Phytodetritus and the abundance and biomass of abyssal nematodes in the central, equatorial Pacific

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Abstract

The abundance and biomass of abyssal (4300–5000 m) nematodes were investigated along a latitudinal gradient of phytodetritus deposition from 0 to 23°N in the central, equatorial Pacific (140–158°W). Nematode abundance in the oligotrophic, central, North Pacific gyre was 50% lower than at the equator while macrofauna abundance increased 6.5 times over the same transect. Nematode abundance and biomass in the surface (0–1 cm) sediment layer were significantly higher at phytodetritus stations than at non-phytodetritus stations. Abundance and biomass were within the range recorded from other sites of comparable depth that also receive an input of phytodetritus. Abundance was also strongly correlated with microbial biomass. An increase in body size was associated with an increase in food supply. The results demonstrate that the equatorial Pacific represents an immense zone of relatively high nematode standing stock. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Nematodes; Phytodetritus; Central Equatorial Pacific

1. Introduction

Surface divergence of upwelled water off the coast of Peru results in a tongue of low-temperature, high-productivity water that can be observed on a coastal zone colour scanner (CZCS) image as

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a band of high phytoplankton pigment concentration. Productivity in this region may account for 20–50% of the global ocean value (Chavez and Barber, 1987; Murray et al., 1994).

During the 1992 US joint global ocean flux study (US JGOFS), abyssal accumulations of phytodetritus were observed, for the first time, by Smith et al. (1996) in the Pacific Ocean along a narrow latitudinal band at 140°W. A number of studies have indicated an association between phytodetritus and marine nematodes in the North Atlantic (Rice and Lambshead, 1994; Lambshead et al., 1995, 2000) and the Indian Ocean (Cook et al., 2000).

Measurement of chlorophyll *a* and excess ^{234}Th activity in phytodetritus from samples taken between the equator and 5°N indicated that the material was recently settled, largely undegraded and so likely to contain significant amounts of labile carbon (see Aller and DeMaster, 1984; Stephens et al., 1997). At 9°N, chlorophyll-*a*-rich phytodetritus was not observed or collected (Smith et al., 1996). These observations indicated that there was a latitudinal gradient in the supply of labile carbon reaching the benthos beneath the transect. Given the known effects of such inputs to shallow water marine systems, such as variations in nematode abundance and diversity (Heip et al., 1985; Jensen, 1987), it was expected that there would be changes in the abyssal nematode fauna that reflected the overlying depositional regime. Thus, nematodes were collected along the 140°W transect to test the following hypotheses. Firstly, that no increase in nematode abundance or biomass should be associated with phytodetritus or microbial biomass. Secondly, that nematodes in the non-phytodetrital locations and deeper in the sediment would not be smaller because of reduced food availability.

2. Materials and methods

Samples were collected at four stations along the JGOFS 140°W transect (Fig. 1, Table 1) during the benthic leg of the US JGOFS equatorial Pacific process study (JGOFS EqPac). These stations were chosen because earlier research had indicated that a gradient in overlying primary productivity, POC flux and sediment accumulation rate existed along the transect, but other characteristics remained approximately constant (Murray et al., 1992).

Additional samples (Fig. 1) were also collected from a reference site under the Hawaiian Ocean time-series ('HOT') station (Karl and Lukas, 1996). This location closely resembles the 9°N JGOFS EqPac station in many physical characteristics of the seafloor. The HOT station is located in the oligotrophic North Pacific gyre, and consequently, we consider it representative of much of the Pacific Ocean abyssal plain, in that it experiences a low organic carbon flux.

