this nematode assemblage indicated the higher values (24–31 species) in the warmer seasons and the lower ones (14–17 species) in the other seasons (mean 19.7 species, SD 5.7). Pielou's evenness index (Fig. 3) reached

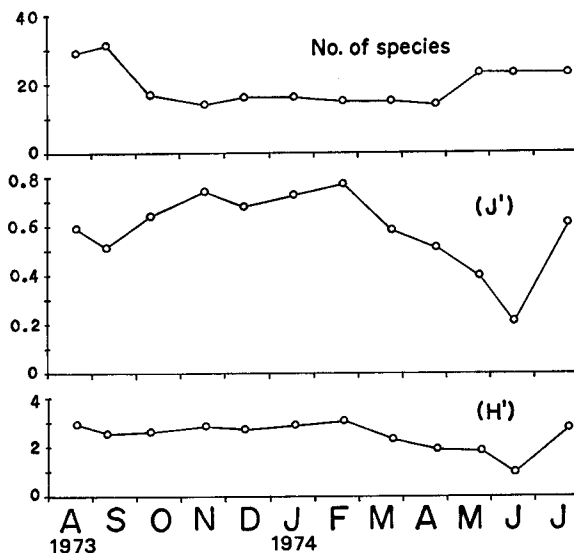


Fig. 3. Seasonal variation in three diversity indices; number of species (species richness), Pielou's evenness (J'), and Shannon-Weaver function (H').

the maximum in February through the gradual increase from autumn to winter, and then it was notably depressed during March-June (mean 0.58, SD 0.15). Shannon-Weaver's function (Fig. 3) expresses the interaction of richness and evenness components. However, it decreased remarkably during March-June, strongly influenced by evenness component, although it showed the intermediate features of both components in the other periods (mean 2.42, SD 0.58). Diversity was very lower when one or two species showed more than 40% of monthly population, i.e. *M. refringens* in March (54.80%), May (58.81%), and June (84.73%), *M. refringens* (40.20%) and *C. heterostomata* (41.73%) in April, while it was higher in the other months without such abundant species.

Faunal Affinity

The trellis diagram (Fig. 4) illustrates that there are two distinct periods, July-January and March-June, which are represented by the high affinity values within each period (mean 68.8 and 70.2%, respectively) but are clearly separated by the low values between both periods (mean 37.4%). From this, it is evident that the species composition was fairly stable during the above two periods, while it changed abruptly from June to July but gradually in the winter.

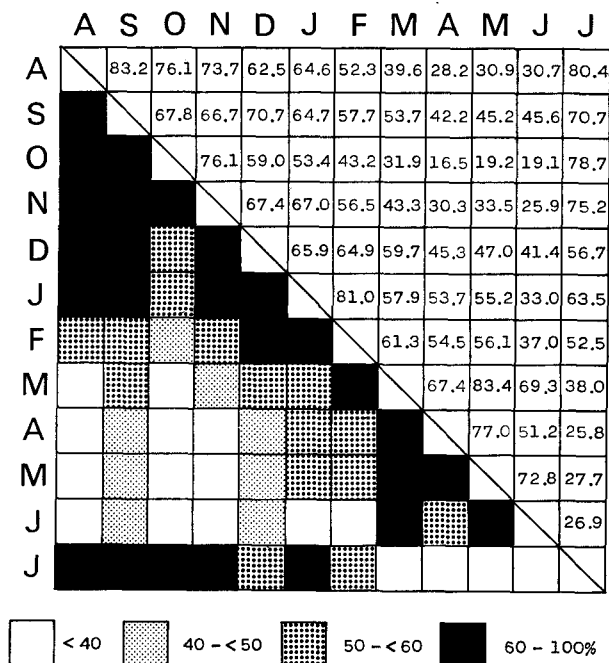


Fig. 4. Trellis diagram for the 12 sampling months from August 1973 to July 1974, showing the degree of faunal affinity among the nematodes.

affinity value was 53.3%, for all possible combinations in the sampling year.

