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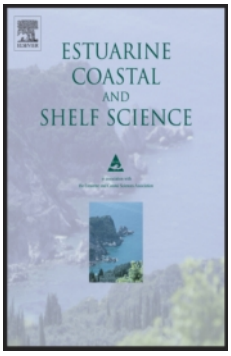

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Authors: M. Hourston, I.C. Potter, R.M. Warwick, F.J. Valesini, K.R. Clarke

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Spatial and seasonal variations in the ecological characteristics of the free-living nematode assemblages in a large microtidal estuary

M. Hourston [a], I.C. Potter [a*], R.M. Warwick [b], F.J. Valesini [a], K.R. Clarke [b],

[a] Centre for Fish and Fisheries Research, School of Biological Sciences and Biotechnology, division of Science and Engineering, Murdoch University, South St, Perth, Western Australia, 6150.

[b] Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth, PL1 3DH, UK

* corresponding author, I. C. Potter:
email: i.potter@murdoch.edu.au
phone: 61 (08) 92398801
fax: 61 (08) 92398899

Abstract

This study has determined the ways in which the density, number of species, species composition and trophic structure of free-living nematode assemblages in the subtidal waters of a large southern hemisphere microtidal estuary change spatially and seasonally, and has explored whether those four biotic characteristics are related to certain environmental factors. Based on data derived from samples collected seasonally at 12 sites throughout the estuary, the densities and number of species of nematodes decreased progressively with distance from estuary mouth, to reach a minimum at sites where salinities were most variable, and then increased slightly in the uppermost part of the estuary where salinities were least. Densities were also generally greatest in spring, due largely to increases in the abundance of epistrate-grazing species at this time and thus when the amount of primary food (microphytobenthos) peaked. The spatial distribution of the composition of the nematode assemblages was closely correlated with salinity and, to a lesser extent, grain-size composition and amount of particulate organic material in the sediment (%POM). Although species composition changed sequentially along the estuary, the change was particularly pronounced between sites above and below the area where salinities started to decline markedly and become more variable and %POM increased markedly. This reflected, in particular, far greater abundances of *Spirinia parasitifera* at the six downstream sites and of *Theristus* sp. 1 at the six sites further upstream. Species composition underwent pronounced seasonal cyclical changes at all sites, presumably reflecting interspecific differences in the timing of peak reproduction and thus of recruitment. The trophic structure of the nematode assemblages changed both spatially and temporally in relation to the relative abundance of different food sources. Thus, for example, non-selective deposit feeders, such as *Theristus* sp. 1, dominated samples in the upper estuary, where %POM was by far the greatest, and was rare or absent at downstream sites. Conversely, epistrate grazers, such as species of the Chromadoridae, were most abundant at downstream sites in spring, when the density of the microphytobenthos reached its maximum.

Keywords: microtidal estuary, nematodes, number of species and density, species and trophic compositions, environmental factors

1. Introduction

Nematodes, which occur in every habitat that can support life, are the most numerous of all metazoans and one of the most diverse metazoan taxa in marine waters (Platt and Warwick, 1980). Free-living nematodes play an important functional role in aquatic ecosystems (Platt and Warwick, 1980; Coull, 1999). For example, they are of major energetic importance in benthic environments as they represent a significant part of the diet of many aquatic organisms (Gee, 1989; Coull, 1990) and facilitate the mineralization of organic matter (Coull, 1999; Riera and Hubas, 2003). Furthermore, as nematodes are highly habitat specific (Findlay, 1981; Joint et al., 1982), changes in the composition of their assemblages are good indicators of when changes are occurring in the environment, either naturally (McLachlan, 1978; Guo et al., 2001; Nozais et al., 2005) or as a result of anthropogenic activities (Coull and Chandler, 1992; Kennedy and Jacoby, 1997; Bongers and Ferris, 1999).

The environmental resources of free-living nematodes are partitioned among those species in different ways, and this is particularly true of its food resources, a feature reflected in the high degree of feeding selectivity exhibited by the various species (Moens and Vincx, 1997). As the latter selectivity is reflected, in turn, by marked differences in the physiognomic characteristics of the buccal cavities of nematode species, the particular characteristics of each species can be used to deduce the functional feeding group to which that species belongs (Wieser, 1953; Moens and Vincx, 1997). The densities of one of these groups, i.e. epistrate grazers, often peak at the time of year when the microphytobenthos is also at its maximum (Tietjen, 1969; Skoolmun and Gerlach, 1971; Hodda and Nicholas, 1986).

The species composition of nematodes in the macrotidal estuaries of temperate regions in the northern hemisphere have been shown to be influenced by salinity and the characteristics of the sediment (Warwick, 1971; Austen and Warwick, 1989; Soetaert et al., 1995). Although the density and diversity of nematodes were also found to be related to salinity in certain of these estuaries (Soetaert et al., 1995), this was not universally the case in this region (Warwick, 1971; Warwick and Price, 1979; Austen and Warwick, 1989). Furthermore, the conclusions drawn as to whether the species compositions of nematodes in these macrotidal temperate estuaries undergo conspicuous seasonal changes have not been unanimous (c.f. Tietjen, 1969; Warwick, 1971). The only study to have specifically explored the ways in which the nematode faunas of a microtidal southern hemisphere estuary vary spatially and seasonally are those of Hodda and Nicholas (1985; 1986). In their study of the fauna in the intertidal zone of the mangrove-dominated

Hunter River Estuary in temperate eastern Australia, those workers found that the densities were correlated most closely with elevation above low tide mark and pollution levels but neither with salinity nor the median grain-size of the sediment. Although the densities and species compositions at the different sampling sites changed during the year, they did not follow a consistent pattern across all sites, which was attributed to the influence of "non-seasonal environmental changes". In another study, Hodda (1990) concluded that variations among nematode faunas at sites in the Hunter River estuary and two other estuaries on the same coast were related to oxygen penetration, organic content and grain-size composition of the sediment.

The large estuaries of south-western Australia, such as that of the Swan River, and like many of those in south-eastern Australia and southern Africa, are microtidal and often comprise three morphologically distinct regions (Chalmer et al., 1976; Bird, 1984; Potter et al., 1990). The lower estuary consists of a short and narrow entrance channel, which opens into a large and wide central basin region that represents the middle estuary. The latter area is fed by tributary river(s), the downstream reaches of which are saline and constitute the upper estuary. The categorisation of the Swan River Estuary into these three regions was based not only on morphological distinctions, but also on the pattern of distribution of the various species of benthic macroinvertebrates (Chalmer et al., 1976). Subsequent work showed that the compositions of the ichthyofauna, and particularly in the upper region of that estuary, undergo pronounced changes between the wet (low salinity) and dry (high salinity) periods of the year (e.g. Loneragan and Potter, 1990). Other studies on the Swan River Estuary have shown that the densities of microphytobenthos were greatest in the lower estuary (Masini and McComb, 2001) and that the amount of particulate organic material was greatest in the upper estuary (M. Wildsmith, pers. comm.) both of which will inevitably influence the structure of the lower trophic levels in those regions.

As the majority of rainfall, and thus also of freshwater discharge, occurs in winter and early spring in south-western Australia, the salinity in the estuaries of this region declines markedly during that period and then increases slowly during the subsequent months as salt water gradually penetrates upstream (Stephens and Imberger, 1996). However, because tidal action within these estuaries is weak, the salinity at any given site does not undergo marked changes during any tidal cycle. These characteristics contrast markedly with those normally found in macrotidal temperate regions of the northern hemisphere, which tend to be funnel-shaped and not divided into distinct regions, and undergo marked changes in salinity and water level during each tidal cycle.

The present study on the Swan River Estuary represents the first concurrent exploration of the ways in which the density, diversity, species composition and trophic categories of the nematode fauna of the nearshore subtidal sediments of a microtidal estuary vary spatially and temporally. The results, which are likely to be applicable to other permanently-open microtidal estuaries in southern Australia and southern Africa, were used to test the following two hypotheses. 1) Biotic variables, such as density, number of species, species composition and trophic structure, change progressively throughout the estuary as environmental variables such as salinity, the amount of organic material and the amount and type of potential food change along the same spatial axis. However, there will also be a tendency for some regional differentiation in the above biotic variables as the biological and environmental characteristics of the lower, middle and upper estuary differ. 2) The changes that occur throughout the year in variables such as temperature and salinity and the potential food sources for nematodes is reflected in cyclical seasonal changes in species compositions and the trophic characteristics of the nematode assemblages.

2. Materials and Methods

2.1. Sampling regime

The Swan River Estuary is located on the microtidal lower west coast of Australia (Fig. 1). The very small tidal regime means that there is essentially no intertidal area throughout most of the length of this estuary. The estuary contains a small amount of seagrass and macroalgae in the channel and basins and riparian vegetation in the upper reaches and no mangroves.

Nematodes were sampled at 12 shallow (< 2 m deep) sites that were located at intervals throughout the length of the Swan River Estuary (Fig. 1) and which each comprised the area within a 100 m radius of a designated point on the shoreline. Five randomly-located replicate samples were extracted from the sub-tidal sediment at each site in the middle each of the four seasons between summer 2004/5 and spring 2005. Samples were collected using a steel corer, which was 3.57 cm in diameter (i.e. covering a surface area of 10 cm^2) and sampled to a depth of 10 cm. In each season, three of the replicate samples at a site were collected on one occasion and the other two at least two weeks later. Each sediment core was immediately fixed in a 5 % formalin / estuary water solution.

[Insert Figure 1]

The same corer was used to obtain three additional sediment samples from each site in each season for determining 1) the depth at which the colour of the sediment changed from light to dark (henceforth referred to as transition zone), 2) the percentage

particulate contribution of organic material (%POM) and 3) the composition of the grain sizes in the sediment. Note that the depth at which the sediment changes colour from light to dark, which is the point where ferric iron is reduced to ferrous iron (Sikora and Sikora, 1982), is deeper than the point at which oxygen is biologically available (Heip et al., 1985). Thus, the entire oxic layer of the sediment, and therefore the vast majority of free-living nematodes, were sampled (Heip et al., 1985).

A further three sediment cores were extracted from each site in each season using disposable plastic corers, 2.8 cm in diameter and 5 cm long, to provide material for calculating the chlorophyll concentration at those sites. The cores were immediately wrapped in aluminium foil to exclude light, stored on ice and frozen.

Temperature, salinity and dissolved oxygen concentration were recorded in the middle of the water column in three regions of each site on each sampling occasion using a YSI 556 Multi-Parameter Handheld Meter.