Samples were not collected at random along a transect, which would be the ideal sampling strategy, but in clusters because of ship requirements. This is a common problem in deep-sea biological and geochemical studies, and the samples are consequently not independent of each other and hence are pseudoreplicates. Sometimes, the only pragmatic approach is to treat the samples as if they were independent and accept the potential for error. A recent example where this analysis strategy has been successfully employed to yield important results is Rex et al. (1993). Where possible, an alternative approach is to mean the data from core samples from a station and use station means as the statistical samples for further analysis. This avoids pseudoreplication as the stations are independent. It is a particularly valuable approach when studying putative nematode patterns over large distances because it removes the high small-scale heterogeneity that
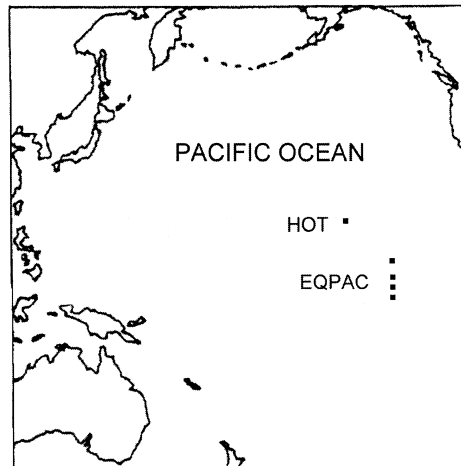
Fig. 1. Site locations for the JGOFS EqPac stations and HOT station.

Table 1
Station locations, water depths and collecting dates for cores that were collected for meiofaunal analysis. The coring device used is also listed

Sample	Location		Water depth (m)	Date	Collecting device
BC4	00°06.00′N	139°43.90′W	4328	15/Nov/92	Box-corer
BC6	00°06.62′N	139°43.96′W	4305	16/Nov/92	Box-corer
BC7	00°06.40′N	139°44.10′W	4307	18/Nov/92	Box-corer
BC8	00°06.98′N	139°43.94′W	4301	19/Nov/92	Box-corer
MC15	00°06.57′N	139°43.42′W	4304	19/Nov/92	Multiple-corer
BC9	02°03.94′N	140°08.94′W	4409	20/Nov/92	Box-corer
BC10	02°04.00′N	140°07.90′W	4414	21/Nov/92	Box-corer
BC11	02°03.96′N	140°08.06′W	4409	22/Nov/92	Box-corer
BC12	02°03.80′N	140°07.90′W	4410	23/Nov/92	Box-corer
BC15	05°05.00′N	139°39.00′W	4447	27/Nov/92	Box-corer
BC16	05°04.42′N	139°38.90′W	4446	28/Nov/92	Box-corer
BC17	05°04.80′N	139°38.50′W	4424	29/Nov/92	Box-corer
BC18	05°04.20′N	139°38.40′W	4320	30/Nov/92	Box-corer
MC26	05°04.30′N	139°38.30′W	4418	30/Nov/92	Multiple-corer
BC19	08°55.08′N	139°52.20′W	4986	03/Dec/92	Box-corer
BC20	08°56.04′N	139°51.55′W	4994	04/Dec/92	Box-corer
BC22	08°55.80′N	139°52.30′W	4991	06/Dec/92	Box-corer
MC1	22°54.69′N	157°49.74′W	4880	29/Jul/92	Multiple-corer
MC2	22°54.95′N	157°49.93′W	4871	29/Jul/92	Multiple-corer
MC4	22°54.74′N	157°50.21′W	4880	31/Jul/92	Multiple-corer
MC6	22°54.64′N	157°49.86′W	4884	01/Aug/92	Multiple-corer

is associated with nematode sampling (Rice and Lambshead, 1994). Cook et al. (2000) and Lambshead et al. (2000) adopted this strategy for analysis of nematode abundance and species richness, respectively, over large distances.

Samples were obtained using either a multiple-corer (similar to that of Barnett et al. (1984) but with 10 cm diameter tubes) or a USNEL-type vegematic box corer, 2500 cm^2 in area (Hessler and Jumars, 1974), divided into subcores of 100 cm^2 (Jumars, 1975). The subdivision of the box-corer is designed to minimise movement of the overlying water during core retrieval. Phytodetritus was observed on the surface of both multiple and box-core samples suggesting that the equipment was adequately sampling the meiofauna without substantial disturbance.

Following recovery, cores were sliced at 1 cm vertical intervals to 5 cm and transferred to formaldehyde, diluted to 4% with seawater. A single multiple-core tube or box-core subcore was used per deployment to ensure randomness. Overlying water was combined with the 0–1 cm sediment layer. Nematodes were extracted using a modified Ludox-TM flotation method (Brown, 1998) on a 45 μm sieve. Nematode abundance was determined by counting all nematodes in a sample using a low-power dissecting microscope. All nematodes extracted from the sediments were mounted in glycerine on slides (Seinhorst, 1959).