Warwick (1977) studied the phytal nematode assemblages among fine intertidal seaweeds, *Asparagopsis armata* and *Falkenbergia rufolanosa* in Scilly, and observed that the two periods separated in dendrograms of faunal affinities alternated seasonally as in the present study. As for the average affinity value throughout a year, Hopper and Meyers (1967a) reported the value 48.1% (Site A) on a turtle grass *Thalassia testudinum* in Florida, and Juario (1975) obtained the very high value 78% (calculated from his Fig. 4 based on Sørensen's Quotient of Similarity) in a subtidal silty sand in German Bight. These data including the present one suggest that phytal nematode assemblages are temporally more variable in faunal composition than bottom sediment nematode assemblages, although the complete picture about the seasonal change of faunal composition in nematode assemblages must be clarified by further information.

Physiognomic Characters

Figure 5 shows monthly distribution of the nematodes within each category of the five physiognomic characters (body length, body setal length, feeding type, visual mechanism, and cuticular structure), and Table 2 summarizes respectively their distribution in the total and the average population.

Although their distribution patterns based on the number of nematode species were almost stable throughout the year, monthly distribution of the number of nematode individuals showed clearly seasonal changes on the characters except for the body length. The distribution patterns of the other four characters, based on the number of individuals, conspicuously varied during March-June, but they were rather stable in the remaining period. *Body length.* This nematode fauna was represented by the nematodes less than 1.5 mm length, which was considered as a length boundary of the highest ecological significance (see Wieser, 1959a). Particularly, proportion of the nematodes belonging to the 0.5–1.0 mm size class always predominated throughout the sampling year. *Body setal length.* Except for the two species, *E. anisospiculus* and *P. pellucida*, all species were equipped with short cephalic setae less than 15 μm ; their somatic setae including cervical ones were within the same or shorter size class than that of the cephalic setae. The species within the two size classes, 0–5 and 5–10 μm , showed similar higher percentages in the total and average, while the nematodes within the shortest class rather dominated, especially in the total. The proportion of the 0–5 μm class increased remarkably in the spring. *Feeding type.* The number of epigrowth feeding species was uniformly most abundant during the course of study. In the number of nematode individuals, on the other hand, the distribution pattern of the four feeding types showed clearly a seasonal change. Epigrowth feeders dominated constantly from the summer to winter, while non-selective deposit feeders conspicuously increased in the spring, particularly constituting about 85% of the nematodes in June. Because of this spring increase, non-selective deposit feeders showed the highest percentage in the total nematodes,

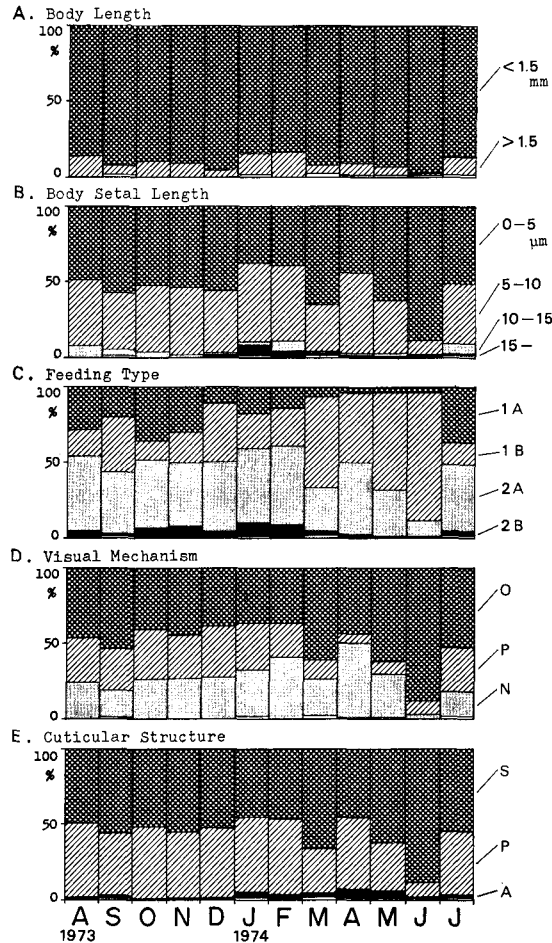


Fig. 5. Monthly distribution of the 5 physiognomic characters. A. Body length, B. Body setal length, C. Feeding type (1A, non-selective deposit feeders; 1B, selective deposit feeders; 2A, epigrowth feeders; 2B, omnivores/predators), D. Visual mechanism (O, ocelli; P, pigments; N, none), E. Cuticular structure (S, smooth; P, punctate; A, annulate).