2.2. Laboratory procedures

The nematodes were separated from the sediment in the cores using the laboratory procedures described in Hourston et al. (2005), except that a decantation step was added prior to using Ludox ™ to increase the efficiency with which nematodes were removed from the sediment. Thus, each sample was suspended in 800 ml of tap water and the larger sediment grains briefly allowed to settle, after which the remaining suspension was decanted through nested sieves of 500 and 63 μm mesh. The sand from which the suspension was decanted was subjected to the above procedure four more times to ensure that all nematodes had been removed. The organisms were separated from the fine sand and debris particles remaining on the 63um sieve using Ludox ™ and preserved in 70% ethanol. The procedures for isolating, subsampling, mounting and identifying the nematodes are given in Hourston et al. (2005). Counts were conducted on sub-samples, generally comprising one quarter of each core. The total number of each nematode taxon in each sample is expressed as a density, i.e. number 10 cm^{-2}.

Each nematode species was assigned to one of the four following functional feeding groups designated by Wieser (1953) on the basis of buccal cavity morphology. 1A. Species without a buccal cavity or with only a narrow tubular buccal cavity and which ingest particles of bacterial size, i.e. the selective deposit feeders. 1B. Species with a large buccal cavity that is not armed with teeth, i.e. non-selective deposit feeders. 2A. Species having a buccal cavity armed with small or moderate sized teeth, i.e. epigrowth or diatom feeders. 2B. Species with large teeth or jaws, i.e. predators/omnivores.

Each of the cores taken for determining %POM and sediment grain size was dried at 100 ºC, weighed to the nearest 0.01 g and ashed at 550 ºC to remove any organic material. Each core was then reweighed to enable the weight and thus %POM to be calculated (Heiri et al., 2001). The ashed sample was wet-sieved through a 63 μm mesh, dried at 70 ºC and reweighed to determine the weight of fines (< 63 μm). The remaining sediment was then wet-sieved through six nested sieves (2000, 1000, 500, 250, 125 and 63 μm) and each fraction dried at 70 ºC and weighed to enable its contribution to the total core weight to be determined.

The top ca 1 cm of the cores collected for chlorophyll analysis was ground in 30 ml of acetone using a mortar and pestle. The resultant slurry was centrifuged and the light absorbances of the supernatant at wavelengths of 664, 647 and 630 m measured using a Hitachi U-1100 spectrophotometer. The concentrations of chlorophyll fractions a, b and c were determined from those absorbances and summed (Parsons et al., 1984)

The sediment from which the chlorophyll had been extracted was dried and weighed, thereby enabling the concentration of chlorophyll to be expressed as mg g^{-1} of sediment.

2.3. Univariate statistical analyses

Two-way Analyses of Variance (ANOVA) were performed to determine whether the following environmental and biotic variables differed significantly among the 12 sites and four seasons, with site and season both considered fixed factors. The environmental variables were water temperature (°C), salinity and dissolved oxygen concentration in the water column (mg L^{-1}), and transition zone depth (cm), POM (%) and chlorophyll concentration in the sediment (mg g^{-1}), while the biotic variables were density and number of species of nematodes. Salinity was measured using the practical salinity scale and is thus dimensionless. All univariate analyses were conducted using the SPSS v 15 statistical software package. Prior to subjecting the data for each dependent variable to ANOVA, the relationship between the mean and standard deviation of each set of replicate samples was examined to determine whether these variables required transformation to meet the test assumptions of normality and constant variance required by ANOVA. In those instances where this was not the case, the appropriate transformation was then applied (Clarke and Gorley, 2006). The H_0 for all ANOVAs, i.e. that significant differences did not exist among a priori groups, was rejected if the significance level (P) was < 0.05.

2.4. Multivariate statistical analyses

All of the following multivariate statistical analysis and routines were carried out using the PRIMER v.6 statistical package (Clarke and Gorley, 2006).

2.4.1 Sediment grain-size composition

The means of the sediment grain size fractions in the three replicate samples obtained from each site in each season were analysed using Principal Component Analysis (PCA) to explore visually the extent of any differences among sites and seasons, and to identify which granulometry fractions were primarily responsible for any such differences. Two-way crossed ANOSIM was conducted using a Euclidian dissimilarity matrix constructed from the same data to ascertain whether the grain size compositions differed significantly among sites and / or seasons.

2.4.2 Comparisons of the species compositions among sites and seasons

The densities of each nematode species in each replicate sample from each of the 12 sites in each season were fourth-root transformed. The means of the transformed densities for each site in each season were used to construct a Bray-Curtis similarity matrix, which was then subjected to group-averaged hierarchical cluster analysis and non-metric multidimensional scaling (nMDS) ordination. The samples were coded for site to assess visually the extent to which the compositions of the samples from the various sites were similar or different.

A second Bray-Curtis matrix, constructed from the densities of each species in the individual replicate samples, was subjected to a two-way crossed Analysis of Similarity (ANOSIM) test to ascertain whether the species compositions of the nematode assemblages differed significantly among sites and/or seasons. For this and all subsequent ANOSIM tests, the null hypothesis that there were no significant differences among groups was rejected if the significance level (P) was <0.05. The R-statistic values determined by ANOSIM for comparisons between those a priori groups that were significantly different were used to ascertain the degree to which those groups were dissimilar. R-statistic values approaching unity demonstrate that the compositions of the groups are very different, while those close to zero show that they are very similar (Clarke, 1993). When ANOSIM detected significant differences among a priori groups, two-way crossed site by season Similarity Percentages (SIMPER) was used to determine the species that typified those groups and those which distinguished each group from each of the others (Clarke, 1993).

As species composition was influenced significantly by both site and season (see Section 3.4), the matrix constructed from the replicate data for the fauna at each of the 12 individual sites was subjected separately to nMDS ordination to show the relationships

between the faunal compositions in the four seasons without the counfounding influence of site. Using the same Bray-Curtis similarity matrices, one-way ANOSIMs were then used to explore whether the species compositions differed among seasons at each site and, if so, the extent of those seasonal differences. To explore the effects of site in each season, nMDS ordinations were constructed for each of the four seasons using the mean densities of each species in each set of five replicate samples for each site. This enabled the question of whether nematode composition changed sequentially along the length of the estuary to be explored visually. The matrices constructed from the replicate data in each season were then subjected to one-way ANOSIMs to determine whether the species composition differed among sites in each season and, if so, the extent of those site differences.

2.4.3. Relationships between nematode fauna composition and environmental variables

Analyses were conducted to determine the extent to which the pattern of spatial differences in the suite of aquatic variables (salinity, temperature and dissolved oxygen concentration) and "non-granulometric" sediment variables (chlorophyll, POM and transition zone depth) matched that exhibited by the nematode fauna. BioEnv, employing mean values for each variable in each season and all seasons collectively, was used to elucidate which of the three aquatic variables, or combination of those variables, was best correlated with nematode compositions, both overall and in each season (Clarke and Ainsworth, 1993). This process was then repeated for the three "non-granulometric" sediment variables. Note that, because there were only 12 sites, only 12 points were available for the matching procedure and that it was thus inappropriate to consider more than three variables in any single test (Clarke et al., 2008). Since the composition of the suite of sediment grain sizes has been reported to influence the composition of nematode assemblages (Coull, 1988), the RELATE procedure was used to determine the extent to which nematode composition is correlated with granulometry as a whole. As both the BioEnv and RELATE routines require complete complementarity of samples, the data for replicates for each of the above variables for each site were averaged. Spearman rank correlation ( ) was employed as the matching co-efficient in the procedures and the null hypothesis, that there is no match in the rank order arrangement of samples between pairs of matrices, was rejected if P was < 0.05.

The mean compositions of the functional feeding groups at the 12 sites in each of the four seasons were subjected to PCA to investigate the extent to which the functional feeding groups of nematodes are distributed according to site in the estuary and which groups were mainly responsible for any spatial and/or temporal differences.

The Euclidian Distance matrix constructed from the compositions of the four functional feeding groups in replicate samples at each site in each season was subjected to two-way crossed ANOSIM to determine whether trophic composition was significantly influenced by site and / or season and, if so, the relative extent of those influences.

3. Results

3.1. Environmental data

Two-way ANOVA demonstrated that water temperature, salinity, dissolved oxygen concentration, transition zone depth, %POM and sediment chlorophyll concentration were each significantly influenced by site and also by season in all cases except %POM (Table 1). There was a significant interaction between site and season for all variables apart from %POM. For each of the variables for which season was significant, the mean squares were greater for that factor than those for site, except in the case of dissolved oxygen, and also than those for the interactions.

[Insert Table 1]

The mean seasonal temperature at all sites except 5 was always greatest in summer, followed by spring and then autumn and winter (Fig. 2a). The same trends were exhibited at site 5, except that the temperature in summer was unusually low and less than during spring, which helps account for the significant interaction between site and season. Although the temperature in summer, and to a lesser extent spring, tended to increase with distance from estuary mouth, the reverse was the case during autumn and to a greater extent winter. The mean seasonal water temperatures ranged from a low of 13 °C at site 12 in winter to 30 °C at site 6 in summer. The mean seasonal salinity at each site was almost invariably greater in summer than autumn, which in turn was greater than in spring and winter (Fig. 2b). The magnitude of differences in this variable also decreased with distance from estuary mouth, with values in summer and autumn declining from close to that of full strength seawater (35) at the downstream sites to about 13 at the most upstream site and those for winter and spring declining from 23-28 near the estuary mouth to ca 3 at the head of the estuary. Dissolved oxygen concentrations were always greatest during spring at sites 1-6, and generally during winter at sites 7-12, and were lowest during summer at 8 of the 12 sites (Fig. 2c). Furthermore, the concentrations in each season were greatest at sites 4, 5 or 6, which are relatively shallow and exposed to wave energy.

The transition zone depth in each season showed no clear tendency to change progressively throughout the estuary or to differ in a consistent manner among seasons

(Fig. 2d). However, the transition zone depths at sites 3-7 were always least in summer and were relatively small in all seasons at site 12. Although the concentration of sedimentary chlorophyll at any given site varied considerably among seasons, it was always greatest in spring at the four most downstream sites, with values at two of those sites in spring being among the three greatest recorded for any site in any season (Fig. 2e). The mean %POM to the sediment at sites 1-7 lay between 0.8 and 1.5%, which was less than those at all sites further upstream, where it peaked at 4.0% at site 9 and 5.2% at site 12 (Fig. 2f).