Nematode dry biomass was estimated by measuring the total length, L, (excluding any filiform section of tails) and width at the base of the oesophagus, W, of 50 randomly chosen individuals from each sample, under a high-power microscope with drawing-tube attachment. Randomisation was achieved by the standard method of mounting all the specimens and selecting slides using a digital random number generator. Individual biomass was then calculated using Andrassy's (1956) formula for body mass with the adaptation of Feller and Warwick (1988) (μg dry wt = $L \times W^2 \times r \times sg/1{,}700{,}000$), assuming a dry mass-to-wet mass ratio (r) of 0.25 and specific

Table 2
The X2 geometric size classes of Warwick (1984) with corresponding nematode biomass

Size class	Biomass (μg)
11	9.537–19.073
10	4.768–9.537
9	2.384–4.768
8	1.192–2.384
7	0.596–1.192
6	0.298–0.596
5	0.149–0.298
4	0.075–0.149
3	0.037–0.075
2	0.018–0.037
1	0.0931–0.018
0	0.0047–0.0931
− 1	0.0023–0.0047
− 2	0.0011–0.0023
− 3	0.00058–0.0011
− 4	0.00029–0.00058

gravity (*sg*) of 1.13. Although a morphometric method suffers the disadvantages of inaccuracies inherent in conversion factors, it permitted preservation of the nematodes for subsequent taxonomic purposes (see Brown et al., in press). Abundance and biomass size spectra were constructed using the X2 geometric size classes of Warwick (1984), where each class is twice the biomass of the class below (Table 2).

Abundance and biomass were recorded for all 0–1 cm samples. Kruskal–Wallis and Mann-Whitney tests (Sokal and Rohlf, 1969) were used as appropriate (with $n - 1$ degrees of freedom where n is the number of samples as shown in Table 1) to assess differences in abundance and total biomass between stations. The level of significance employed for rejection of the null hypothesis was $p \leqslant 0.05$. Correlation analysis was carried out using the Pearson's product moment correlation coefficient, r (Sokal and Rohlf, 1969).

3. Results

Mean nematode abundance and total biomass in the 0–1 cm sediment layer were significantly greater ($p = 0.0109$, $p = 0.0109$, respectively) at phytodetritus stations (0–5°N) than at non-phytodetritus stations (9–23°N). The greatest abundance in the top centimetre was found at 2°N, while biomass was greatest in the top centimetre at 5°N. There was no significant difference in mean abundance or biomass among individual stations (Table 3), but this may be a type I error due to the high intra-station variability and small number of cores from some stations.

Values of microbial biomass measured at the same time (Smith et al., 1997) were used to determine whether nematode abundance was associated with microbial biomass. There was a high positive correlation between nematode abundance and microbial biomass ($r = 0.931$, $p < 0.025$, Fig. 2).

Table 3
Surface (0–1 cm) abundance, A (ind./10 cm²) and total biomass, B (µg/10 cm²) for each core with Kruskal–Wallis test statistic, Z[a]

|	0°		2°N		5°N		9°N		23°N	
	A	B	A	B	A	B	A	B	A	B
	9	0.998	76	1.992	64	18.394	20	10.25	46	1.170
	102	4.876	90	15.050	73	2.095	26	8.73	28	0.835
	21	0.412	60	8.125	72	10.989	88	37.71	39	4.300
	92	2.706	160	7.772	54	1.295			49	1.452
	75	6.385			60	10.907				
Mean	60	3.075	96	8.234	64	8.736	45	1.890	40	1.939
S.D.	42.26	2.537	44.06	5.343	7.83	7.116	37.70	1.631	9.17	1.594
1 S.E.	18.90	1.135	22.03	2.671	3.50	3.182	18.85	0.942	5.30	0.797
Z	0.25	−0.83	1.88	1.61	0.33	1.65	−1.01	−1.31	−1.61	−1.34