in despite of the dominance of epigrowth feeders in the average. *Visual mechanism.* The nematodes equipped with visual mechanisms comprised over 80% of the total population though they belonged to only 11 species, of which nine were equipped with ocelli and two were equipped with pigments. The nematodes lacking visual mechanisms dominated in February and April, but in the other months the nematodes with ocelli were most abundant, especially constituting about 90% of

Table 2. Distribution of the five physiognomic characters based on the number of species and individuals in the total nematodes; the average percentage throughout the year in parentheses. Nematodes with uncertain characters were not listed in this table.

Physiognomic characters	species		individuals	
	no.	%	no.	%
Body length				
0-0.5 mm	2	4.1 (2.0)	3.72	0.1 (0.4)
0.5-1.0	19	38.8 (49.5)	3572.55	91.8 (87.3)
1.0-1.5	6	12.2 (9.6)	93.10	2.4 (3.2)
1.5-2.0	10	20.4 (15.6)	114.26	2.9 (3.2)
2.0-3.0	5	10.2 (9.3)	69.27	1.8 (2.9)
3.0-	7	14.3 (13.9)	28.69	0.7 (2.7)
Body setal length				
0-5 μ m	23	46.9 (40.2)	2666.30	68.5 (55.1)
5-10	20	40.8 (44.8)	1120.10	28.8 (40.2)
10-15	5	10.2 (11.2)	81.71	2.1 (3.0)
15-	1	2.0 (3.8)	13.48	0.3 (1.4)
Feeding type				
1A	7	14.3 (13.2)	379.03	9.7 (18.1)
1B	8	16.3 (19.2)	2345.94	60.3 (36.8)
2A	23	46.9 (48.6)	1112.56	28.6 (40.9)
2B	11	22.4 (19.0)	44.06	1.1 (3.9)
Visual mechanism				
ocelli	9	18.4 (22.9)	2625.17	67.4 (51.0)
pigments	2	4.1 (9.3)	534.28	13.7 (22.6)
none	38	77.5 (67.8)	722.14	18.5 (26.1)
Cuticular structure				
smooth	21	42.9 (42.2)	2677.45	68.8 (56.9)
punctate	17	34.7 (40.7)	1104.74	28.4 (40.2)
annulate	11	22.4 (17.1)	99.40	2.6 (2.5)

the population in June. *Cuticular structure.* Both species with smooth and punctate cuticle were subequally abundant in the present fauna but the nematodes with smooth cuticle were more abundant than those with punctate cuticle in the total nematodes. A significant change of the distribution pattern occurred in the period, March to June, in which the nematodes with smooth cuticle occupied more than 90% of the population in June.

Discussion

The phytal nematode assemblage on the *Sargassum* thalli in Oshoro Bay displayed seasonal changes in a variety of structural attributes. The nematode population density showed higher values during the warmer seasons and attained significant peaks in the spring and early autumn, in either of which the common species showed their maximum occurrence. Those two peaks were evidently different in faunal composition, species diversity, and distribution of physiognomic

