

# Meiobenthic community underneath the carcass of a stingray: a snapshot after natural death

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**ABSTRACT:** The impact of large food falls and carrion on meiobenthic communities remains little understood. The objective of the present study was to investigate whether the carcass of a stingray, encountered fortuitously in an Australian estuary, affects the underlying meiobenthic community, in particular nematode assemblages. The integrity of the skeleton and the low redox values observed under the carcass suggest that the cadaver had been slowly and chiefly decomposed by microbes. The abundance and number of meiofaunal taxa, as well as nematode abundance and nematode-species richness, were significantly lower under the carcass when compared to samples outside the carcass. Nonetheless, a few nematode species, typical of hypoxic/anoxic sediments, were more abundant under the carcass. Interestingly, all these species were absent or rare in samples near, but not under, the carcass, suggesting that they may take advantage of the reduced environment created by the carcass and the consequent lack of competition to prosper. As observed for other marine environments, carcasses in estuaries create a microhabitat that supports a characteristic meiobenthic fauna, distinct from those inhabiting the surrounding sediments, but similar to those of reduced habitats.

**KEY WORDS:** Meiofauna · Food fall · Nematode communities · Estuary · Australia

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## INTRODUCTION

Nekton carcasses from fishes, birds, cetaceans and other large animals have pronounced effects on benthic organisms from a variety of aquatic environments (Ramsay et al. 1997). Once deposited on the bottom, carcasses attract several opportunist species and are usually consumed within a few days. In the deep sea, for instance, the carcasses of whales attract dense aggregations of mobile scavengers, including dramatically increased numbers of macrofaunal species, several being unique to the carcasses (Smith et al. 2002, Smith & Baco 2003, Dahlgren et al. 2004, Glover et al. 2005, Fujikura et al. 2006). In the North Sea, the fish discards produced by the beam-trawl fishery attract several species of invertebrate scavengers, such as brittle stars, starfish, gadoids, and hermit and swimming crabs (Kaiser & Spencer 1994, Groenewold & Fonds 2000). In the same way, the upstream migration and

subsequent death of salmon and other cyprinids attracts the larvae of different insects (Chaloner et al. 2002). Although the importance of carcass decomposition as a transfer mechanism for nutrients and energy across trophic levels and ecosystem boundaries has been widely recognized (King et al. 2007), benthic studies focusing on its ecological importance have predominantly investigated the effect of carcasses on macroorganisms. To date there are few data available on the impact of carcasses on smaller meiobenthic organisms (organisms retained by 0.32 µm mesh and passing through 0.5 mm mesh; Giere 2009), the numerically dominant metazoans representative of the benthos of most marine and brackish water habitats (Heip et al. 1985).

Studies on the meiofauna associated with carrion showed varying results. In the deep sea, the abundance of the dominant group of meiofauna, the nematodes, was negatively affected by whale carcasses

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(Debenham et al. 2004, Pavlyuk et al. 2009). Shallow-water studies, on the other hand, did not observe significant differences in nematode abundances between samples with and without carrion (Gerlach 1977, Ólafsson 1992, Franco et al. 2008). A common finding among these studies is that carrion significantly affected nematode composition, favoring a few genera but not others (Gerlach 1977, Ólafsson 1992, Franco et al. 2008, Pavlyuk et al. 2009). In addition to these studies, there is evidence from the North Sea that the free-living marine nematode *Pontonema vulgare* is attracted to dead and moribund organisms (Lorenzen et al. 1987, Prein 1988). Given such paucity of data, the effect of carrion on meiobenthic organisms remains little understood.

The objective of the present study was to investigate how the carcass of a stingray, encountered fortuitously in an Australian estuary, affected the meiobenthic community, in particular nematode assemblages. Specifically, the study examined the hypothesis that no differences occur in meiofaunal and nematode abundances, number of taxa, or faunal composition between samples taken underneath this carcass and those taken nearby. Additionally, the present study aimed at investigating whether there is a specialized nematode scavenger assemblage or whether opportunistic/generalist species take advantage of the new environment created by the carcass.

