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The impact of whale falls on nematode abundance in the deep sea

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Abstract

Abundance of nematode assemblages from the sediment surrounding an experimentally implanted whale carcass in the Santa Cruz Basin were investigated at 1.5 and 18 months after placement. Samples were taken at 0, 1, 3, 9 and 30 m distance away from the carcass.

Abundance is positively correlated with distance from the carcass out to at least 30 m. Analyses of nematode abundance at 18 months after implantation showed a non-linear inverse pattern to that of the macrofauna implying that enhanced macrofaunal activity immediately around the carcass was decreasing nematode abundance through predation or competition. The increased nematode abundance at 30 m after 18 months may be a response to organic enrichment from the whale fall occurring where macrofaunal abundance no longer limits nematode densities.

Keywords: Deep sea; Nematoda; Organic enrichment; Whale fall; Abundance; Pacific ocean

1. Introduction

The fall of large whale carcasses results in intense pulses of labile organic matter to the food-impoverished deep-sea floor. For example, the organic carbon contained in a single 4×10^4 kg whale ($\sim 2 \times 10^6$ g C_{org}) is equivalent to 100–200 years worth of typical organic flux from the euphotic zone to 1×10^4 m^2 of abyssal sea floor. Population level calculations suggest that such whale falls are relatively common on regional scales (Smith and Baco, 2003). Whale fall events attract dense aggregations of mobile scavengers and yield dramatically increased abundance of polychaetes and other macrofauna (20,000–45,000 m^{-2} within 1 m of the skeletons) during the first 4–18 months in what has been called the 'enrichment-opportunist successional stage' (Smith and Baco, 2003; Smith et al., 2002).

Nematodes are often the most abundant metazoan taxon in deep-sea sediments, becoming proportionally more important with increasing water depth (Carman et al., 1987). In typical marine sediments, they may account for 90–95% of individuals and 50–90% of meiofaunal biomass (Giere, 1993).

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Little is known about the effects of large pulses of organic enrichment on deep-sea nematodes and the enriched sediments surrounding deep-sea whale-fall carcasses in particular have not been investigated. Modest organic enrichment through phytodetritus input is known to affect nematode spatial distributions and abundance (Brown et al., 2001; Cook et al., 2000; Lambshead et al., 1995; Rice and Lambshead, 1994; Soetaert et al., 1997; Thiel, 1983; Vincx et al., 1994).

This study tests the hypothesis that organic enrichment in the form of a whale-fall event will cause an increase in the abundance of deep-sea benthic nematodes.

2. Materials and methods

The study site was an experimentally implanted sub-adult gray whale carcass (*Eschrichtius robustus* Gray, 1864), which weighed approximately 35×10^3 kg when it was placed at 1675 m depth in the Santa Cruz Basin (33° 29.6′ N, 119° 22.0′W; Fig. 1) in April 1998 (Smith and Baco, 2003). The sediment surrounding the carcass was sampled by DSRV *Alvin* at 1.5 and 18 months after implantation, in June 1998 and October 1999, from the R.V. *Atlantis*.

Transects were randomly selected radiating outward from the whale carcass. Along each transect tube cores of 6.7 cm internal diameter (35.26 cm^2) were taken at distances of 0, 1, 3, 9 and 30 m. All meiofaunal samples were collected along a subset of the macrofaunal transects. Samples obtained are listed in Table 1.

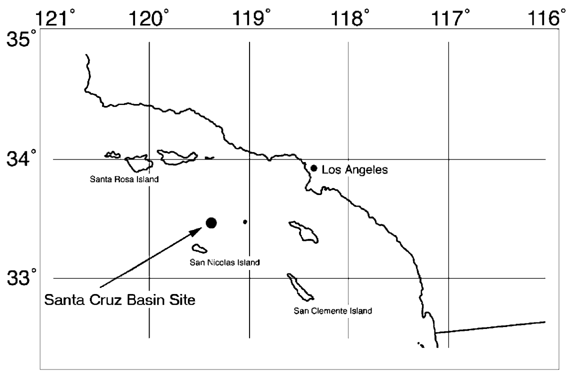

Fig. 1. Map of the study area showing the location of the whale carcass.