characters, although the number of species (species richness) was abundant in both periods. The spring nematode populations represented homogeneous features in faunal structure because of the remarkable dominance of one species, *M. refringens* (together with *C. heterostomata* in April). While, the other density peak in September was rather composed of a heterogeneous population chiefly due to subequal occurrence of the three species, *M. refringens*, *C. nudicapitata*, and *A. elegans*. In the same way, the distribution of physiognomic characters are strongly influenced by the foregoing four dominant species; *M. refringens* (body length 0.5–1.0 mm, body setae 0–5 μm , feeding type 1B, visual mechanism 0, cuticular structure S), *C. nudicapitata* (0.5–1.0, 5–10, 2A, P, P), *C. heterostomata* (0.5–1.0, 5–10, 2A, N, P), and *A. elegans* (0.5–1.0, 0–5, 1A, 0, S). The spring and early autumn populations, therefore, showed peculiar distribution patterns of the physiognomic characters except for the body length, of which the 0.5–1.0 mm size class always predominated. The spring populations were represented by conspicuous increase of the individuals belonging to the categories, 0–5 μm long body setae, non-selective deposit feeders, ocelli, and smooth cuticle, greatly due to *M. refringens*, although in April *C. heterostomata* temporarily increased the proportion of the 5–10 μm long body setae, epigrowth feeders, no visual mechanisms, and punctate cuticle. On the other hand, the nematodes belonging to the categories, 0–10 μm long body setae, deposit and epigrowth feeders, ocelli and pigments, smooth and punctate cuticle were abundant in September chiefly due to occurrence of the three species with subequal density, *M. refringens*, *C. nudicapitata*, and *A. elegans*.

The species composition and abundance of phytoplankton marine nematode populations are directly dependent on the morphology of seaweeds, e.g. growth form, coarseness, and texture (Wieser, 1951, 1952, 1959a; Ott, 1967; Moore, 1971; Warwick, 1977). More complex and well-grown weeds provide epiphytic organisms including nematodes with more heterogeneous and greater habitable space; moreover, organic matters (detritus, etc.) which are available as food resources for nematodes are densely accumulated in that space (see also Dahl, 1948, Nagle, 1968, especially for amphipods; Heck and Westone, 1977, for macroinvertebrates; Hicks, 1977a, b, 1980, for harpacticoid copepods). The present study also indicated the presence of a close relationship between the structural complexity of algal habitat and the number of species and individuals of the nematodes living therein: here the standing crop of *S. confusum* is considered as a measure of structural complexity (after Heck and Westone, 1977). The number of species increased clearly between May and September when the *Sargassum* showed a more complex growth form (Kito, 1975) and were remarkably polluted by various deposit matters. This species increase was mostly due to the rare species which occurred restrictedly in the warmer seasons. These facts suggest that complex algal structure and a variety of food resources increased the potential useful niche resources for nematodes, to which the rare species immigrated from the other habitats within the *Sargassum* region: Hopper and Meyers (1967a, b) and Jensen (1981) also suggest the occur-

rence of seasonal movement of nematodes between the phytal and the sediment habitats, based on the field works or laboratory experiments. The present observed fluctuation of nematode abundance may be interrupted likewise as a product of a correlation between habitat complexity and available food resources. The total nematode density per 10 cm² reached the maximum value in May-June, following the synchronous increase of the standing crop of *Sargassum* and the amount of detritus. On the other hand, the density was not so abundant in the other peak September when the *Sargassum* was rather poor in standing crop but was densely coated with detritus. Considering that the density per gram algae in September was rather higher than those in May-June, it is apparently presumed that the spring populations could obtain the maximum density for the sufficient habitable space and available foods, while the autumn one remained on the rather low level for the scarcity of habitable space, despite of a great amount of food resources. The summer radical decrease in density is presumably caused by the defoliation or washout of portions of the *Sargassum* thalli harboring numbers of nematodes (see Mukai, 1971, 1976, for whole phytal animals and mollusks on *S. serratifolium*, respectively).