## MATERIALS AND METHODS

**Study area and the carcass.** The carcass of a stingray was found in December 2009 at 0.5 m water depth in Basin View, St. Georges Basin, in the southeast of New South Wales, Australia (35° 5' 43" S, 150° 33' 29" E). The basin covers an area of approximately 42 km<sup>2</sup> and has a catchment area of 348 km<sup>2</sup>. St. Georges Basin is relatively shallow (0 to 10 m water depth), mesotrophic to eutrophic, and incorporates a wide variety of sedimentary habitats: sand banks, saltmarshes, seagrasses, rocky reefs, mangroves, intertidal flats, fluvial delta and a channel (Murray et al. 2005). Like other Australian estuaries, St Georges Basin receives little input of freshwater and is highly saline throughout the year (35 psu at the sampling site) (Hutchings 1999). The basin is permanently open to the ocean, with little water exchange due to the long and narrow outlet. The benthic environment at the basin is variable; overall, diatoms are the primary source of organic matter, and the organic matter in the sediment is mainly degraded by anaerobiosis (Murray et al. 2005).

The carcass was found lying on bare sediment and was partially degraded (Fig. 1). The skeleton was intact, and the flesh was partially decomposed, mainly on the wings

and tail. The nose was partially covered with sediment and intact. The cadaver formed a black halo in the sediment, indicating the lack of oxygen and presence of sulfides. The skeleton of the carcass measured approximately 60 cm in width. The dead animal probably belonged to the species *Dasyatis brevicauda* Hutton, 1875 or *D. thetidis* Ogilby, 1899 (M. McGruther pers. comm., Australian Museum). Both are widespread, temperate, Southern Hemisphere species recorded in Australia, New Zealand and southern Africa, occurring in a wide variety of habitats including shallow coastal bays, estuaries, lagoons, large inlets, coastal rocky reefs, offshore islands and open sea floor (Duffy & Paul 2003, Stevens 2008). Although very little is known about their populations, during summer, *D. brevicauda* forms large aggregates for mating (Duffy & Paul 2003). Recreational fishers and bycatch from inshore trawling are probably the main causes of their decline and the production of cadavers (Stevens 2008).

**Sampling and sample processing.** Four samples (core of 2 cm inner diameter and 3 cm in depth) of meiofauna were taken from underneath the stingray, and 4 samples were taken from adjacent sediments outside the carcass. No samples were taken inside or on the carcass. The samples 'outside' the carcass were randomly taken up to 1 m from the cadaver. Another 3 samples of the same size were taken under and outside

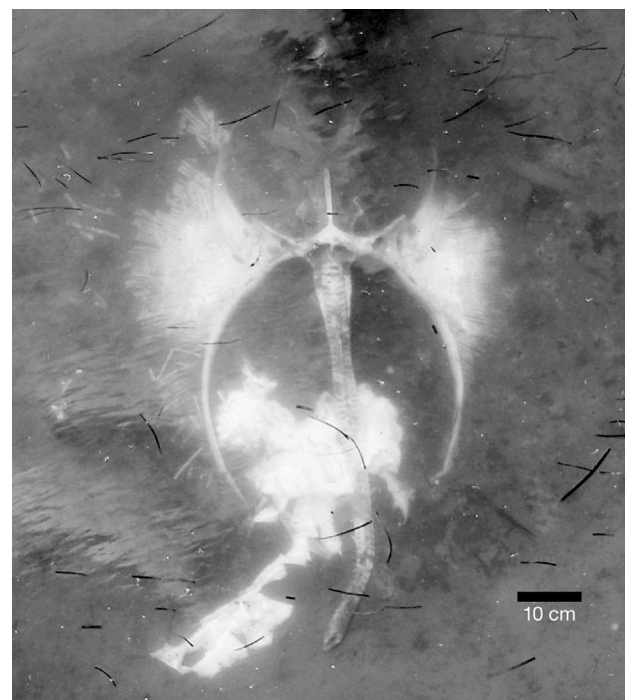


Fig. 1. Carcass of a stingray measuring ca. 60 cm in width found at a water depth of 0.5 m in St. Georges Basin, NSW, Australia. Black strips on the water surface are leaves of *Zoostera capricorni* from adjacent areas

