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1 **Nematode community dynamics over an annual production cycle**
2 **in the central North Sea**

3

4 M. Schratzberger*, R. M. Forster, F. Goodsir, S. Jennings

5

6 *The Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory,*

7 *Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK*

8

9 * Corresponding author: Tel. +44(0)1502-527743, Fax. +44(0)1502-513865

10 *E-mail address:* michaela.schratzberger@cefas.co.uk (M. Schratzberger)

11 **Abstract**

12

13 Nematode species composition, trophic structure and body size distributions were followed
14 over an annual production cycle in the central North Sea; to test responses to temporally
15 changing food quality and quantity in the sediment. Changes in the phytoplankton
16 concentration in the water column were quantitatively reflected in the concentration of
17 chlorophyll *a* and breakdown products in the sediment, with higher concentrations in spring
18 and autumn following blooms, and lower concentrations in summer and winter. The
19 taxonomic and trophic structure of nematode communities differed significantly among
20 stations over relatively short distances, potentially masking some of the temporal dynamics.
21 Spatio-temporal differences in nematode species composition were linked to changes in the
22 quality and quantity of organic material reaching the seabed, reflecting a species-specific
23 response to the nutritional quality of sedimenting organic material and the biochemical
24 changes in the sediment associated with its decomposition. The size distributions of selected
25 nematode species indicated that most species bred continuously throughout the sampling
26 period, although one species, the epigrowth feeder *Spilophorella paradoxa*, had periods of
27 increased growth following the deposition of the spring phytoplankton bloom. There was no
28 consistent temporal relationship between the trophic composition of nematode communities
29 and spring chlorophyll *a* or carbon sedimentation, most likely a result of the trophic plasticity
30 of most feeding types and the capacity of the community to use both freshly sedimented
31 material as well as the subsequent breakdown products and refractory organic matter.
32 Community metrics implied that there were small responses to the seasonal production cycle,
33 but these belied strong responses of a few species with life histories that allowed them to
34 track the availability of suitable food resources.

35

36 *Key words:* Nematodes; Taxonomic and functional community composition; Benthic-pelagic
37 coupling; Food quality; Food quantity; North Sea

38

39 **1. Introduction**

40

41 The ecology of marine food webs at higher latitudes is strongly influenced by broadly
42 predictable production cycles, driven by changes in nutrient supply, solar radiation and wind
43 stress (Colebrook and Robinson, 1961). The production cycle in stratified temperate seas is
44 characterised by one or more distinct phytoplankton blooms. The spring bloom is often
45 dominated by larger-celled groups such as diatoms, followed by proliferation of nano- and
46 picoplankton populations throughout the summer and autumn. The fate of carbon generated
47 by phytoplankton depends on whether energy and nutrients fixed during blooms are recycled
48 in the water column, exported to higher trophic levels or transferred to the seabed (Jago et al.,
49 2007). After the bloom, fresh organic material sinking to the bottom is partly incorporated
50 into the sediment as detrital particles or becomes adsorbed to sediment grains.

51 Sedimentation of organic matter represents the major input of production to the benthic
52 community on an annual basis and is a major factor influencing benthic community structure,
53 biomass and metabolism (Graf et al., 1982). Energy produced during annual production
54 cycles propagates through the food web, with increasing lag and attenuation as it passes to
55 larger animals with slower turnover times (Pope et al., 1994). Smaller benthic animals are
56 likely to track the production cycle most closely, as their high relative rates of consumption
57 and fast turnover times allow them to rapidly assimilate available production. The ecology
58 and life histories of meiofauna (invertebrates that pass through a 500 – 1000 μm mesh sieve
59 but are retained on a 32 – 63 μm mesh sieve; Giere, 1993) suggest that their population and
60 community dynamics will respond to the seasonality of production.