Two or more closely related species of marine nematodes are generally found in natural communities as the previous authors have already noted (e.g. Wieser, 1960; Ott, 1972; Boucher, 1972; Juario, 1975). If applying the competitive exclusion principle (Hardin, 1960), they seem to coexist in the same community because of their different ecological requirements for space, time, food resources, and so on. In the present phytal nematode assemblage, there are two pairs of closely related abundant species, *M. refringens* and *M. disjuncta*, and *C. nudicapitata* and *C. heterostomata*. Although both the *Monhystera* species having unarmed, somewhat cylindrical buccal cavity are non-selective deposit feeders (according to Wieser, 1953), they showed a difference in food preference; *M. disjuncta* takes primarily fine soft materials (see also Chitwood and Marphy, 1964; Gerlach and Schrage, 1971), while *M. refringens* has large, hard materials such as pennate diatoms besides soft materials (unpublished data). Such the difference seems to result from different width of their mouth openings which is apparently deduced from the length of head diameter (Levy and Coull, 1977): $hd=5-7\ \mu m$ in *M. disjuncta*, $10-12\ \mu m$ in *M. refringens* (after Kito, 1981). The wider food preference of *M. refringens* may be one of the possible cause why it predominated in this nematode assemblage. On the other hand, the two epigrowth-feeding species of the *Chromadora* appear to coexist in this habitat by having asynchronous fluctuation patterns in reproductive activity; *C. nudicapitata* maintained higher reproductive activity from May to September while *C. heterostomata* obtained it just in April and May. There is no clear difference of gut contents between the two species which probably scrap the surface of algae or suck out the cell-liquid of the food objects such as benthic diatoms (see Wieser, 1953). However, they may also depend on their own peculiar food resources because they are obviously different in the morphology of buccal armatures, which of *C. heterostomata* is more complicated and larger than that of *C.*

nudicapitata. Besides the above features, *M. refringens* and *C. nudicapitata* are equipped with ocelli or pigments respectively, while *M. disjuncta* and *C. heterostomata* have neither visual mechanisms. Such the presence or absence of the visual mechanisms also seems to concern their coexistence in the present algal habitat, since the visual mechanism is available for nematodes to fix the position to light (Wieser, 1959a; Warwick, 1977).

Since Wieser (1953, 1959a) approached the characterization of different marine habitats by using physiognomic characters of nematodes, many authors have studied the distribution of those characters, especially feeding types, in various habitats (for sediments: Wieser, 1960; King, 1962; Hopper and Meyers, 1967b; Tietjen, 1969, 1971, 1976; Warwick and Buchanan, 1970; Coull, 1970; Boucher, 1974; Juario, 1975; Platt, 1977a, b; for seaweeds: Hopper and Meyers, 1967a; Ott, 1967; Moore, 1971; Warwick, 1977). Most of the works dealt with those distribution based on the total data from one particular season or a limited number of months. Phytoplankton nematode assemblage, however, varies seasonally not only in faunal structure and population density but also in distribution of physiognomic characters, as suggested by Warwick (1977) and also revealed through the present study. For this reason, the variability in the distribution of physiognomic characters should be taken into consideration when comparing phytoplankton nematode assemblages. Figure 6, for example, shows a comparison of the distribution patterns of

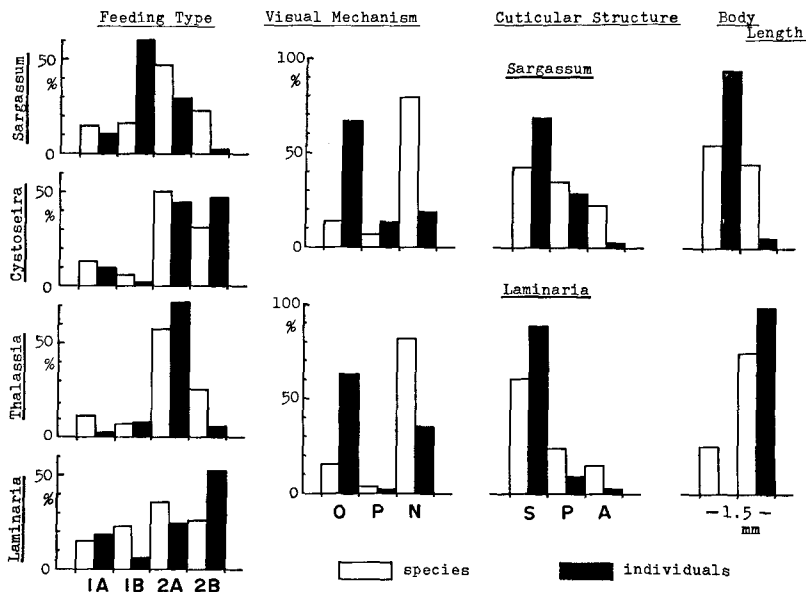


Fig. 6. Comparison of distribution of certain physiognomic characters among four phytoplankton nematode faunas (see text and Fig. 5 for explanation).