the carcass to determine total organic matter and redox potentials. Redox potentials were analyzed in the surface layer.

Samples for the investigation of meiofauna were fixed in 10% formalin immediately after sampling. In the laboratory, samples were washed through a 45  $\mu\text{m}$  sieve, extracted by flotation with a solution of colloidal silica (LUDOX TM-50; density: 1.18  $\text{g cm}^{-3}$ ), stained with Rose Bengal and sorted under a low-power stereo microscope (Heip et al. 1985). All nematodes from samples under the carcass were picked out, transferred to anhydrous glycerol and mounted on permanent slides for identification. From samples outside the carcass, 10% of all nematodes were randomly picked out and mounted on permanent slides for identification. Nematodes were identified under the microscope to genus level (Warwick et al. 1998) and were separated into putative morphospecies, while the other groups were identified to a higher taxonomic level (phylum or class). All material has been deposited in the Australian Museum.

Sediment total organic matter (OM) was estimated by dry weight after combustion at 550°C for 4 h. Redox potential was measured at the sediment surface using a Metrohm AG 9109 Herisau Combined Pt-wire electrode, with an Ag/AgCl reference electrode. The instrument was calibrated using Orion Application Solution ORP Standard 967961, and all redox readings were corrected for  $\text{E}^{\text{H}}_{\text{Ref}} = -210 \pm 3 \text{ mV}$ , i.e. reported redox potentials are versus that of the hydrogen electrode,  $\text{E}^{\text{H}}_0 = 0 \text{ mV}$ .

**Data analysis.** As univariate descriptors of the fauna, abundance, number of higher meiofaunal taxa and number of nematode species were considered. ANOVA was applied to test for differences in all univariate measures between under the carcass and outside the carcass. Differences in the multivariate structure of meiofaunal communities and nematode assemblages were analyzed by means of analysis of similarity (ANOSIM; Clarke & Gorley 2006). Multivariate analyses were conducted on Euclidean-distance similarity matrices. For the meiofauna, presence/absence data were used to remove the relative importance of nematodes. For nematodes, data were standardized to eliminate the effect of density, and no transformation was applied. To visualize the multivariate structure of the meiofaunal and nematode assemblages, non-metric multidimensional scaling ordination (nMDS) was performed based on the same Euclidean-distance similarity matrix. To identify which nematode species were the most important in characterizing differences between samples from under and outside the carcass, a similarity percentage (SIMPER) analysis was conducted. All multivariate analyses were performed with PRIMER v6.0 (Clarke & Gorley 2006).

## RESULTS AND DISCUSSION

The integrity of the skeleton, the presence of remaining flesh and the apparent absence of macroinvertebrates on the carcass (Fig. 1) suggest that the cadaver had been slowly and chiefly decomposed by microbes. Although no macrofaunal or microbial samples were taken, the low redox values observed in surface sediments underneath the carcass in comparison to the samples from outside the carcass (Fig. 2) provide additional evidence for strong microbial degradation of the stingray cadaver, as this was probably a result of higher oxygen consumption due to microbial decomposition of the carrion (Tang et al. 2006). Larger scavengers, like starfish, fish and amphipods can consume large amounts of food falls in <5 d (Kaiser & Moore 1999). However, microbial decomposition is much slower, taking several weeks to months, depending on the local conditions, to completely decompose a fish carcass (Minshall et al. 1991, Parmenter & Lamarra 1991, Fenoglio et al. 2005, Premke et al. 2010). This much slower decomposition is partly due to the fact that scavenger microbes produce noxious chemicals that deter animal scavengers (Burkepile et al. 2006).