61 Meiofauna play an important role as intermediaries between the microbial/detrital
62 compartments (by influencing bacterial density and biomass; Mikola, 1998), and larger
63 organisms (by serving as major food sources for higher trophic levels; Danovaro et al., 2007)
64 in food webs (Chardy and Dauvin, 1992; Schmid-Araya et al., 2002). However, little is
65 known about how food quality and quantity affect natural populations (Findlay, 1982;
66 Danovaro and Gambi, 2002). Seasonal data on meiofauna abundance, reproduction and

67 species composition are essential for conceptualising and modelling trophic dynamics
68 (Fleeger, 1985) but to date, relationships between faunal characteristics and phytoplankton
69 sedimentation have proven elusive. This is partly a result of the rarity of surveys which
70 monitor phytoplankton sedimentation and faunal responses adequately. Thus most ecological
71 studies of meiofauna have focused on intertidal or shallow subtidal habitats. When deeper
72 water environments were studied, sampling designs rarely permitted repeated sampling at
73 multiple stations or over more than one season (e.g. Vanaverbeke et al., 2004a and references
74 therein).

75 Phytoplankton sedimentation is likely to affect meiofauna communities as many species live
76 close to the sediment surface, feeding on diatoms and epigrowth (i.e. algal cells attached to
77 particles). Fresh organic material is expected to reach deeper dwelling, deposit and bacteria
78 feeding species during later stages of phytoplankton decomposition (Graf et al., 1982;
79 Rudnick, 1989). Indeed, temperature and food availability are the factors most often invoked
80 to explain seasonal changes in meiofaunal abundance (Heip et al., 1985; Ólafsson and
81 Elmgren, 1997).

82 Taxon-based approaches are commonly used to study temporal dynamics of meiofauna.
83 Aggregating taxonomically similar species or different developmental stages of the same
84 species, however, does not take account of the diverse biology and autecological requirements
85 of the organisms (Schratzberger et al., 2007). These issues have been taken into account by
86 adopting functional and size-based approaches. The functional group approach classifies
87 organisms by morphological characteristics that are thought or known to represent an
88 important ecological function (Chalcraft and Resetarits, 2003). However, links between
89 morphology and function can be weak and inconsistent, in some cases leading to an uncertain
90 separation of taxonomic and functional approaches. The size-based approach focuses on the
91 aggregation of organisms based on individual body weight, often independent of their
92 taxonomy. Size is linked to processes such as metabolism and productivity, but size-based
93 approaches may not reflect complex differences in the feeding ecology of different sized
94 organisms.

95 Since taxonomic, functional and size-based approaches focus on different aspects of
96 assemblage structure, a combination of all three methods is likely to provide better
97 understanding of seasonal changes in assemblage structure, dynamics and responses to
98 changing food supply. Here, we study meiofaunal nematode community dynamics in the
99 central North Sea to assess how taxonomic, trophic and biomass distribution patterns varied
100 during a seasonal production cycle. We relate community changes to changing food quality
101 and quantity in the sediment to investigate two questions:

102 (1) Does a local increase in food promote consistent temporal changes in the taxonomic,
103 trophic and size structure of nematode communities?

104 (2) Do selected nematode species, representing the main taxonomic and trophic categories
105 available to the phylum, respond in a differential way to a pulsed food supply?

106

107 **2. Material and methods**

108

109 *2.1. Study site*

110

111 We studied nematode communities in the Silver Pit, central North Sea (Fig. 1). The Silver Pit
112 is predominantly 60 – 80 m deep with a muddy-sand substratum and the water column
113 stratifies in summer months. Parts of the Silver Pit are fished by beam trawlers but there is
114 limited evidence that trawling disturbance has significant effects on nematode community
115 structure. Thus a previous experimental study in the Southern North Sea, investigating acute
116 effects of trawling disturbance on nematodes, showed that seasonal changes in assemblage
117 structure were greater than those attributed to trawling (Schratzberger et al., 2002). Sub-
118 surface temperature at 35 m depth at the sampling stations was low during spring and summer
119 (6 – 8 °C February to June, 9 – 10 °C in July), peaked in late summer (11 – 16 °C August to
120 October) and declined again during autumn and winter months (8 – 10 °C November to
121 January) (Paul McCloghrie, unpublished data).