certain physiognomic characters among four phytal nematode faunas: those on *Sargassum confusum* (the present study, Sea of Japan) and *Thalassia testudinum* (Hopper and Meyers, 1967a, Florida, USA) are based on the total nematodes throughout a year, while those on *Cystoseira spicata* (Ott, 1967, Adriatic, Yugoslavia) and among the holdfasts of *Laminaria hyperborea* (Moore, 1971, North Sea, UK) are based on the temporal fauna collected during one sampling period. These four phytal nematode faunas show similar distribution patterns of feeding types in species number (dominance of epigrowth-feeding species), but each is represented by one or two peculiar feeding types in individual abundance, i.e. non-selective deposit feeders on the *Sargassum*, epigrowth feeders on the *Thalassia*, epigrowth feeders and omnivores/predators on the *Cystoseira*, and omnivores/predators among the *Laminaria* holdfasts. The phytal nematode fauna on the *Sargassum* is also distinguishable from that among the *Laminaria* by the different distribution pattern in body length (shorter nematodes less than 1.5 mm are dominant on the former, while larger forms among the latter), although both faunas are alike in the distribution of visual mechanisms and cuticular structures. However, these different or similar distribution of physiognomic characters are probably not actual characteristics for each phytal nematode assemblage because the character distribution tends to vary temporally as well as the faunal composition and population density as observed above. These variation in phytal nematode assemblage is closely related with the peculiarity of algal habitats themselves, especially with the changes of their size and shape through the course of their own life cycles, and with the seasonal fluctuations of other environmental factors such as temperature, salinity, light penetration, water movement, amount and component of detritus, etc. In order to discuss phytal marine nematode assemblages, further investigation should be aimed to analyze precisely the corresponding seasonal variation between the nematode assemblages and the physical and biological environments in the seaweed region.

Summary

1) The structure and seasonal fluctuation of the phytal marine nematode assemblage on the thalli of a brown alga, *Sargassum confusum* Agardh, were studied throughout one year, August 1973-July 1974, in the *Sargassum* region of Oshoro Bay, Hokkaido, Japan.

2) A total of 49 species were identified, of which the 12 species occurred beyond the average of 1% in relative abundance throughout the year. The 4 dominant species, *Monhystera refringens*, *Chromadora nudicapitata*, *Chromadora heterostomata*, and *Araeolaimus elegans*, numerically comprised 90% of the total nematode population.

3) The population density was abundant in the warmer seasons, and it increased significantly in the spring and early autumn (maximum 1290 individuals/10 cm² in May and 370 individuals/g algae in September), in either of which the

12 common species showed their maximum occurrence.

4) The spring and the early-autumnal nematode populations were different each other in faunal composition, diversity, and distribution patterns of the physiognomic characters of nematodes. The spring populations were predominated by one or two species while the autumnal one was represented by some abundant species, although the number of species was rich in both periods. The categories of each physiognomic characters, 0–1.5 mm body length, 0–5 μm body setae, non-selective deposit feeders, ocelli, and smooth cuticle, increased their proportion in the spring, while in September the categories, 0–10 μm body setae, deposit and epigrowth feeders, ocelli and no visual mechanisms, smooth and punctate cuticle were abundant.

5) The seasonal fluctuations in a variety of structural attributes of the phytoplankton marine nematode assemblage seem to be closely related to changes in the physical and biological environmental factors, e.g. water temperature, structural complexity of algal habitat, available food resources in the seaweed region. It was emphasized that, in order to discuss phytoplankton marine nematode assemblages, the seasonal variability of the assemblage structure should be taken into consideration.

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