Following recovery, nematode cores were transferred to a constant temperature room (2–4°C) where they were sliced at 1 cm vertical intervals down to a final sediment horizon of 5 cm. The samples were fixed in formaldehyde buffered with sodium borate and diluted to 4% v/v with filtered seawater.

Nematodes were extracted in two stages: by water decantation to eliminate the clay fraction and larger particles such as sand grains, pebbles and general detritus, followed by extraction in Ludox-TM 50 (specific gravity = 1.15) to separate the nematodes from the finer silt fractions (Platt and Warwick, 1983). Extracted nematodes were counted under a low-power dissecting microscope and, where abundance was high, the sample was placed in a sample splitter and sub-sampled (Elmgren, 1973). The 0–1 cm sediment horizon of all samples was analysed for nematode abundance. In addition, the vertical pattern of nematode abundance was determined in the deeper sediment horizons (1–2, 2–3, 3–4 and 4–5 cm) of a single sample taken adjacent to the carcass (0 m), see Table 2.

Macrofauna were collected with 7 cm diameter core tubes (38.48 cm^2 in area) or 100 cm^2 Eckman cores. Cores were taken, as with the nematode samples, along transects starting from random points around the carcass. The top 10 cm of sediment were extruded from each core, fixed in 4% formaldehyde–seawater solution, washed on a 300 μm sieve, stained in Rose Bengal and then sorted under dissecting microscopes (Smith et al., 2002).

Statistical analyses, including regressions and Student's *t*-tests, were carried out using the MINITAB® statistical package and curves were fitted with CurveExpert.

3. Results

After both 1.5 and 18 months, nematode abundance increased with distance from the carcass (Table 1 and Fig. 2). The data are highly variable (see standard deviations in Table 3) as is

Table 1
Sample information and nematode abundance as numbers per core and per 10 cm^2 from the 0–1 cm sediment horizon on each of the two sampling occasions

Year	Sample	Distance from carcass (m)	Abundance (ind. /core)	Abundance (ind. /10 cm^2)
1998	AD 3227 TC 7	0	242	68.69
	AD 3227 TC 8	0	90	25.55
	AD 3227 TC 13	0	166	47.12
	AD 3227 TC 9	1	301	85.43
	AD 3227 TC 10	1	128	36.34
	AD 3227 TC 17	3	306	86.86
	AD 3227 TC 14	9	806	228.78
	AD 3227 TC 15	9	735	208.63
	AD 3227 TC 18	9	181	51.38
1999	AD 3483 TC 18	0	88	24.98
	AD 3484 TC 1	0	136	38.60
	AD 3484 TC 6	0	155	43.99
	AD 3483 TC 2	1	73	20.73
	AD 3484 TC 5	1	57	16.18
	AD 3483 TC 10	3	75	21.29
	AD 3484 TC 15	3	42	11.92
	AD 3484 TC 12	9	73	20.73
	AD 3484 TC 13	9	71	20.16
	AD 3485 TC 1	9	2261	641.79
	AD 3485 TC 19	30	5552	1575.95
	AD 3485 TC 20	30	4272	1212.61

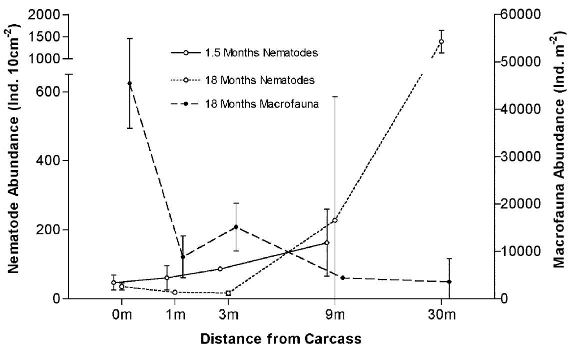

Fig. 2. Mean nematode abundance in the 0–1 cm sediment horizon (at 1.5 and 18 months) and mean macrofaunal abundance at 18 months ± 1 standard error (Smith et al., 2002) plotted against distance from whale carcass. NB There are no error bars given for the nematode point for 1.5 months at 3 m as only one replicate was available.