[Insert Figure 2]

Two-way crossed ANOSIM, using the matrix derived from replicate samples, showed that sediment granulometry differed significantly among sites (P<0.001, R-statistic = 0.723), but not seasons. Principal Components Analysis (PCA) of the data for the various sediment grain size fractions, demonstrated that 84 % of the total variation was encompassed by principal component axes 1 and 2. Although samples from certain site(s), e.g. 4, 6-8, 10 and 11, showed a very marked tendency to group together on the PCA plot, the samples from the various sites were not arranged sequentially on that plot according to distance from the estuary mouth (Fig. 3). The orientation of the eigenvectors demonstrated, for example, that the group of sediment samples from sites 10 and 11 contained large contributions of the coarsest grain-size fractions (500 µm and 1 and 2 mm), whereas those from sites 6, 7 and 8 comprised greater amounts of the 250 µm fraction.

[Insert Figure 3]

3.2. Densities and percentage contributions of the nematode species at the twelve sites

Over 150 000 nematodes belonging to 76 species were collected during seasonal sampling between summer 2004 and spring 2005 of the sub-tidal sediments of the twelve sites that were distributed throughout the Swan River Estuary. The mean density (No. 10 cm $^{-2}$) of nematodes, derived from pooled data for all seasons, decreased in a largely sequential manner from 1139 at site 1, close to the estuary mouth, to a minimum of 160 at site 9, the most downstream site in the upper estuary and then increased to between 297 and 668 at the three uppermost sites (Table 2). The number of species recorded at the 12 sites also declined in an essentially sequential manner from sites 1 and 2 (49) to site 10 (21), and then increased slightly further upstream (Table 2).

[Insert Table 2]

The dominant species at sites 1-6 in the lower and middle reaches of the estuary were similar (Table 2). Thus, in terms of abundance, *Spirinia parasitifera* ranked first at

sites 1, 2, 3, 5 and 6, where it contributed between 26 and 44 % to the total number of individuals, and *Theristus* sp. 2 always ranked in the top five species at sites 1-6 (5-16 %). *Comesoma arenae* also made substantial contributions at sites 1, 2 and 4 (7-9 %) and the same was true of *Bathylaimus australis* at sites 2 and 3 (6 and 11 %) and *Chromadorina* sp. at sites 1 and 2 (5 and 18 %).

Although *Dichromadora* sp. made a considerable contribution to the number of individuals at site 1 (8 %), it tended to be more common further upstream where it ranked in the top five contributors at each of sites 4-9 (5-29 %). Similarly, while *B. australis* and *Viscosia glabra* were present in moderate numbers at some of the downstream sites, they made their greatest contributions further upstream at sites 7 (35 %) and 10 (21 %), respectively (Table 2).

The nematode assemblages at the upper estuary sites (7-12) were all dominated by *Theristus* sp. 1, where this species always ranked either first or second (Table 2). This was particularly the case at the uppermost site (12), at which this species comprised 60% of all individuals. Other species that contributed substantially to the nematode assemblages in upstream areas were *Metadesmolaimus* sp. 2 at sites 9-11 (8-15 %), *Pierrickia* sp. nov. at sites 8, 10 and 12 (6-17%), *Metalinhomoeus* sp. at sites 9, 11 and 12 (6-12 %), *Nannolaimoides decoratus* and *Parodontophora aurata* sp. nov. at sites 11 and 12 (5-7 % and 4-8 %, respectively) and *Gomphionema typicum* at site 8 (11%).

3.3. density and Number of species

Two-way ANOVA demonstrated that the density and number of species of nematodes differed significantly among sites and that the former also differed significantly among seasons (Table 1). Although there was a significant interaction between site and season for both of these biotic variables, the mean squares for each of these interactions were far less than those for the main effects that were significant. The densities tended to be greater at sites 1-6 than at 7-10 and then increased at the uppermost sites, and were also greater in spring than in the other seasons at eight of the 12 sites (Fig. 4a). However these trends were not entirely consistent, as is reflected in the significant interaction between site and season for this variable. The number of species showed a similar overall trend to density and thus declined progressively from lower estuary sites (except site 3) to sites 8 and 9 and then showed a slight increase. The significant interaction between site and season reflects the fact that this biotic variable did not obviously tend to follow the same order in terms of season at each site and, atypically for the lower reaches, was low in all seasons at site 3 (Fig. 4b).

[Insert Figure 4]

3.4. Comparisons of species compositions among sites and seasons

Two-way crossed ANOSIM, using the matrix constructed from the replicate densities of nematode species obtained from each site in each season, demonstrated that species composition differed significantly among both sites and seasons ($P = 0.001$) and that the differences were greater for site (R-statistic = 0.834) than for season (R-statistic = 0.592). Pair-wise tests showed that the composition of the assemblages at each site was significantly different from that at each of the other sites ($P = 0.001$). Furthermore, the R-statistic values demonstrate that the compositions of the nematode faunas at sites located relatively close to each other tended to be far more similar to each other than were those that were further apart, e.g. the R-statistic for sites 1vs 2 was 0.304, whereas that for sites 1 vs 12 was 0.996. Likewise, R-statistic values showed that the compositions in widely-separated seasons, i.e. summer vs winter and spring vs autumn (0.728 and 0.634, respectively) were greater than those between consecutive seasons (< 0.610).

In the dendogram produced by Cluster Analysis of the similarity matrix constructed using the means for the densities of the nematode species at each site in each season, the samples separated, at a similarity level of 33 %, into two discrete groups, i.e. those from sites 1-6 and 7-12 (Fig. 5a). Furthermore, the samples from a particular site or neighbouring sites tend to cluster together. The clear separation between the samples from upstream and downstream sites is present in dendograms produced using data for each season separately (Figs not shown). On the nMDS ordination plot, derived from the same matrix, the samples show a very marked tendency to progress from left to right according to their distance from the estuary mouth (Fig. 5b).

[Insert Figure 5]

The site component of the two-way crossed SIMPER showed that the assemblages at many sites, or pairs of sites, contained a species that both characterised and consistently distinguished the assemblage at that site from those of all other sites. Thus, this role was performed by *Comesoma arenae* at sites 1 and 2, *N. decoratus* at site 3, *Pseudochromadora cazca* at site 4, *Halichoanolaimus duodecimpapillatus* at sites 5 and 6, *Metadesmolaimus* sp 1 at site 7, *Bathylaimus australis* at sites 7 and 8, *Gomphionema typicum* at site 8, *Pierrickia* sp. nov. at site 10, *Paradontophora aurata* sp. nov. at site 12 and by *Metalinhomoeus* sp. at sites 11 and 12. Three species made an important contribution to the distinction between the samples for sites in different regions of the estuary on the ordination plot shown in Fig. 5, namely, *Spirinia parasitifera* at sites 1-6 and 8, *Theristus* sp. 2 at sites 3-6, and *Theristus* sp. 1 at sites 7-12. The seasonal

component of the two-way crossed SIMPER showed more subtle trends than that for the site component.

The nematode fauna present in each season was characterised by a similar suite of species and those in any given season tended to be distinguished from those of the faunas in each of the other seasons by differences in the densities of those same species. For example, *Dichromadora* sp., which distinguished the fauna in each season from that in every other season, occurred in greater densities in spring than winter, which in turn were greater in summer and then autumn. Likewise, *N. decoratus* was most common during spring, followed by summer, winter and finally autumn, while *Chromadorina* sp. was most prevalent in spring, then summer, autumn and winter. Note that the above three species each attained their highest densities during spring and that each belong to the epistrate grazing functional feeding group.

One-way ANOSIM tests demonstrate that the compositions of the nematode assemblages differed significantly among seasons at every site ($P = 0.001$), being particularly well defined at site 6, for which the R-statistic was greatest, i.e. 0.852 (Fig. 6f). The magnitude of the seasonal differences tended to be greater in the middle estuary, with the R-statistics for sites 4, 6, 7 and 8 being the largest and always > 0.7. On the separate MDS ordination plots for each of the twelve sites, the samples for each season often show a marked tendency to form distinct groups (Fig. 6). The samples for successive seasons often underwent clear progressive cyclical changes on the ordination plots, a feature well displayed on the plots for sites 1, 6, 10, 11 and 12.

[Insert Figure 6]

3.5. Relating nematode assemblage patterns to environmental characteristics

When the matrices constructed from the mean densities of the nematode species at the 12 sampling sites were subjected to ordination, the points for the samples at the various sampling sites in each season progressed in a largely linear manner on the resultant plots according to location of site in the estuary (Fig. 7). Thus, on each ordination, those from the most downstream sites lie on the left, while those from the most upstream sites lie on the right, with the distance between points for sites 6 and 7 always being relatively large, and the greatest for any pairs of sites in three of the four seasons. RELATE tests demonstrated that the patterns of differences in the compositions of the nematode assemblages among sites were significantly correlated with distance from estuary mouth ($P = 0.001$), both overall (= 0.764) and in each season, with that in spring exhibiting the closest match, (=0.805), followed by autumn (= 0.801), winter (= 0.739) and then summer (= 0.582). The relatively lower correlation in summer largely

reflects the fact that the point for site 7 lies well to the right of those for all other sites (Fig. 7a).

[Insert Figure 7]

The use of BioEnv demonstrated that, among the aquatic variables, the pattern of rank-order of similarity in the compositions of the nematode assemblages at the various sites was significantly and most highly correlated overall with that of salinity, (= 0.775, $P = 0.010$), and that the correlation was not improved by the inclusion of temperature and/or dissolved oxygen concentration. Furthermore, salinity was also identified as the best matching variable in separate tests for autumn (= 0.828, $P = 0.010$), winter (= 0.866, $P = 0.010$) and spring (= 0.859, $P = 0.010$), but not summer where no significant match was found ($P = 0.440$), with the improvement in match in the former three seasons being negligible by including one or both of the other aquatic variables. In the case of the non-granulometric sedimentary variables, BioEnv demonstrated that the pattern of rank-order of similarity of the compositions of the nematode assemblages was significantly correlated overall with %POM (= 0.335, $P = 0.040$), but not with transition zone depth or chlorophyll concentration. Seasonal tests for the non-granulometric sedimentary variables showed that a combination of %POM and chlorophyll concentration provided the best match with the compositions of the nematode assemblages in each season, but that the correlation was significant in only autumn and spring ($P < 0.05$), and that those correlations were always lower than 0.390.

The RELATE test demonstrated that the pattern of rank-order of similarity between the compositions of the nematode assemblages at the 12 sites was significantly correlated with that for the grain size compositions of the sediments ($P = 0.001$) and that the degree of correlation was relatively low (= 0.353).

3.6. Analysis of functional feeding groups

Two-way crossed ANOSIM demonstrated that the contributions of the four FFGs differed significantly among sites and seasons (both $P = 0.001$), with the R-statistic being greater for site (0.541) than season (0.361). Sixty three of the 66 pairwise comparisons among sites were significant, and in general, were greatest between sites that were widely separated, with those for each of sites 1 and 2 vs each of sites 9-12 being greater than ca R = 0.5. The R-statistics for seasonal pairwise comparisons demonstrated that the FFG composition of the samples from spring were the most distinct, with values for spring vs each other season always exceeding 0.450 and being greater than between any other two seasons.