Although there was a significant reduction in redox potential under the stingray, an indication of lack of oxygen and presence of sulfides, sediment samples near the carcass were also anoxic (Fig. 2). These values were nevertheless within the range reported for vegetated and unvegetated sites in St. Georges Basin (below -100 mV; Murray et al. 2005, McKinnon et al. 2009), suggesting that values sampled outside the carcass are natural for the study area and probably free of effects from the carcass itself. There were no significant differences in the concentrations of sediment

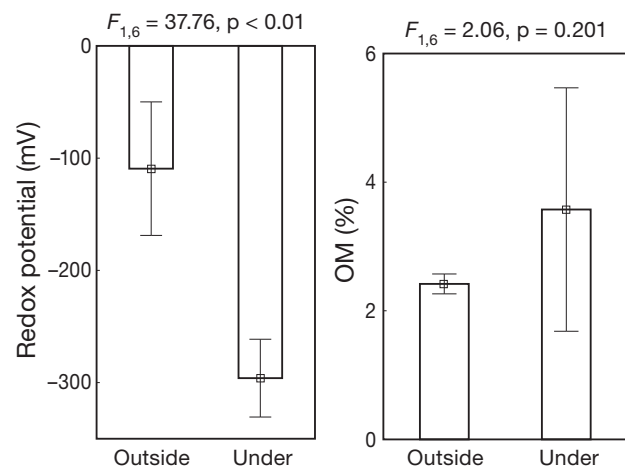


Fig. 2. Redox potentials and organic matter content (OM) from samples taken outside and under the carcass of a stingray. Data are mean  $\pm$  SD. ANOVA results are given above each panel

organic matter between samples taken under and outside the stingray (Fig. 2). This was probably due to the high variability in organic matter values from samples underneath the carcass, since a mosaic of spots with and without remaining flesh was observed. Outside the carcass no flesh was observed.

A total of 12 meiofaunal taxa were encountered (Appendix 1). Meiofaunal abundance and the number of meiofaunal taxa per core were significantly lower underneath the carcass compared to samples outside (Fig. 3a,b). Additionally, meiofaunal composition underneath the carcass was significantly different from samples taken outside the carcass ( $R = 0.839$ ,  $p < 0.05$ ; Fig. 4a). Whereas no meiofaunal taxon occurred exclusively under the carcass, several taxa such as nauplii, turbellarians, oligochaetes, isopods and kinorhynchs were only found in samples outside the carcass (Appendix 1). Other taxa, such as acari and polychaetes, were found only once (as singletons in only 1 sample) under the stingray carcass, but otherwise were restricted to samples outside the carcass. As observed for other aquatic systems (Debenham et al. 2004, Pavlyuk et al. 2009, Premke et al. 2010), the encountered stingray carcass had a negative impact on meiofaunal abundances. Such a negative impact is probably due in part to hypoxia and the presence of toxic sulfides in sediments underneath the carcass, since most of the affected taxa (i.e. taxa that were found in control samples but were not sampled underneath the ray) are known to be more abundant in oxic than in anoxic conditions (Modig & Ólafsson 1998, Fonseca et al. 2011).

Among the meiofaunal taxa that occurred in sediments underneath the carcass, nematodes dominated all samples, representing 82.2 to 94.7% of all organisms collected per sample. In total, 29 nematode species were identified (Appendix 1). They showed similar trends to those of total meiofauna (i.e. significantly lower abundance and species richness under the carcass; Fig. 3c,d). Likewise, samples from outside and under the carcass also showed distinct nematode assemblages ( $R = 0.59$ ,  $p < 0.01$ ; Fig. 4b). In contrast to other meiofaunal taxa, however, there were some nematode species that occurred exclusively under the carcass, such as *Adoncholaimus* sp. 1, *Calomicrolaimus* sp. 1 and *Microlaimus* sp. 1 (SIMPER analysis; Table 1, Appendix 1). *Adoncholaimus* species are facultative predators that exhibit a variety of feeding strategies (Moens et al. 1999). *A. thalassophygas* De Man, 1876, for example, can benefit from the fermentation products (acetate) of anoxic habitats (Riemann et al.