normally found in nematode abundance data (Rice and Lambshead, 1994). The linear regression of nematode abundance with distance from the carcass as the predictor is $y = 154x - 177$, $R^2 = 83.4\%$, $p = < 0.001$. The regression for the 1.5 month data alone is $y = 45.2x + 168$, $R^2 = 52.1\%$, $p = < 0.028$, and for the 18 month data $y = 164x - 228$, $R^2 = 87.1\%$, $p = < 0.001$.

However, the 18 month data show low abundance adjacent to the carcass and out to the 3 m distance before rising to a higher abundance at the 9 m distance than that recorded at the 1.5 month sampling period. This pattern is best fitted by a second-order polynomial ($y = 16.288x^2 - 71.279x + 123.97$, $R^2 = 99.9\%$, $p = < 0.01$).

Measured over 0–9 m, mean nematode abundance at 18 months (303 $sample^{-1}$) was not significantly different from that at 1.5 months (328 $sample^{-1}$) using Student's *t*-test. This result is probably due to the high variability in the abundance values recorded at 9 m and, in particular, to a single high value (2261 $sample^{-1}$) recorded at 18 months (Table 1). Omitting the 9 m stations from this analysis, the resulting mean nematode abundance over 0–3 m at 18 months (mean = 89.4 sample^{-1}) was significantly lower from that at 1.5 months (mean = 205.5 sample^{-1}) using a t-test ($p = 0.028$).

Nematode abundance at 18 months shows an inverse non-linear relationship to the macrofaunal abundance at the same point (Fig. 2). The relationship between macrofauna and nematode abundance is shown in Fig. 3 ($y = 18.57x^{(1239/x)}$, $R^2 = 99.7\%$).

Nematodes were distributed superficially within the sediment horizons from a single core adjacent to the whale carcass at 18 months (Table 2). Over 80% of all individuals were found in the upper 2 cm of sediment, the majority of which (66.7%) were found in the upper centimetre.

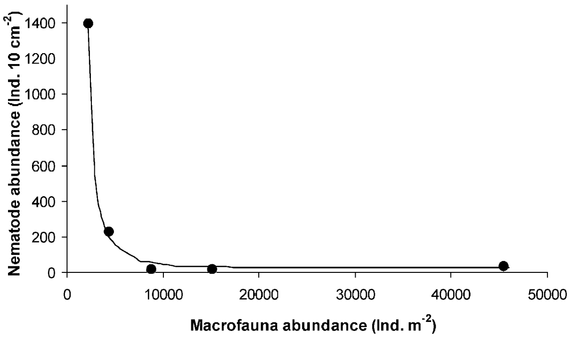

Fig. 3. Nematode abundance (10 cm^{-2}) plotted against macrofauna abundance (m^{-2}) at 18 months (no macrofauna data are available from 1.5 months).

Table 2
Vertical distribution of nematodes in 1 cm sediment horizons in core AD3483 TC 18 (18 month sample) adjacent to the whale carcass

Sediment horizon (cm)	Abundance (ind. /core)	Abundance (ind. /10 cm^2)	Abundance (%)
0–1	88	24.98	66.67
1–2	20	5.67	15.15
2–3	14	3.97	10.61
3–4	6	1.70	4.55
4–5	4	1.13	3.03

4. Discussion

The experimental design of this study was primarily the result of sample availability and replication was either limited or not possible. Given the known patchiness of deep-sea nematode populations (Rice and Lambshead, 1994) this is a serious limitation. Nevertheless, because nothing is known of the impact of whale falls on any meiofaunal taxa we considered it worthwhile to carry out a preliminary investigation with the limited cores available.

The original hypothesis that nematode abundance would be increased by organic input from the carcass between 1.5 and 18 months is rejected as the reverse occurred (the hypothesis would suggest that nematode numbers should increase with proximity to the carcass). However, the null hypothesis, that the carcass should have no effect on nematode abundance, is also rejected.