When the mean contributions of the various functional feeding groups at the 12 sites in the four seasons were subjected to PCA, the 2 dimensional plot encompassed 84 % of the total variation in the data (Fig. 8). The samples from sites 7-12 formed a group in, or close to, the upper right quadrant of the PCA plot and were positively correlated with the eigenvector for the 1B FFG (Fig. 8a). In contrast, the majority of the samples for sites 1-6 were widely distributed through the other three quadrants of the plot and were thus more positively correlated with the eigenvectors for the 1A and 2A FFGs. The four seasonal samples from each of sites 7-12 showed a much greater tendency to group together than did those from each of sites 1-6. When the data were coded for season, 11 of both the autumn and winter samples and 9 of the 12 summer samples lay in the upper half of the plot, whereas 7 of the 12 spring samples lay in the bottom half of the plot (Fig. 8b)

[Insert Figure 8]

4. Discussion

This study is the first to explore statistically the ways in which the densities, numbers of species and species compositions of nematode assemblages in subtidal waters differ throughout the length of a microtidal estuary and the extent to which those three biotic variables change in this type of estuary during the year. This enabled emphasis then to be placed on exploring which environmental variables were mainly responsible for influencing the spatial and temporal distributions of those nematode assemblages. Our study also represents the first time that the trophic compositions of nematode assemblages numerous sites throughout an estuary have been analysed, with a view to elucidating how the contributions of the various functional feeding groups change with location and season and which factors are responsible for any such changes.

4.1 Spatial variation

Our results demonstrated that, while the species compositions of the nematode assemblages in the Swan River Estuary are influenced markedly by both site and season, the first of these factors is by far the most important. In the context of site, it is relevant that the ordination plots shown in Fig. 7 demonstrate that, in each season, species composition changes progressively along the estuary. This point is emphasised by the R-statistic values for comparisons between the compositions of assemblages at the proximal and distal ends of the estuary being close to 1, whereas those for the compositions at sites close together were far lower. The very pronounced differences in the compositions at the extreme ends of the estuary are reflected in the horseshoe-like distribution of the samples on the ordination plot that utilised data for all four seasons

(Fig. 5). This pattern of distribution reflects the fact that the mechanics of the ordination procedure are influenced by the very high dissimilarity between samples at the extremes in a gradient (Seber, 1984; Clarke and Gorley, 2006). As with nematodes, the species composition of the benthic macroinvertebrate and fish faunas in the lower and upper reaches of the Swan River Estuary are differ markedly (Loneragan and Potter, 1990; Wildsmith pers. comm.)

The change in the species compositions of nematodes through the estuary was shown by BioEnv to be closely correlated with changes in salinity, thereby paralleling the situation with nematode faunas in macrotidal estuaries in Europe (Warwick, 1971; Austen and Warwick, 1989). However, Cluster analysis emphasised that the compositions at the various sites constituted two very distinct groups, namely those in the entrance channel and lower basin (sites 1-6) vs those in the upper basin and riverine parts of the estuary (sites 7-12). This regional distinction, with the point of separation occurring where the estuary becomes very constricted and thus separates the large downstream and upstream basins, parallels that found with the fish faunas that are likewise located in nearshore waters (Loneragan et al., 1989). As salinity influences the composition of nematode faunas, it is relevant that, in each season apart from summer, salinity declines progressively and markedly upstream of site 6 and that it exhibits the greatest intra-annual variation at sites 7-9. It is therefore suggested that the species that characterise the fauna of the assemblages upstream of site 6 are particularly well adapted to the osmotic stress produced by the lower and more variable salinities that are found in that part of the estuary. The conclusion that variation in salinity is important in influencing the composition of the nematode fauna of the Swan estuary parallels that drawn by Armenteros et al. (2006) for meiofaunal assemblages in the mangroves of a Cuban gulf that exhibited spatial differences in salinity.

The distinction between the compositions at sites 1-6 and 7-12 was shown by SIMPER, and by the data for the percentage contributions and ranking by abundance for each species in Table 2 to be due to marked differences in the abundances of certain species. This shift was due to in particular to a pronounced decline in the importance of *Spirinia parasitifera* and *Theristus* sp. 2 and to a marked increase in the importance of *Theristus* sp. 1. Thus, *S. parasitifera* and *Theristus* sp.2 contributed 30 and 11% respectively, to the total number of nematodes recorded at sites 1-6, but only 6 and 3%, respectively, to those collected from 7-12, whereas *Theristus* sp. 1 contributed only 4% to the numbers at sites 1-6 compared with as much as 36% at sites 7-12. Although *S. parasitifera* is a very cosmopolitan species, it was not recorded during extensive

studies of the sediments in nearshore waters along the coast outside the Swan River Estuary, as were neither of the other two species (Hourston et al., 2005).

Although salinity was the most important of the factors which influenced the species compositions of nematode assemblages in the Swan River Estuary, those compositions were also influenced by sediment granulometry and POM. In the case of the macrotidal Exe estuary (UK), a combination of transition zone depth, salinity and granulometry (as reflected by median particle size) of the sediment provided the strongest relationship with the species composition of nematode assemblages (Warwick, 1971; Clarke and Ainsworth, 1993). In macrotidal estuaries, the strong tidal activity typically leads to the development of a strong spatial gradient in sediment composition, with sediments at the mouth being coarse and well-oxygenated, whereas those at the head are finer and poorly oxygenated (McLusky and Elliott, 2004). However, our data show that grain-size composition does not change in a comparable sequential manner along the Swan River Estuary, presumably reflecting variations among locations in such factors as flow soil type and extent and type of vegetation. This accounts for changes in the compositions of the nematode assemblages along the estuary being far less strongly correlated with that of granulometry than with that of salinity, which does change progressively with increasing distance from estuary mouth.

The positive correlation between the compositions of the nematode assemblages and %POM reflects the fact that the fauna in the lower and upper halves of the estuary constituted relatively distinct groups and that the levels of POM are far greater in the latter part of the estuary. This point further emphasises that there is a regional component to the pattern of distribution of nematode species within the overall trend for compositions to change sequentially along the longitudinal axis of the estuary.

It was conspicuous that the number of nematode species at site 3 was relatively low in all seasons as this ran counter to the strong trend for the values at the other downstream sites (1, 2, 4 and 5) to be high. This apparent anomaly can almost certainly be explained by the fact that Tributyl-tin, which is known to be toxic to nematodes (Schratzberger et al., 2002), was present in high levels in nearby sediments, having been used as an antifoulant on boats in a nearby marina.

The tendency for the number of nematode species in the Swan River Estuary to decrease with declining salinity and then to show a slight increase at the lowest salinities broadly parallels the Remane paradigm that was based on an analysis of the changes in the number of species along a salinity gradient in the Baltic Sea (Remane, 1934). It also parallels the trends exhibited by nematodes in a Japanese coastal lake system that is

connected to the sea (Yamammuro, 2000) and by the meiofauna in the Thames Estuary in the United Kingdom (Attrill, 2002). However, Attrill (2002) concluded that the diversity of subtidal meiofauna (and macrofauna) of the Thames estuary was influenced more by variation in salinity than by absolute salinity, which parallels our conclusions regarding species composition (see earlier). The importance of the magnitude of change in salinity was also considered by Armenteros et al. (2006) to influence meiofaunal community structure in a tropical mangrove system to a greater extent than does absolute salinity per se.

4.2. Seasonal variation

The high Global R-statistic of 0.592 in the global two-way crossed ANOSIM with site shows that species composition undergoes considerable seasonal variation. Furthermore, the distributions of the samples for the four seasons on the ordination plots shown in Fig. 6 demonstrate that the composition of the nematode fauna at the 12 sites in the Swan River Estuary undergo progressive cyclical changes during the year, thereby paralleling the situation with the fish faunas in nearshore waters of the same estuary (Hoeksema and Potter, 2006). Variations in the composition of the fish fauna of the Swan River Estuary are due, in part, to interspecific differences in the timing of recruitment of juveniles, often as a result of differences in the temperatures that stimulate spawning in the various species.

As reproduction, maturation and development of two co-occurring nematode species were shown to be differentially influenced by temperature (Moens and Vincx, 2000), the changes in species composition of the nematode fauna of the Swan Estuary may likewise reflect temperature-related differences in the reproductive success and/or recruitment of the various species. However, since salinity had a differential impact on the viability of juveniles of the two species studied by Moens and Vincx (2000), changes in this environmental variable may also influence the relative abundances of the various species in the Swan River Estuary and thus also contribute to the cyclical changes in the composition of its nematode assemblages. Seasonal variation in salinity is also likely to be a more important factor in influencing seasonal changes in nematode assemblages in microtidal estuaries such as the Swan, more so than in macrotidal estuaries where the shorter-term variation in salinity over diurnal and lunar time-scales may be greater in magnitude than the seasonal changes. The seasonal changes in the composition of the nematode assemblages partly reflected the marked increase that occurred in the population of the epistrate grazing species *Dichromadora* sp., *Nannolaimoides decoratus*

and *Chromadorina* sp. in spring, when the density of microphytobenthos peaks in the Swan River Estuary (Montani et al., 2003).

The very conspicuous seasonal changes undergone by the species compositions of nematode assemblages throughout the Swan River Estuary parallel the situation recorded in two macrotidal estuaries in the north-eastern region of the United States (Tietjen, 1969). Furthermore, the seasonality in the two North American estuaries, and also in an estuary in Germany (Skoolmun and Gerlach, 1971), likewise reflected increases in the densities of epistrate-grazing species in spring and/or summer, when benthic microflora production was at its maximum. However, conspicuous seasonal variations were not found in the nematode assemblages of two macrotidal estuaries in Europe (Warwick, 1971; Warwick and Price, 1979). Although the composition of the nematode assemblages in the Hunter River estuary, which is located in eastern Australia at a similar latitude to the Swan, varied through the year, the trends were not consistent across all study sites, which was attributed to differences in non-seasonal environmental changes in the estuary (Hodda and Nicholas, 1986). Our ability to demonstrate that nematode compositions underwent cyclical seasonal changes in the Swan River Estuary and identification of the species responsible for those changes benefited greatly from the development of nMDS ordination plots, ANOSIM tests and SIMPER, which were not available to some earlier workers. It would be worthwhile to use contemporary multivariate statistical techniques to explore whether the compositions of nematode assemblages in all types of estuaries typically vary seasonally.