[a]Abundance $p = 0.202$, biomass $p = 0.106$.
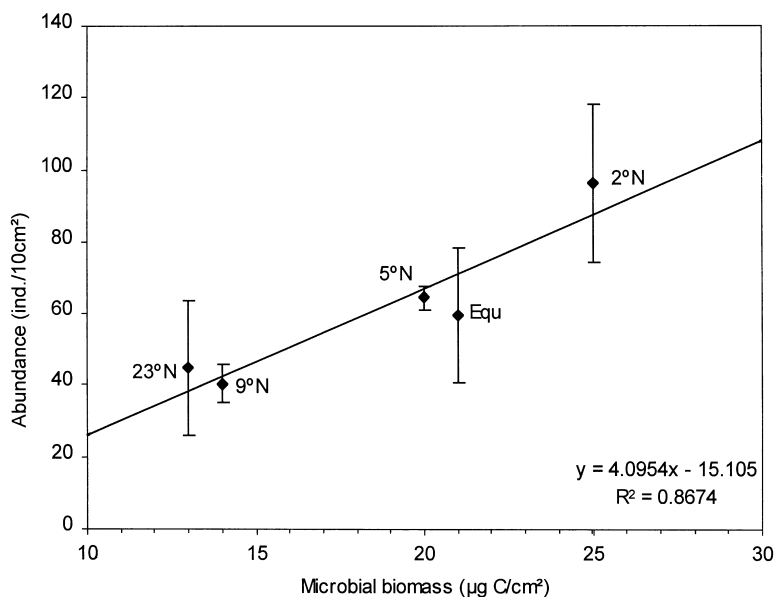
Fig. 2. Nematode abundance in 0–1 cm sediment layer correlated with microbial biomass. Microbial biomass values are taken from Smith et al. (1997). Error bars are $\pm$ 1 S.E. Regression line equation is shown on the chart.

A single, large predator/scavenger nematode (*Mesacanthion* sp.) accounted for a high proportion of the total 0–1 cm biomass at 5°N. Removing this individual from the data set reduced the mean measured biomass from 7.8 ± 6.5 to $3.8 \pm 3.3\,\mu g$ (sample size $10\,cm^2$). However, the decision was made to leave this individual in the data set as it was felt that (1) the 50 individuals used for biomass measurement had been chosen randomly and thus were considered to be representative of the sample population and (2) as a predator/scavenger type, this individual may feed directly on the phytodetritus in addition to other nematodes (Jensen, 1987) and hence may well be an important consumer of organic carbon within the population.

Individual biomass size spectra were constructed for stations 0, 5 and 9°N along the phytodetrital gradient (Fig. 3). At the equator, the same sized nematodes were found at all horizons in the sediment. However, at 5 and 9°N, below the 2 cm horizon there was a pronounced 'spike' that represented many individuals in the 0.0047–$0.0093\,\mu g$ size class indicating a smaller nematode body size. Additionally, at 9°N, there were fewer of the large individuals that were observed at phytodetritus stations. Overall, there was a general trend towards greater body size at phytodetritus stations compared with non-phytodetritus stations.
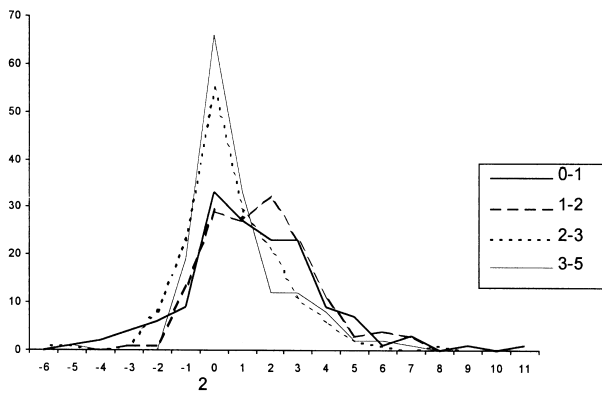
4. Discussion

A significant increase in nematode abundance and biomass occurred at stations enriched by phytodetritus, when compared with stations with little input in the equatorial Pacific in November–December, 1992. Overall, the annual abyssal POC flux exhibited a four-fold increase between