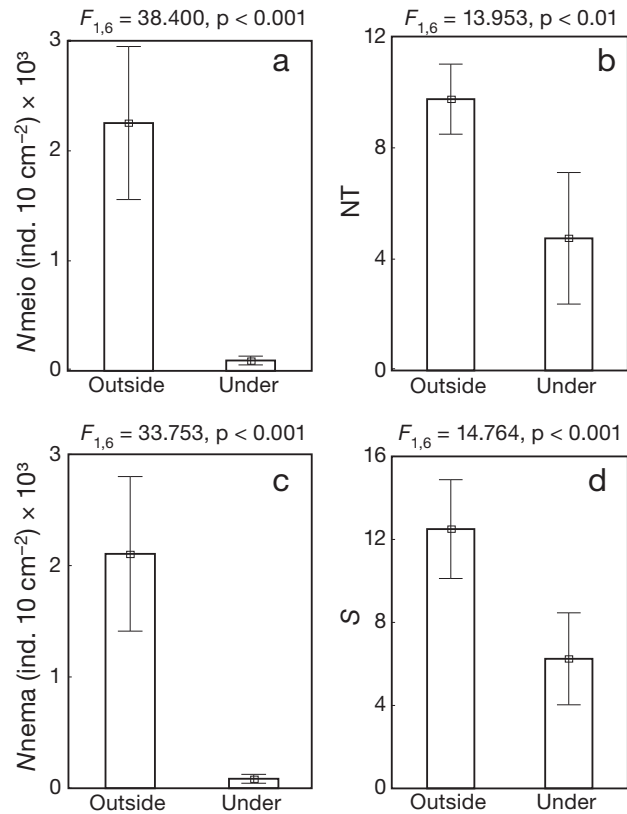


Fig. 3. Meiofaunal and nematode abundances (*Nmeio* and *Nnema*, respectively), number of higher taxa (NT) and number of nematode species (*S*) in samples taken outside and under the carcass of a stingray. Data are mean  $\pm$  SD. ANOVA results are given above each panel

1990) and are attracted to patches of intense microbial degradation (Riemann & Schrage 1988). Studies on other co-familial genera (*Oncholaimidae*) have also reported members of this family scavenging on dead and moribund macrofauna, as well as being associated with rotted seaweed (*Ulva* sp.), and occurring in highly polluted areas (Lorenzen et al. 1987, Bett & Moore 1988, Prein 1988), under seagrasses (Fonseca et al. 2011) and under the noxious seaweed *Caulerpa taxifo-*



Fig. 4. Ordination plots of multidimensional scaling for (a) the meiofaunal community (presence and absence) and (b) nematode assemblages (standardized data) from samples taken outside (black dots) and under the carcass of a stingray (open squares)

Table 1. Similarity percentage (SIMPER) results for the nematode assemblage of samples from outside vs. samples from under the carcass. Average dissimilarity = 60.33. Av.N: average abundance (10 cm<sup>2</sup>); Cont%: contribution for the dissimilarity in percentages

Species	Outside Av.N	Under Av.N	Cont%
<i>Metalinhomoeus</i> sp. 1	5.89	29.74	19.76
<i>Terschellingia</i> sp. 1	17.26	29.76	18.82
<i>Perspiria</i> sp. 1	33.50	12.39	18.64
<i>Gomphonema</i> sp. 1	11.54	4.72	6.79
<i>Daptonema</i> sp. 1	7.06	10.07	6.36
<i>Adoncholaimus</i> sp. 1	0.00	6.94	5.76
<i>Parodontophora</i> sp. 1	6.06	0.00	5.02
<i>Sabatieria</i> sp. 1	6.44	0.68	4.78
<i>Thalassomonhystera</i> sp. 1	3.76	0.00	3.12
<i>Calomicrolaimus</i> sp. 1	0.00	3.63	3.01