4.3. Trophic structure

Because free-living species of nematode tend to be selective in the food they ingest, the presence of large amounts of a particular type of food at a locality would favour colonisation by species that belong to a particular trophic group or groups. The distributions of the seasonal samples for the 12 sites on the PCA plot, derived from the percentage contributions of each of the four Functional Feeding Groups (FFGs), suggest that the types of food ingested by the nematode species in the downstream and upstream reaches of the estuary differ markedly. The great importance of non-selective deposit-feeding species, such as *Theristus* sp. 1 to the nematode fauna upstream of site 7 presumably reflects the presence of greater amounts, and sometimes markedly so, of their main food source (POM) in the sediments of those sites than in those further downstream. In comparison to the situation upstream, the trophic compositions of the nematode assemblages in the lower reaches was far more seasonally variable, with those in spring being the most distinct and characterised by epigrowth feeders such as *Dichromadora* sp.,

Nannolaimoides decoratus and *Chromadorina* sp.. This peak in abundance of epistrate feeders in the lower estuary corresponds, both temporally and spatially, to where the concentration of sedimentary chlorophyll and therefore density of microphytobenthos was greatest. The co-occurring density peaks of microphytobenthos and epistrate grazing nematodes is consistent with the proposal that the members of this feeding group are more susceptible to variation in their food source than the other three groups (Tietjen, 1969; Austen and Warwick, 1995).

5. Conclusions

In summary, this study has demonstrated that the species composition of nematode assemblages of the Swan River Estuary changes largely in a linear manner along the length of this system and that these changes are closely related to the overall decline in salinity and, to a lesser extent, the increase in the percentage of organic material in the sediment with increasing distance from the estuary mouth. Species composition is also moderately related to sediment grain-size composition, even though that variable does not change in a similar progressive manner. This suggests that certain species prefer certain sediment types which, through differences in factors that affect granulometry, tend to differ among areas in this microtidal estuary. The density and number of species tended to decline with increasing distance from estuary mouth, to reach a minimum in the area where salinity started decreasing markedly and exhibited the greatest intra-annual variation, and then rose slightly in the uppermost reaches. The spatial and temporal variations recorded in the compositions of the different functional feeding groups were related to differences in the relative abundances of the different types of food present.

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List of Tables

Table 1. Mean squares and significance levels for two-way ANOVAs of five abiotic and two biotic variables recorded at twelve sites in each of the four seasons between summer 2004/5 and spring 2005. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

Table 2. Functional feeding group (FFG) of each nematode species, and the mean density (No. 10 cm^{-2}), percentage contribution and rank by abundance of those species at each of the twelve sampling sites in the Swan River Estuary, derived from pooled data for all seasons. The five most abundant species at each site have been shaded. Data are restricted to those species which contributed > 0.5% to the total number of individuals in any region.

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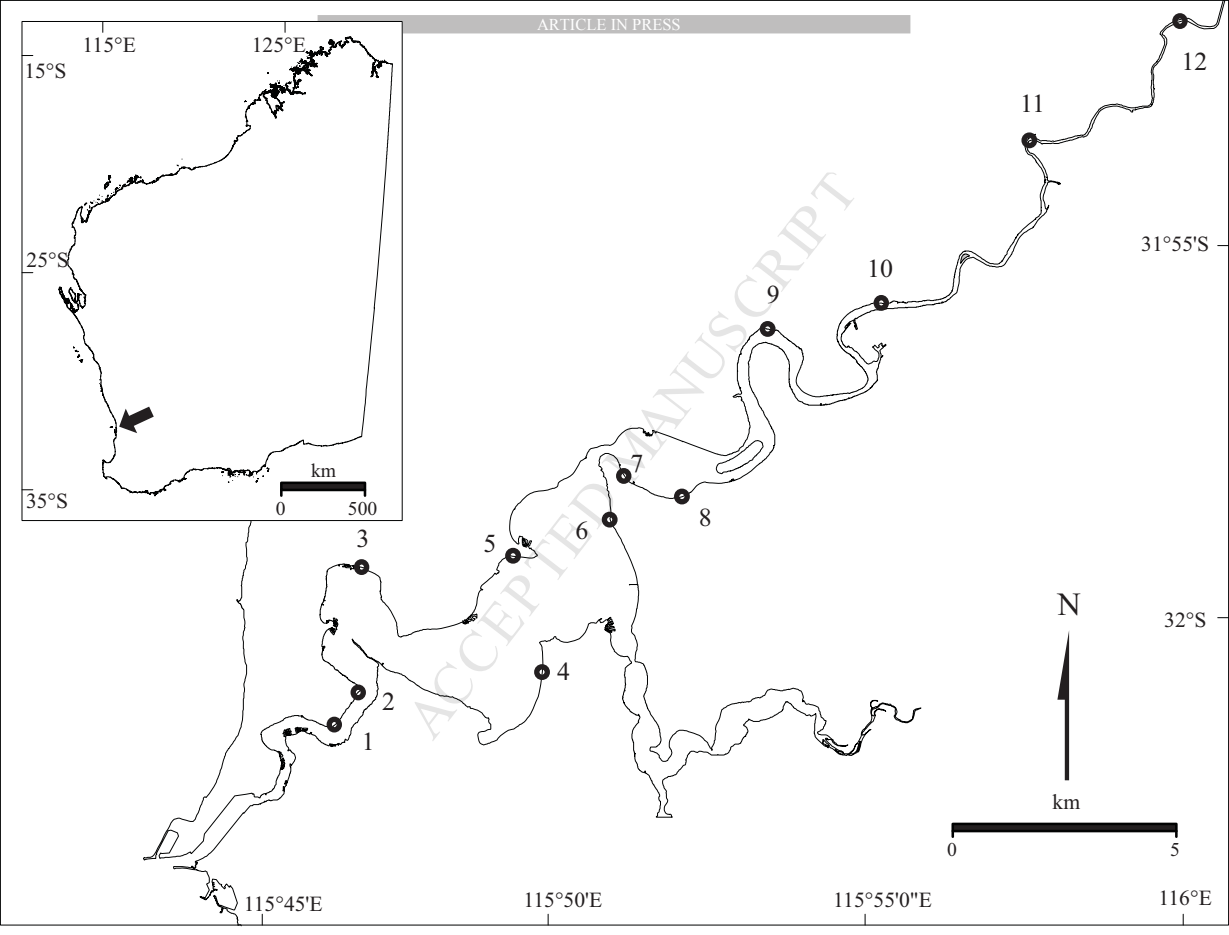
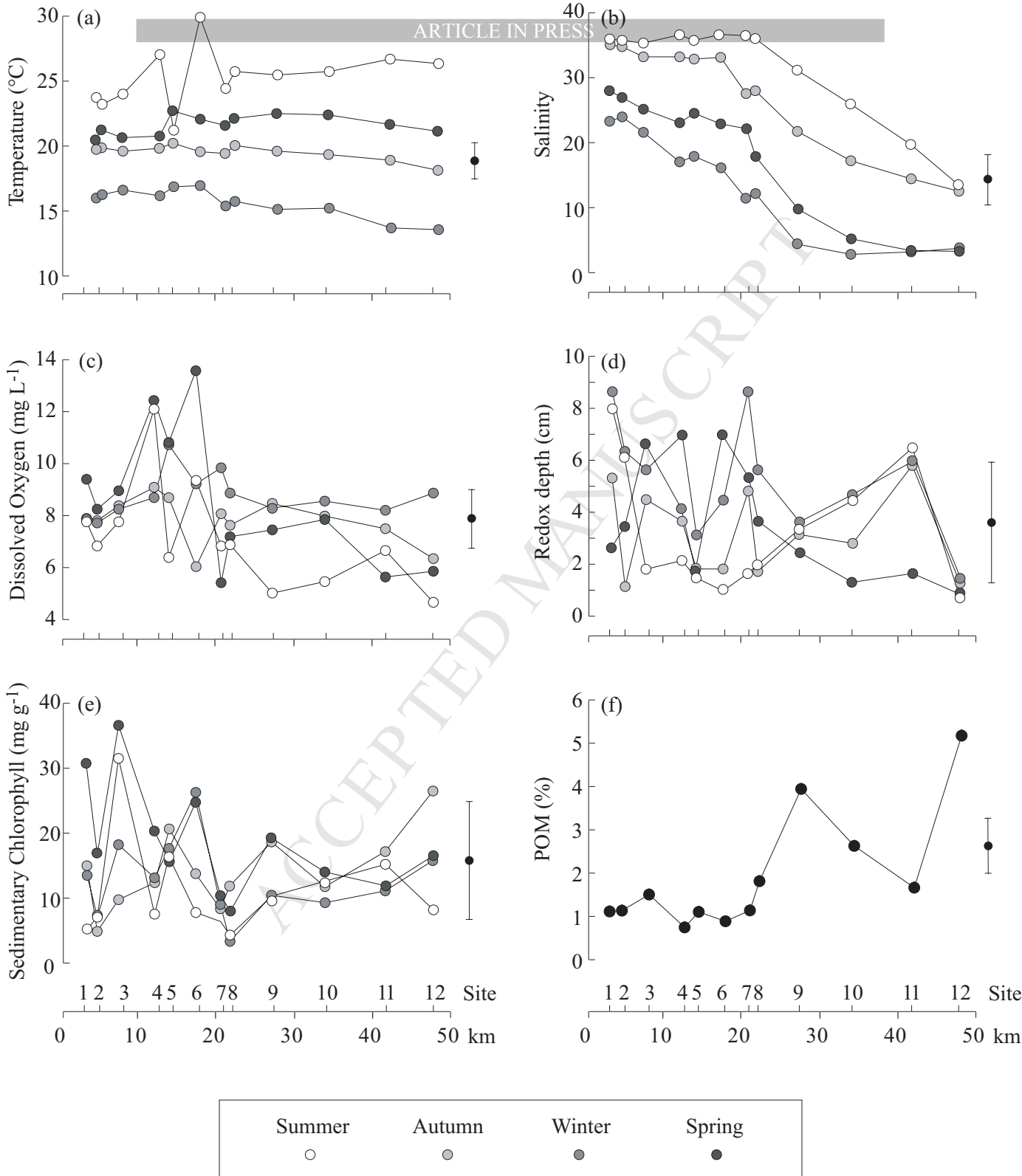
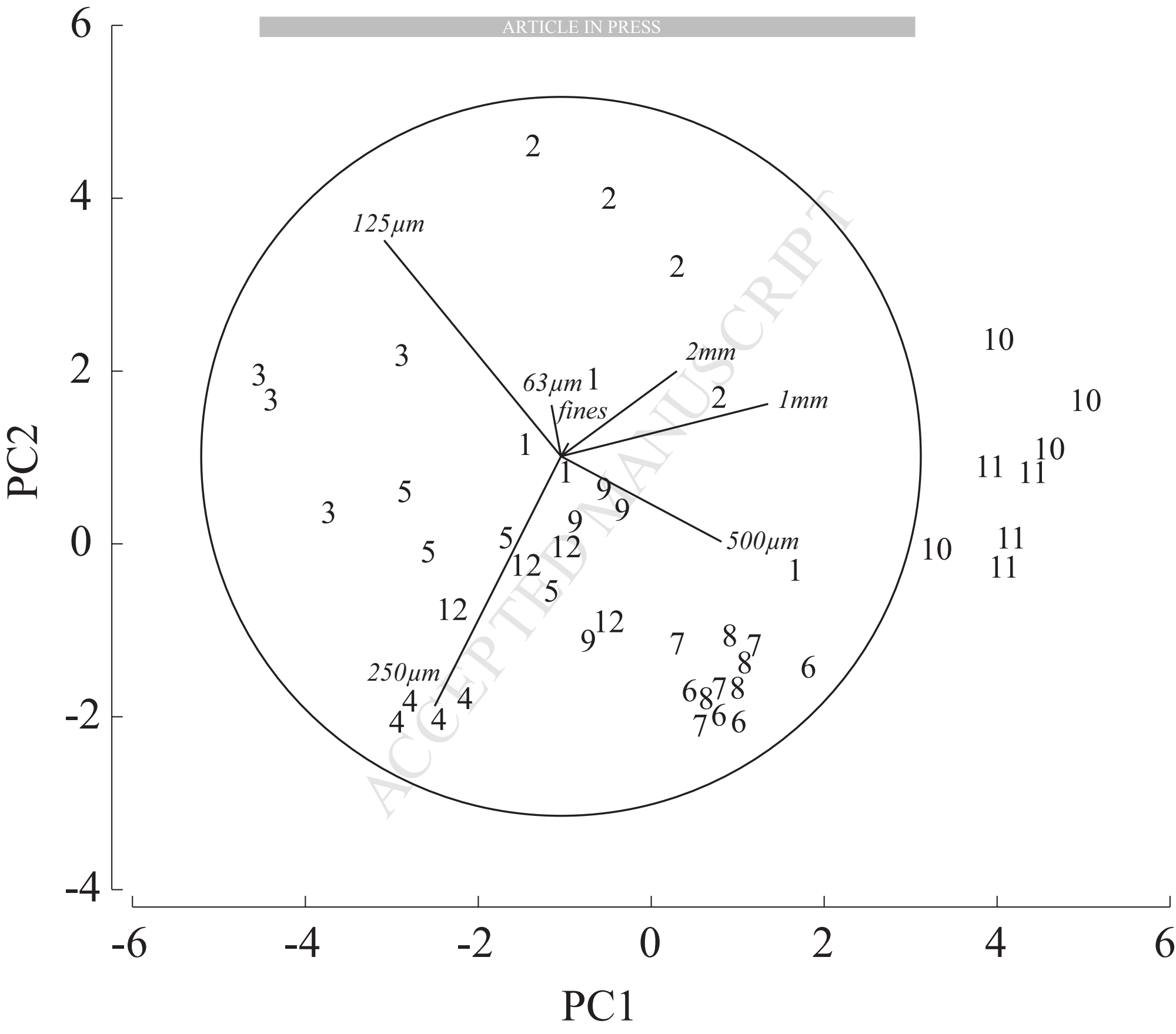
Figure 8 Principal component analysis plot derived from the mean percentage contributions of each of the four functional feeding groups to the total number of nematodes in the samples at each site in each season. Samples have been coded for (a) site and (b) season. Principal component axes 1 and 2 collectively accounted for 84.5% of the total variation present