The positive correlation between nematode abundance and distance from the carcass, which appeared to operate out to at least 30 m distance, would suggest that the presence of the carcass has decreased nematode abundance in its immediate vicinity.

Table 3 shows nematode abundance from some of the few bathyal locations thus far studied. Nematode abundance immediately around the whale-fall (0–3 m) is the lowest ever recorded at these depths and is significantly lower than that in the nearby San Diego Trough, which was itself unusually low (Lambshead et al., 1994). Although the difference in the means is small (Table 3), it is statistically significant. The single core analysed for nematode vertical abundance in the sediment horizons to 5 cm (Table 2) suggests that the low 0–1 cm abundance is not caused by vertical migration of the nematodes to deeper depths (Gooday et al., 1996; Moodley et al., 2000; Vanreusel et al., 1995).

Mean nematode abundance at 30 m (1394.28 per 10 cm^2) was almost as high as at the heavily phytodetritus-enriched, oxygen-minimum zone in the Arabian Sea (1658.0 per 10 cm^2) (Cook et al., 2000) and an order of magnitude higher than the abundance reported from the Atlantic and Mediterranean (ca. 250 per 10 cm^2) (Soetaert et al., 1991, 2002). There is thus an implication that, at

Table 3
Bathyal nematode abundance with standard deviations from the present study and for a station in San Diego Trough (Lambshead et al., 1994), two combined stations in the Rockall Trough (Lambshead et al., 1994), two stations in the Arabian Sea (Cook et al., 2000), one station in the Mediterranean (Soetaert et al., 1991), and 6 stations from the Galician Margin (Soetaert et al., 2002). Where possible, the mean nematode abundance at the seven sites is compared with the 0–3 m whale fall abundance, from both the 1.5 and 18 month sampling periods, using a Student's *t*-test

Station	Sampling depth (m)	Mean nematode abundance (ind. /10 cm^2 and ± 1 SD)	Significantly greater than (>) or less than (<) abundance 0–3 m from whale fall
Whale Fall Abundance 0–3 m	1675	40.6 ± 25.3	
Whale Fall Abundance 9 m	1675	195.1 ± 837	
Whale Fall Abundance 30 m	1675	1399.2 ± 257	
San Diego Trough	1050	68.5 ± 19.49	> ($p = 0.022$)
Rockall Trough	835 and 1474	231.0 ± 109	> ($p = 0.008$)
Arabian Sea	700 and 1250	1658.0 ± 919	> ($p = 0.008$)
Mediterranean Sea (NB 0–5 cm sediment horizon)	1220	267.5	Data not available
NE Atlantic Galician Margin	733–2625	251.0 ± 132	> ($p = 0.003$)

this distance from the whale-fall, the nematode abundance is enhanced by organic enrichment.

Lambshead et al. (1994) discussed why the bathyal region off southern California might show low nematode abundance. These authors rejected low oxygen as a cause and further work by Cook et al. (2000) in the Arabian Sea has supported the view that low oxygen has little effect on nematode abundance. Lambshead et al. (1994) suggested that unusually high biological activity from larger benthos had caused low nematode abundance through competition or predation. Similar results have been reported from shallow water studies (Hanson et al., 1981; Tietjen, 1971; Warwick et al., 1986). The inverse relationship between macrofauna and nematodes as shown in Fig. 3 might reflect predation, competition or other interactive effects. This suggestion has been made to explain the similar inverse relationships between macro- and meiofaunal biomass in the Baltic Sea (Elmgren, 1978).

The inverse relationship between macrofauna and nematode abundance is consistent with a hypothesis that nematode abundance is suppressed in the immediate vicinity of the carcass at 18 months because of high macrofaunal activity. The increased nematode abundance at 30 m after 18 months may be a response to organic enrichment from the whale fall occurring where macrofaunal abundance no longer limits nematode densities.

These results suggest that biological interactions can be important in structuring meiofaunal assemblages in the deep sea and that simple measures of nematode abundance may be misleading.

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