122

123 *2.2. Sample collection*

124

125 Sediment samples were collected with a NIOZ corer on six cruises in 2005 and 2006 (21 – 26
126 May, 12 – 16 July, 29 September – 4 October, 5 – 10 November 2005; 13 – 17 February, 26
127 April – 5 May 2006) from seven randomly chosen locations within 50 m of each of three
128 stations (Fig. 1). The NIOZ corer takes a circular core of 0.1 m² to a depth of > 30 cm. The
129 surface of the sediment core is relatively undisturbed, and the corer retains a few cm of the
130 overlying water.

131 From each deployment, two sediment sub-samples were collected with a perspex corer (2 cm
132 diameter, 3.14 cm² surface area) to a depth of 5 cm. On each sampling date, sub-samples were
133 combined by station and frozen at -20 °C prior to the analysis of particle size and organic
134 carbon content. From each of the first three deployments, two further sub-samples were
135 collected, one for the analysis of sediment chlorophyll *a*, the other for the analysis of
136 sediment porosity. These sub-samples were frozen separately at -20 °C pending analysis. As
137 sediments reflect a time-averaged input of phytodetritus to the benthic system, sediment
138 chlorophyll *a* concentrations are likely to show a more reliable pattern of annual algal
139 biomass and sedimentation than near-bottom water samples. Boon et al. (1998) and Franco et
140 al. (2007) showed that the typical algal spring bloom is quantitatively reflected in the
141 chlorophyll *a* concentration of the majority of North Sea sediments.

142 From each of the last four deployments at each location, a meiofauna sub-sample was
143 collected with a 5.5 cm internal diameter perspex tube (surface area 23.76 cm²) to a depth of 5
144 cm. All faunal samples were fixed and preserved in 10 % formalin in filtered seawater.

145

146 *2.3. Sample processing*

147

148 After thawing, sediment samples were wet sieved through a 500 μm sieve, and the fraction >
149 500 μm was oven dried at 90 $^{\circ}\text{C}$ for 24 h. This fraction was then dry sieved at 0.5 phi
150 intervals, down to 1 phi (500 μm). The fraction < 500 μm was freeze dried and analysed on a
151 Coulter LS 130 Laser sizer. The laser sizer results were combined with the dry sieve results to
152 give the full particle size distribution. The mean particle size diameter (hereafter referred to as
153 grain size) was calculated from these results (Dyer, 1986). The total organic carbon content of
154 the sediment fraction < 63 μm was determined with a Leeman CE 440 elemental analyser.
155 Total organic carbon in the sediment consists of a variety of compounds with different
156 decomposition rates based on their structures and susceptibility to biological attack (Henrichs
157 and Doyle, 1986). Organic matter in the majority of marine sediments is complex and
158 generally of less degradable (i.e. refractory) nature (Fabiano and Danovaro, 1994).
159 Defrosted sediment chlorophyll *a* samples were extracted in neutralised 90 % acetone for 24 h
160 at 4 $^{\circ}\text{C}$ in the dark. Measurements of extracted chlorophyll fluorescence were made (before
161 and after acidification with 8 % hydrochloric acid to distinguish phaeopigments) using a
162 Turner Design (Model 10 AU) filter fluorometer (Tett, 1987). Sediment chlorophyll *a* and
163 phaeopigment concentrations in the interstitial water were corrected for porosity, determined
164 from the dry weights and wet weights of known volumes of sediment. Sediment chlorophyll *a*
165 concentrations were used as an index of phytodetrital concentration (Boon and Duineveld,
166 1998). Temporal changes in chlorophyll *a* breakdown products (phaeopigments) and
167 chlorophyll *a*:phaeopigment ratios were tracked as indices of phytoplankton bloom
168 degradation.
169 After washing the meiofauna samples onto a 38 μm sieve, fauna were extracted with Ludox
170 TM 40 (Somerfield and Warwick, 1996). The extraction was repeated three times. The
171 extracts were sub-sampled following the method described by Somerfield and Warwick
172 (1996). Sub-samples of 5 % of the extracted material (containing 85 – 448 nematodes,
173 average = 226 nematodes) were evaporated slowly in anhydrous glycerol and mounted on
174 slides for further analysis. The numbers of individuals identified should give reasonable, and
175 comparable, estimates. Nematodes consistently comprised > 95 % of total meiofauna

176 abundance in all samples. Temporal dynamics of nematode communities in the Silver Pit
177 were investigated by analysing changes in their taxonomic and trophic composition as well as
178 changes in their size distribution.