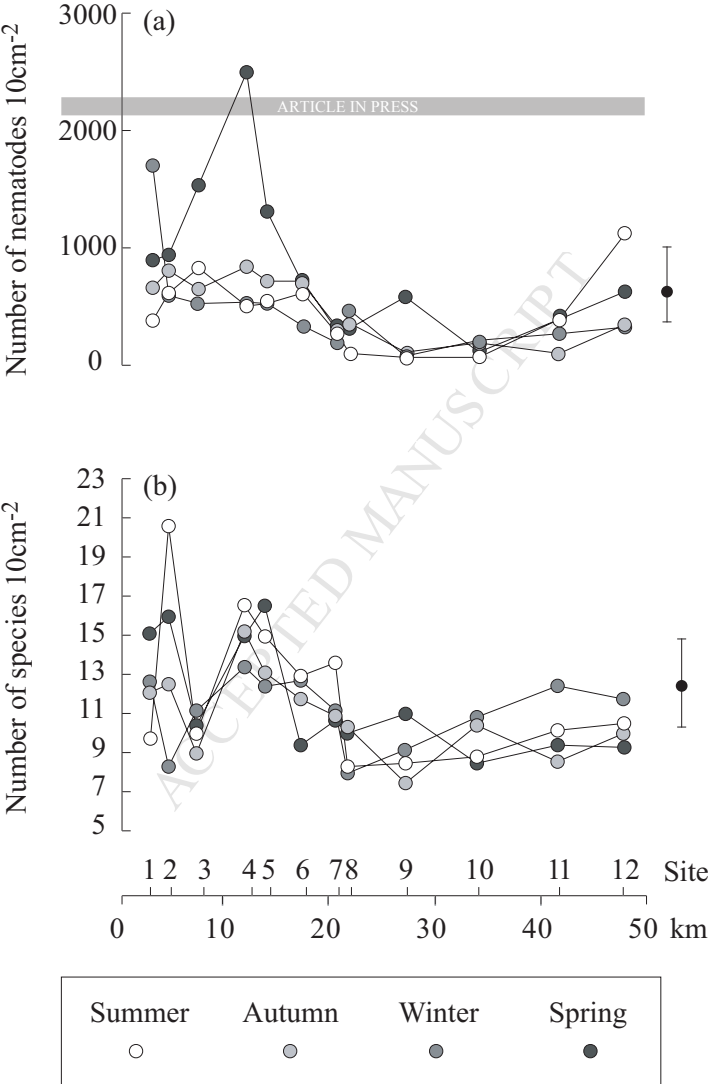
	Site (Si)	Season (Se)	Si x Se Interaction	Residual
Factor type	Fixed	Fixed	Fixed	
Degrees of freedom	11	3	33	192
Abiotic				
Temperature	4.559 ***	554.658 ***	5.375 ***	1.455
Salinity	766.811 ***	2450.548 ***	20.488 ***	11.755
Dissolved Oxygen	0.483 ***	0.269 *	0.205 ***	0.031
Redox Depth	23.009 ***	42.341 ***	9.596 ***	4.087
%POM	21.099 ***	0.855 ns	1.502 ns	1.230
Chlorophyll concentration	283.584 ***	459.235 ***	102.635 *	62.928
Biotic				
Density	11.447 ***	7.343 ***	1.749 ***	0.473
Number of Species	1.837 ***	0.266 ns	0.440 ***	0.123