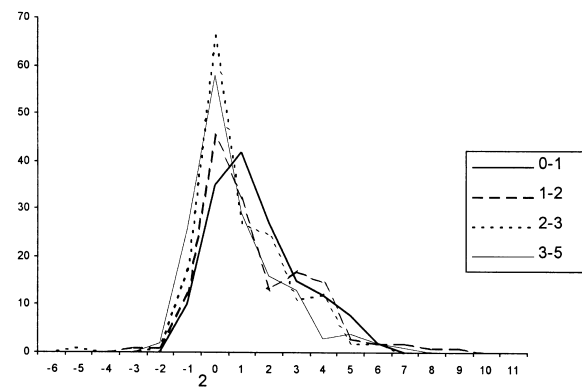**Equator**
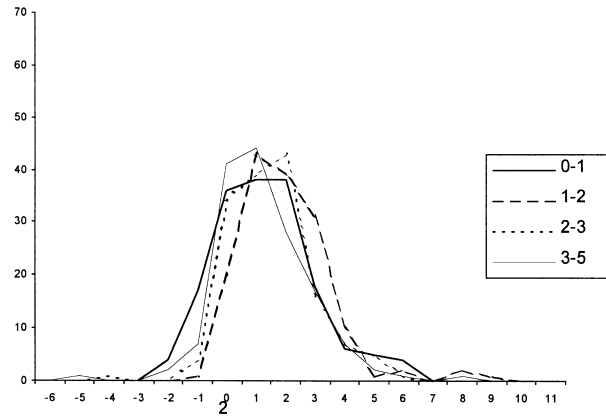
5°N

9°N

Fig. 3. Abundance–biomass size spectra at three JGOFS EqPac stations. Size spectra for vertical profiles are also shown. X2 geometric size classes are as described by Warwick (1984, Table 2).

9°N and the equator (Dymond and Collier, 1988; Honjo et al., 1995). The hypothesis that phytodetritus is not associated with an increase in nematode abundance and biomass is therefore rejected.

Besides our present study, only two other deep-sea sites in the Pacific Ocean (both without evidence of phytodetritus) have been sampled for nematode abundance or biomass (Table 4), allowing only limited comparisons with our equatorial Pacific data. The abundance of nematodes at the non-phytodetritus stations (9 and 23°N) fell within the range recorded for the Clarion–Clipperton fracture zone (Renaud-Mornant and Gourbault, 1990), which is located at 14°N, 130°W. Both abundance and biomass values across the JGOFS EqPac transect (0–9°N) fell within the range recorded off Japan at 5500–5800 m (Shirayama, 1984). This station very likely has an enhanced terrigenous POC input, which probably accounts for the similarity in nematode abundance between this site and the Pacific phytodetritus stations examined here.

Nematode abundance and biomass at Pacific phytodetritus stations were lower than those at phytodetritus locations in the NE Atlantic (Table 4). The Pacific values perhaps may be explained by the lower quantity of phytodetrital material that arrives at the seafloor compared with the NE Atlantic. At the Porcupine Seabight in the NE Atlantic, for example, phytodetritus can occur in uniform greenish carpets up to 1 cm thick (Billett et al., 1983; Lampitt, 1985), and the phytodetritus standing crop can attain 32 mmol organic $C m^{-2}$ at the BIOTRANS site (at 47°N, 20°W, close to the Porcupine Seabight, 50°N, 13°W) during the spring bloom event (Thiel et al., 1988/89). In contrast, the phytodetritus in the equatorial Pacific appeared as patchy, gelatinous aggregates that had become trapped in surface pits and furrows, or as a very thin veneer and the maximum recorded standing crop of phytodetritus reached only 2.6 mmol organic $C m^{-2}$ (Smith et al., 1996).

Table 4
Comparison of nematode abundance previously recorded from sites in the Pacific and eastern Atlantic Oceans (abundance is shown as ± 1 s.d.)