*lia* (F. Gallucci et al. unpubl. data). These observations suggest that oncholaimids tolerate the presence of sulfides, are attracted to putrefied conditions and are able to utilize (parts of) the nutritious mixture of the body remains of dead organisms, bacterial epigrowth, dissolved glucose and the end products of fermentation (Lopez et al. 1979, Riemann et al. 1990, Moens et al. 1999).

The other 2 species restricted to the carcass, *Calomicrolaimus* sp. 1 and *Microlaimus* sp. 1 (Appendix 1), are classified as epigrowth feeders, feeding mainly on diatoms and microalgae (the 2A feeding group; Wieser 1953). *Calomicrolaimus* is one of the dominant genera in anoxic sediments on the Isle of Sylt, Germany (Wetzel et al. 1995), and *Microlaimus* is considered an opportunistic genus (Lee et al. 2001, Gallucci et al. 2008), which is also associated with naturally hypoxic environments such as sediments colonized by seagrasses (Fonseca et al. 2011) and algal mats (Wetzel et al. 2002). The study area of St. Georges Basin is characterized by large areas of seagrasses (3.170 km<sup>2</sup>), salt-marshes (0.149 km<sup>2</sup>) and mangroves (0.276 km<sup>2</sup>) (Murray et al. 2005), all known to have naturally anoxic sediments. The fact that these 3 species were not encountered in the samples near the carcass suggests they are probably rare in bare sediments and were originally from the surrounding vegetated sites where the sediment is also depleted in oxygen. These species took advantage of the 'favorable' conditions created by carcass decomposition to flourish. Like *Adoncholaimus*, these genera probably do not feed directly or exclusively on the carcass, but take indirect advantage of the lack of competition in the reduced and toxic environment. Other nematode genera that were favoured under the carcass were *Terschellingia* sp. 1 and *Metalinhomoeus* sp. 1 (SIMPER analysis; Table 1). Both genera are well known to contain species that can tolerate

anoxic conditions and organic enrichment (Steyaert et al. 2007). Finally, all 5 species mentioned above are long and slender, a morphological adaptation of 'thiobios' nematodes to low oxygen tension and high concentrations of dissolved organic matter (Jensen 1986, 1987, Wetzel et al. 1995).

The present study is limited in the number of experimental units (i.e. carcasses), and we have no information about when the carcass was deposited, hindering full assessment of the effects of carcasses on the meiobenthos. Nonetheless, the results demonstrate that a carcass in estuarine sediments may support a characteristic nematode fauna, distinct from that inhabiting the surrounding sediments, but similar to those of reduced environments. Similar observations have been made for meiofauna of sand beaches (Gerlach 1977), estuarine intertidal areas (Franco et al. 2008) and subtidal areas (Ólafsson 1992). In all these studies it was determined that the nematode species associated with carrion were inhabitants of reduced habitats, which are commonly designated as 'thiobios' (Giere 2009). Such similarity between habitats gives further support to the hypothesis that carrion maintains a specialized set of species across a variety of marine environments (Britton & Morton 1994), and is of primary importance regarding the distribution of meiobenthos (Ólafsson 1992).