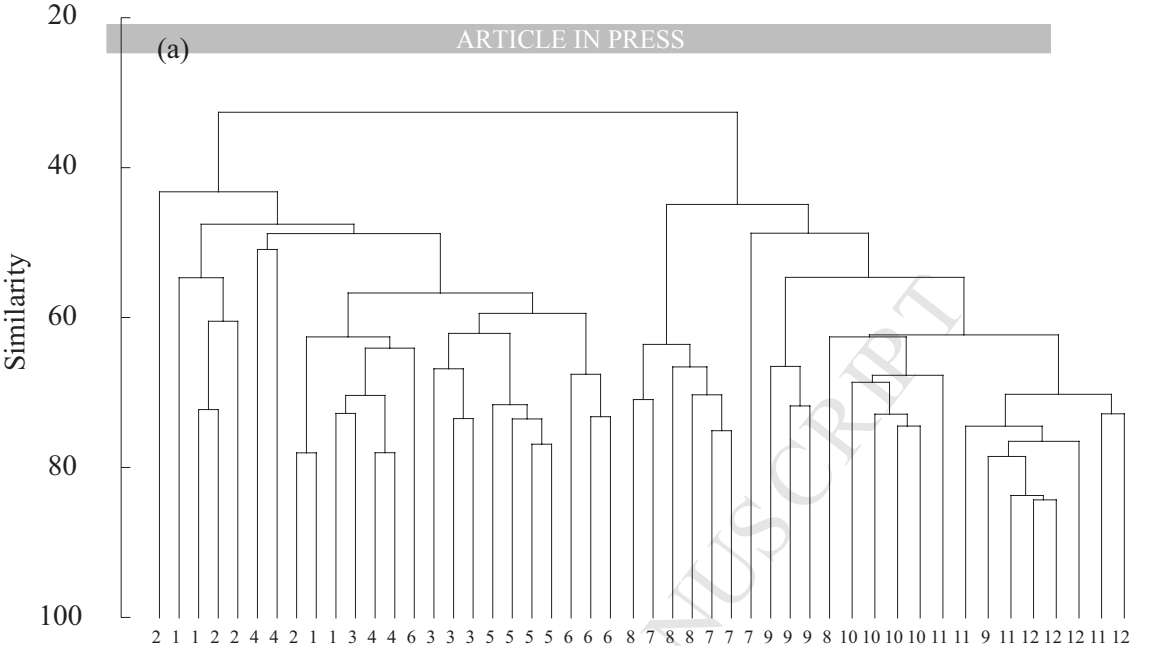
		Site																																	
		1			2			3			4			5			6			7			8			9			10			11			12		
	FFG	X	%	Rk	X	%	Rk	X	%	Rk	X	%	Rk	X	%	Rk	X	%	Rk	X	%	Rk	X	%	Rk	X	%	Rk	X	%	Rk	X	%	Rk	X	%	Rk
Spirinia parasitifera	1A	499	44	1	227	26	1	327	35	1	29	3	11	271	34	1	256	41	1	11	3	7	18	6	6	20	8	4	1	<1	15	<1	<1	17	2	<1	14
Theristus sp. 2	1B	141	12	2	48	5	5	151	16	2	120	11	2	67	8	3	65	10	2	16	5	6	5	2	14	4	2	11	-	-	-	-	-	-	-	-	-
Dichromadora sp.	2A	96	8	3	24	3	9	46	5	6	331	29	1	84	11	2	53	9	3	31	9	3	24	8	4	14	5	5	8	5	7	11	3	7	15	2	7
Comesoma arenae	1B	78	7	4	82	9	3	<1	<1	20	76	7	5	26	3	10	7	1	15	1	<1	16	<1	<1	21	2	<1	14	-	-	-	1	<1	16	1	<1	15
Chromadorina sp.	2A	61	5	5	162	18	2	21	2	10	48	4	9	15	2	13	9	1	14	7	2	8	5	2	13	2	<1	15	4	2	10	2	<1	15	<1	<1	16
Bathylaimus australis	1B	18	2	10	53	6	4	106	11	4	3	<1	20	1	<1	20	12	2	11	117	35	1	13	4	8	7	3	8	-	-	-	<1	<1	19	-	-	-
Nannolaimoides decoratus	2A	18	2	10	14	2	13	116	12	3	66	6	6	31	4	9	30	5	5	2	<1	12	1	<1	18	2	<1	17	3	2	11	17	5	5	47	7	3
Halichoanolaimus duodecimpapillatus	2B	25	2	8	20	2	10	50	5	5	47	4	10	34	4	8	26	4	6	2	<1	14	<1	<1	20	2	<1	16	3	2	13	5	1	10	10	2	9
Viscosia glabra	2B	31	3	7	20	2	12	24	3	9	108	10	3	36	5	7	40	7	4	<1	<1	18	10	3	10	4	1	12	33	21	1	5	1	12	4	<1	13
Metadesmolaimus sp. 1	1B	35	3	6	47	5	6	36	4	7	95	8	4	46	6	6	18	3	9	26	8	4	20	7	5	-	-	-	<1	<1	17	-	-	-	-	-	-
Terschellingia sp.1	1A	13	1	15	20	2	11	33	4	8	24	2	12	52	7	4	10	2	12	<1	<1	17	2	<1	17	1	<1	18	9	6	6	5	2	9	4	<1	12
Pontonema sp.1	2B	1	<1	26	2	<1	23	<1	<1	17	50	4	8	48	6	5	21	3	8	17	5	5	17	6	7	4	2	10	11	7	5	4	1	13	6	<1	11
Theristus sp. 1	1B	1	<1	27	<1	<1	26	4	<1	12	-	-	-	3	<1	17	26	4	7	81	24	2	79	27	1	93	36	1	29	18	2	176	54	1	404	60	1
Pierrickia sp. nov.	1A	-	-	-	<1	<1	27	-	-	-	<1	<1	25	11	1	14	5	<1	16	<1	<1	21	37	13	2	11	4	6	26	17	3	6	2	8	43	6	4
Gomphionema typicum	2A	<1	<1	29	-	-	-	1	<1	13	14	1	13	20	3	11	<1	<1	20	2	<1	15	32	11	3	-	-	-	-	-	<1	-	-	<1	-	-	-
Metadesmolaimus sp. 2	1B	-	-	-	-	-	-	-	-	-	3	<1	18	-	-	-	10	2	13	4	1	11	5	2	12	39	15	2	13	8	4	27	8	2	21	3	6
Metalinhomoeus sp.	1B	14	1	13	8	<1	16	<1	<1	20	-	-	-	11	1	15	<1	<1	23	<1	<1	19	8	3	11	32	12	3	7	4	8	20	6	4	60	9	2
Parodontophora aurata sp. nov.	2B	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	24	-	-	-	2	<1	13	11	4	9	9	4	7	3	2	12	26	8	3	25	4	5
Monhysterida sp. 4	1B	3	<1	21	-	-	-	6	<1	11	-	-	-	-	-	-	<1	<1	22	6	2	10	3	<1	16	6	2	9	1	<1	16	5	1	11	14	2	8
Parascolaimus breviseta sp. nov.	1B	-	-	-	-	-	-	<1	<1	20	-	-	-	-	-	-	<1	<1	23	<1	<1	22	<1	<1	23	3	1	13	7	4	9	13	4	6	9	1	10
Oncholaimus domesticus	2B	2	<1	25	7	<1	17	1	<1	15	<1	<1	23	-	-	-	-	-	-	7	2	8	5	2	15	-	-	-	3	2	14	3	<1	14	<1	<1	16
Neochromadora sp. 1	2A	2	<1	23	45	5	7	<1	<1	20	3	<1	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	18
Paracomesoma sipho	2A	6	<1	19	1	<1	24	1	<1	14	13	1	14	<1	<1	22	3	<1	17	<1	<1	23	-	-	-	-	-	-	-	-	-	<1	<1	18	-	-	-
Camacolaimus sp.	1A	9	<1	16	8	<1	14	-	-	-	<1	<1	24	<1	<1	23	1	<1	19	<1	<1	19	<1	<1	23	<1	<1	19	-	-	-	<1	<1	20	-	-	-
Subsphaerolaimus sp. nov.	1B	-	-	-	-	-	-	<1	<1	17	-	-	<1	16	2	12	-	-	-	-	-	-	<1	<1	25	-	-	-	<1	<1	18	-	-	-	-	-	-
Epacanthion georgeii	2B	2	<1	24	5	<1	19	-	-	-	12	1	15	<1	<1	24	<1	<1	25	-	-	-	-	-	-	<1	<1	19	-	-	-	-	-	-	-	-	-
Chromadorida 2	2A	13	1	14	37	4	8	<1	<1	17	2	<1	22	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	21	-	-	-	-	-	-	-	-	-
Pomponema sp.1	2A	5	<1	20	7	<1	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	19	-	-	-	-	-	-	-	-	-	-	-	-
Onyx cephalispiculum sp. nov.	2A	16	1	12	3	<1	22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	22	-	-	-	-	-	-	-	-	-	-	-	-
Pseudochromadora cazca	2A	2	<1	22	<1	<1	25	-	-	-	57	5	7	3	<1	18	17	3	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Choniolaimus papillatus	2B	<1	<1	29	<1	<1	27	-	-	-	5	<1	17	7	<1	16	2	<1	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Neochromadora sp 2	2A	<1	<1	29	-	-	-	1	<1	15	9	<1	16	-	-	-	<1	<1	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Daptonema sp.	1B	<1	<1	28	5	<1	19	<1	<1	20	2	<1	21	2	<1	19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Monhysterida sp. 3	1B	20	2	9	-	-	-	-	-	-	-	-	-	<1	<1	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pomponema sp.2	2A	7	<1	17	4	<1	21	-	-	-	<1	<1	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mesacanthion sp. nov.	2B	6	<1	18	8	<1	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mean total density (No. 10cm^{-2})		1138.9			877.5			931.4			796.7			618.8			335.4			297.5			256.8			160.0			328.3			668.4			297.5		
Total number of species		49			49			30			41			36			31			25			27			24			21			25			22		