Location	Water depth (m)	Abundance (ind./10 cm²)	Reference
Western Pacific	5580–5820	145 ± 108	Shirayama (1984)
Clarion–Clipperton fracture zone, eastern, central Pacific	4905–5140	35 ± 15	Renaud-Mornant and Gourbault (1990)
HOT Station, central Pacific	4871–4884	40 ± 9	This study
JGOFS EqPac transect 0–5°N,[a] Equatorial Pacific	4301–4447	72 ± 36	This study
JGOFS EqPac transect 9°N, Equatorial Pacific	4986–4994	45 ± 38	This study
Porcupine Seabight,[a] NE Atlantic	4167–4850	345 ± 103	Pfannkuche (1985)
Porcupine Abyssal Plain[a], NE Atlantic	4843–4850	118 ± 35	Lambshead et al. (1995)
BIOTRANS,[a] NE Atlantic	4330–4561	117 ± 63	Soltwedel et al. (1996)
DORA,[a] NE Atlantic	4000–4800	473 ± 142	Rutgers van der Loeff and Lavaleye (1986)

[a]Seafloor receives a significant input of phytodetritus.

A significant, positive correlation was obtained between nematode abundance and microbial biomass in the central, abyssal Pacific. The hypothesis regarding no association between nematode abundance and microbial biomass is, therefore, rejected. A large proportion of the nematodes along the JGOFS EqPac transect were feeding type 1A, putatively classed as selective deposit-feeders (Wieser, 1953), so a positive association was anticipated. 1A nematodes are predominately small-sized individuals and so do not contribute greatly to community biomass. It is suggested that elevated microbial biomass, acting as a food source for 1A nematodes, triggers a reproductive response at phytodetritus stations, resulting in greater nematode abundance.

At 5°N, a substantially greater proportion (78%) of the total 0–5 cm biomass was found in the 0–1 cm layer compared with the equator and 9°N stations (41 and 50%, respectively). The occurrence of greater biomass without increased abundance in the 0–1 cm layer at 5°N suggested that a few large individuals had migrated upwards, perhaps to take advantage of the increased food availability caused by phytodetritus. At a shallow-water site, an upward migration of meiofauna was observed following a food input (Shulz, 1983 in Graf, 1992), but previous studies at deep-sea phytodetritus stations in the NE Atlantic have not reported such a 'shoaling' effect (Lambshead et al., 1995; Gooday et al., 1996).

There was also a discernible shift in biomass size spectra towards an increase in mean individual body size at phytodetritus stations in the equatorial Pacific. The results of the present study are, therefore, in agreement with Thiel's (1975) hypothesis. There is a general trend of increasing abundance of smaller-sized individuals with decreasing food availability, horizontally and vertically, with a corresponding decrease in the numbers of larger-sized nematodes and so our second hypothesis is rejected.

Thiel (1975) proposed that "Associations governed by constantly limiting food availability are composed of small individuals on average". This concept was originally based upon the widespread observation that meiofauna increased in importance relative to the macrofauna with increasing water depth, but may also explain the small mean body size of deep-sea nematodes (Jensen, 1988). Some studies have been based upon comparisons of the fractions of fauna retained upon sieves of decreasing mesh sizes. For example, Pfannkuche (1985) found a significant increase in the abundance of nematodes in the 46–60 μm fraction and a corresponding decrease in the > 150 μm size fraction with increasing depth in the Porcupine Seabight. This was attributed to the decrease in food availability with increasing depth. Similarly, along a depth gradient in the Mediterranean, not only the arithmetic mean size of nematodes, but also the median, geometric mean and modes of length and weight spectra decreased with decreasing organic supply (Soetaert and Heip, 1989). The results of two studies of nematode size spectra from a number of locations in the NE Atlantic, including two locations receiving inputs of phytodetritus, support the important controlling effect of food supply on nematode size (Vanreusal et al., 1995; Soltwedel et al., 1996).

The phytodetrital input to the abyssal sediments of the central equatorial Pacific was associated with a significant increase in nematode abundance and biomass compared with non-phytodetritus stations. We suggest this result reflects utilisation of bacteria by abundant selective deposit feeders in the nematode communities at phytodetritus stations. An increase in food supply was also associated with an increase in individual body size.

To conclude, the equatorial Pacific represents an immense zone with a relatively high standing stock of free-living nematodes, and it is surprising that nematode abundance in the oligotrophic central North Pacific gyre is only 50% lower than at the equator. This is a different pattern from

the macrofauna, whose abundance drops approximately sevenfold from the equator to 23°N (Smith et al., 1997).

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