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**Appendix 1.** Absolute abundance of higher meiofaunal taxa (ind. 10 cm<sup>-2</sup>) and relative abundance of nematode species in each replicate (A to D) encountered outside and under the carcass of a stingray in St. Georges Basin, NSW, Australia

	Outside the carcass				Under the carcass			
	A	B	C	D	A	B	C	D
<b>Higher meiofaunal taxa</b>								
Nematodes	7272	8183	7605	3391	339	393	110	232
Copepods	226	430	308	327	6	22	16	19
Nauplii	82	25	66	72	0	0	0	0
Ostracods	31	6	6	25	6	3	3	3
Kinorhynchs	19	19	28	13	0	0	0	0
Polychaete larvae	13	0	31	13	0	0	0	3
Polychaetes	9	9	9	0	3	0	0	0
Isopods	9	3	0	3	0	0	0	13
Turbellarians	9	0	9	0	0	0	0	0
Oligochaetes	9	3	0	6	0	0	0	0
Acari	6	0	6	3	0	0	0	3
Gastropods	0	0	3	3	3	0	0	6
<b>Nematode species</b>								
<i>Perspiria</i> sp. 1	19.6	32.7	53.8	15.9	3.6	8.7	8.0	15.5
<i>Terschellingia</i> sp. 1	15.0	35.4	7.1	5.3	47.0	20.2	0.0	27.6
<i>Metalinhomoeus</i> sp. 1	13.8	5.0	2.0	3.8	15.7	35.6	32.0	12.1
<i>Daptonema</i> spp.	6.7	1.5	8.7	18.9	10.8	12.5	12.0	1.7
<i>Gomphonema</i> sp. 1	14.2	3.8	6.7	27.3	7.2	4.8	0.0	3.4
<i>Sabatieria</i> sp. 1	14.2	3.1	4.7	5.3	2.4	1.0	4.0	1.7
<i>Parodontophora</i> sp. 1	6.7	7.7	3.2	7.6	0.0	0.0	0.0	1.7
<i>Adoncholaimus</i> sp. 1	0.0	0.0	0.0	0.0	0.0	0.0	20.0	0.0
<i>Thalassomonhystera</i> sp. 1	2.1	1.2	4.0	6.1	0.0	1.0	0.0	0.0
<i>Theristus</i> spp.	1.7	2.3	1.2	0.8	2.4	0.0	4.0	0.0
<i>Pseudochomadora</i> sp. 1	0.4	1.5	0.4	3.8	0.0	0.0	4.0	1.7
<i>Calomicrolaimus</i> sp. 1	0.0	0.0	0.0	0.0	2.4	5.8	0.0	3.4
<i>Ptycholaimellus</i> sp. 1	1.3	0.4	2.4	3.0	0.0	2.9	0.0	0.0
<i>Cobbia</i> sp. 1	2.1	0.4	2.4	0.8	0.0	0.0	0.0	1.7
<i>Paracyatholaimus</i> sp. 1	2.1	0.0	1.6	0.0	0.0	0.0	0.0	1.7
<i>Spirinia</i> sp. 1	0.0	0.0	0.4	0.0	0.0	2.9	0.0	1.7
<i>Prochromadorella</i> sp. 1	0.0	0.0	0.0	0.0	0.0	1.0	4.0	0.0
<i>Chromadora</i> sp. 1	0.0	0.4	0.0	0.0	0.0	0.0	4.0	0.0
<i>Dorylaimidae</i> sp. 1	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0
<i>Eurystomina</i> sp. 1	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0
<i>Microlaimus</i> sp. 1	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0
<i>Linhomoeus</i> sp. 1	0.0	0.0	0.4	0.0	1.2	0.0	0.0	0.0
<i>Comesa</i> sp. 1	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0
<i>Megadesmolaimus</i> sp. 1	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0
<i>Paralinhomoeus</i> sp. 1	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0
<i>Paracomeseoma</i> sp. 1	0.4	0.4	0.4	0.0	0.0	0.0	0.0	0.0
<i>Chromadorina</i> sp. 1	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0
<i>Desmolaimus</i> sp. 1	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0
<i>Sphaerolaimus</i> sp. 1	0.0	0.4	0.4	0.0	0.0	0.0	0.0	0.0