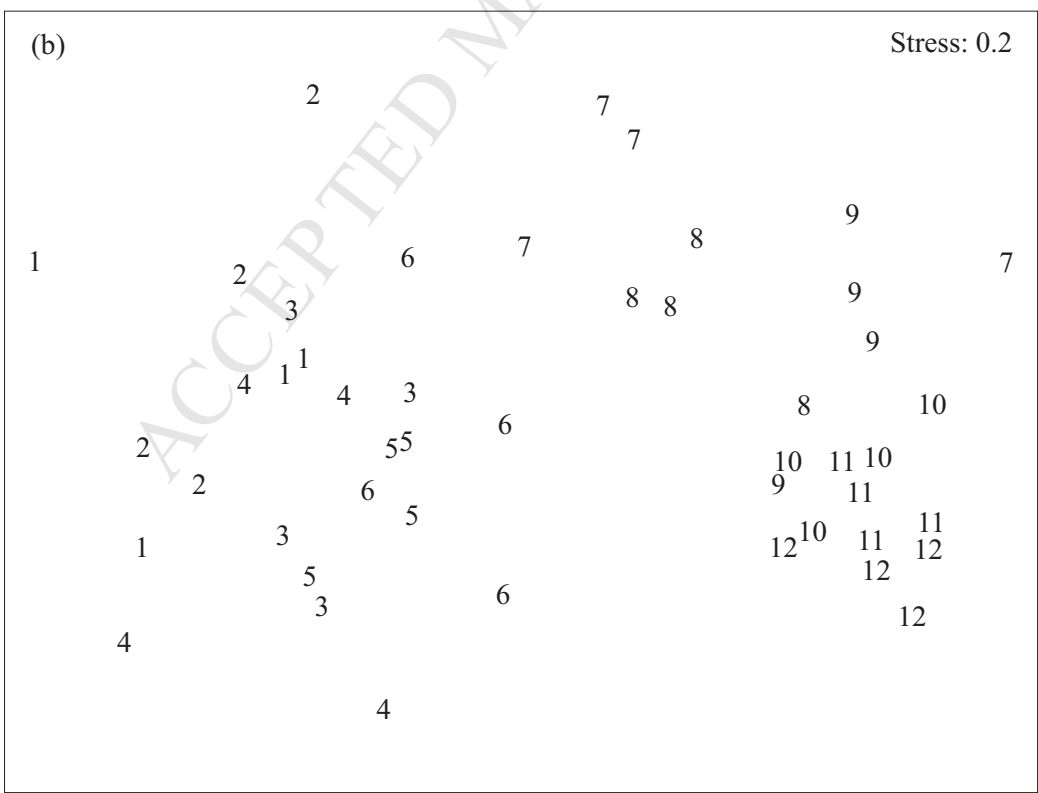


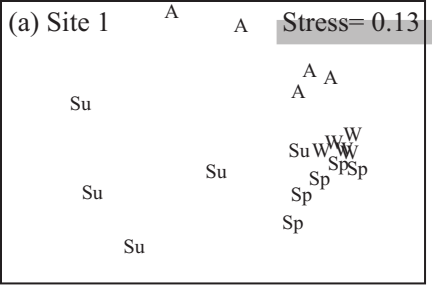


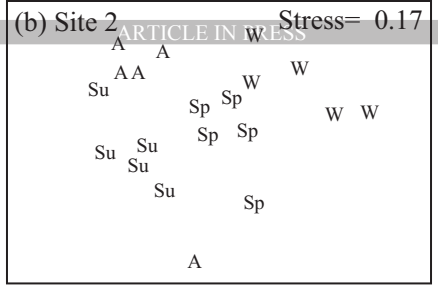


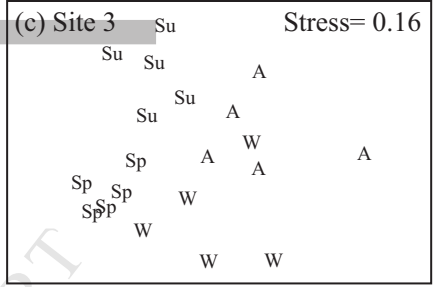


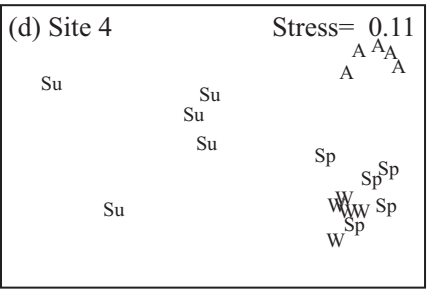


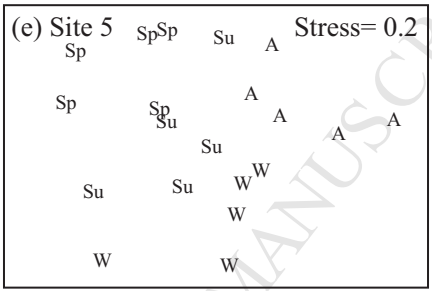


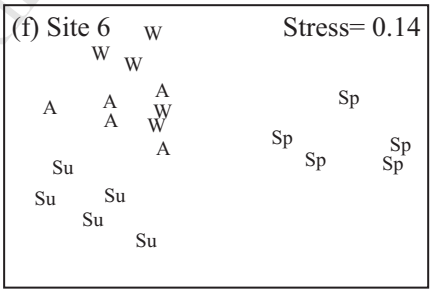


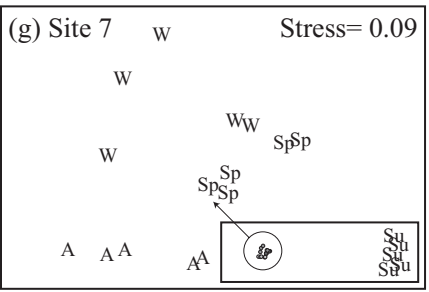


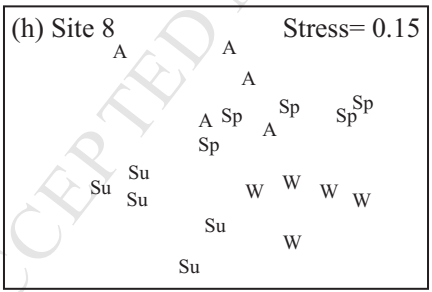


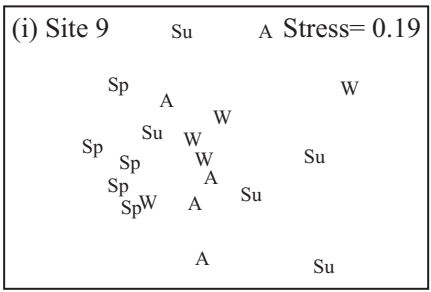


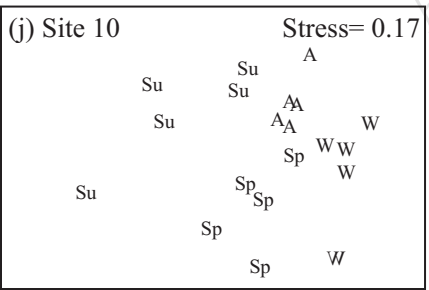


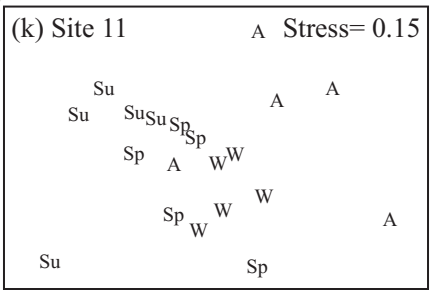


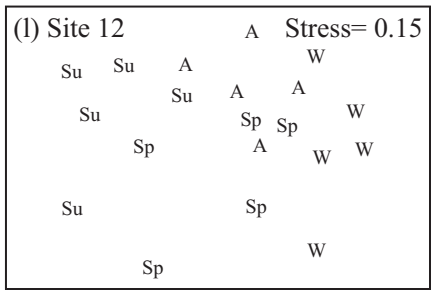


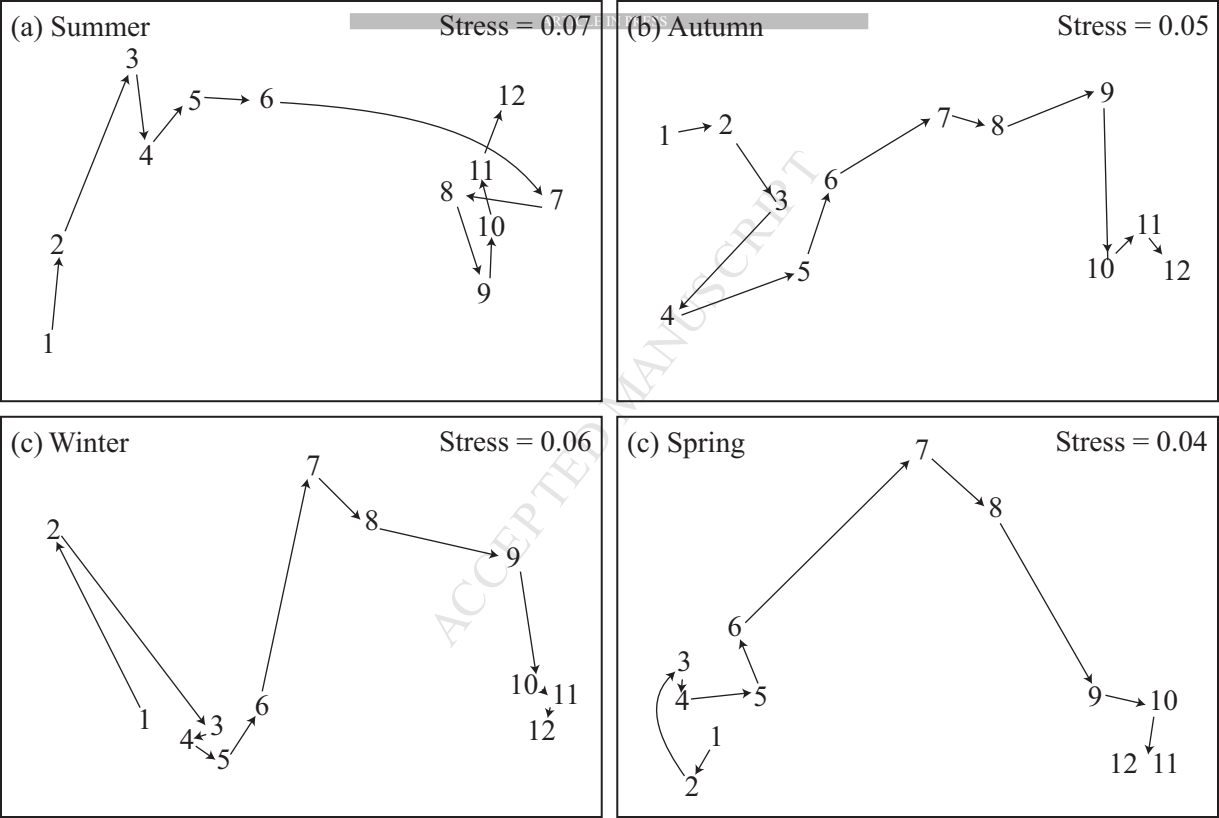


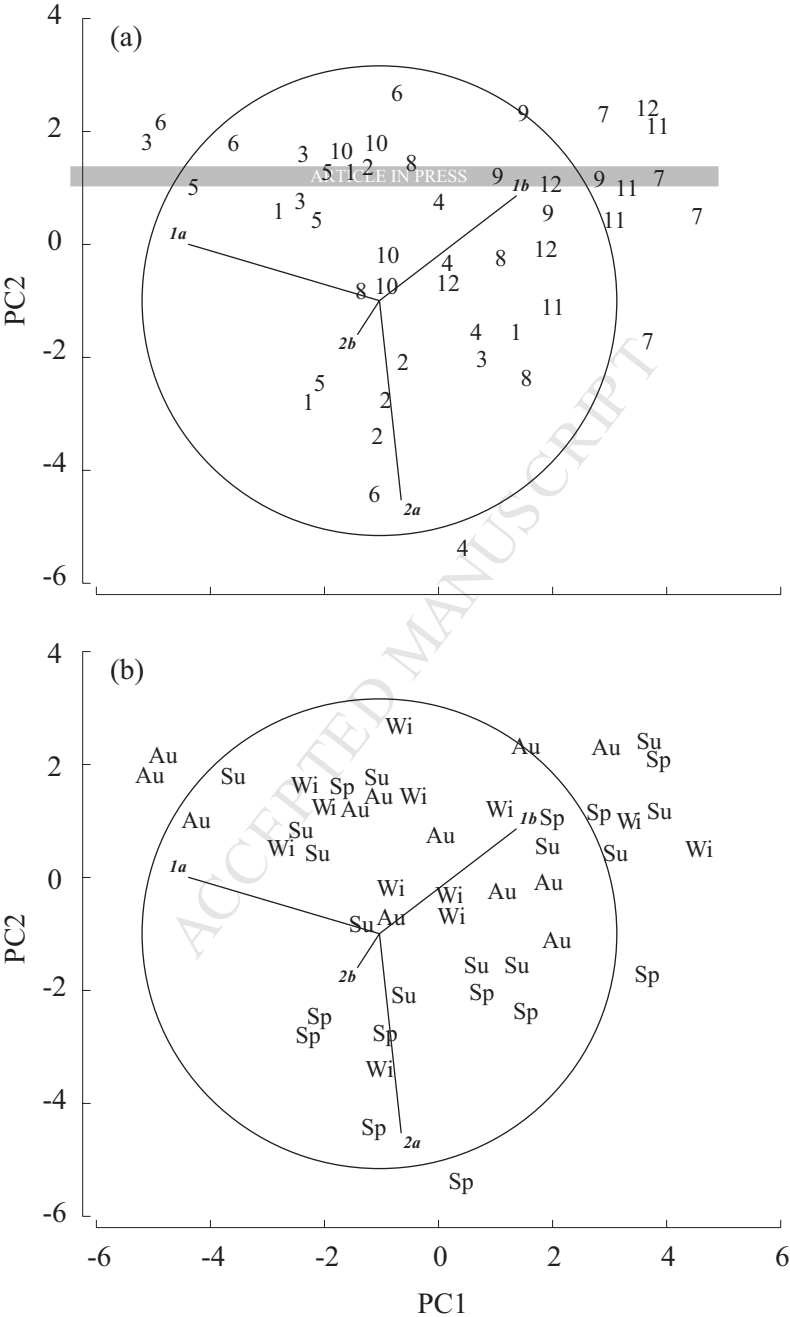








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