179

180 *2.3.1. Taxonomic analysis*

181 All nematodes in each sub-sample were identified to genus or species level, using the
182 taxonomic keys of Platt and Warwick (1983, 1988) and Warwick et al. (1998) and the online
183 information system NeMys (Deprez, 2005; www.nemys.ugent.be). These are based on a
184 phylogenetic classification scheme, where the structure of the taxonomic tree approximates
185 the evolutionary relationships among organisms. Changes in phylogenetic diversity of species
186 assemblages, however, are not explicitly linked to changes in functional diversity and so their
187 ecological significance can be difficult to assess (Walker et al., 1999; Warwick and Clarke,
188 2001)

189

190 *2.3.2. Trophic analysis*

191 Despite the uniform organisation of free-living nematodes, a great diversity in mouth
192 structure exists which reflects the ecological role of the species (Heip et al., 1985). Based on
193 these morphological characteristics, Wieser (1953) devised a classification of feeding types
194 including selective deposit feeders consuming bacteria and small-sized organic particles, non-
195 selective deposit feeders also feeding on organic deposits but targeting larger-sized particles,
196 epigrowth feeders scraping food off surfaces or feeding on diatoms and microalgae and
197 predators feeding on nematodes and other small invertebrates. The disadvantage of this
198 scheme is that it confines species to a single trophic role when many non-selective deposit
199 feeders are known to be omnivores. For example, while the omnivores may feed on particles
200 of a restricted size, their food can include bacteria, small flagellates and non-living
201 aggregates. Moreover, many selective deposit and epigrowth feeders feed on diatoms but
202 these are only numerous in shallow sediments and little is known about their diet in deeper
203 sediments (Heip et al., 1985) and some genera classed as predators may scavenge dead

204 organic material as juveniles. Thus various authors have revised and modified Wieser's
205 classification (Romeyn and Bouwman, 1983; Jensen, 1987; Moens and Vincx, 1997; Moens
206 et al., 2004). However, in the absence of experimental evidence to describe the feeding habits
207 of most species, Wieser's scheme remains the most feasible trophic classification of free-
208 living marine nematodes from a variety of habitats.

209

210 2.3.3. Size-based analysis

211 Many biological and ecological processes are related to body size (Peters, 1983; Brown et al.,
212 2004). In contrast to taxonomic and functional approaches, size-based analyses assume that
213 all organisms of the same size, independent of their taxonomic or functional identity, will
214 behave in approximately the same way in bioenergetic terms.

215 Individual body sizes were determined for nematodes in three of the four faunal replicates.
216 One percent of all nematodes in each replicate (corresponding to a total of 2454 individuals),
217 irrespective of species identity, were randomly selected for the calculation of individual body
218 mass from allometric relationships linking body dimensions to mass. Nematode length
219 (except long, filiform tails where present) and maximum width were measured using image
220 analysis (Image Pro Plus version 4.5). The body mass of individuals was then calculated with
221 the formulae of Andrassy (1956). Although more laborious, this volumetric, as opposed to a
222 gravimetric, method was chosen since it is non-destructive and keeps measured specimens
223 intact for taxonomic identification and the analysis of size distributions (Udalov et al., 2005).
224 Nematode size distributions were described for each sample by assigning individuals to log₂
225 body-mass classes and calculating the proportion of all individuals in each class.

226 The similarities percentages procedure (SIMPER; Clarke, 1993) was used to identify species
227 that consistently contributed to spatio-temporal differences between assemblages. These
228 included the epigrowth feeder *Spilophorella paradoxa*, the non-selective deposit feeder
229 *Sabatieria punctata* and the selective deposit feeder *Leptolaimus elegans* and individual body
230 mass was therefore also estimated for these species separately. The percentages of organisms
231 measured were 3 % of all *Sabatieria punctata* (corresponding to a total of 1479 individuals)

232 and 5 % of all *Spilophorella paradoxa* and *Leptolaimus elegans* (corresponding to a total of
233 372 and 1129 individuals respectively).

234

235 *2.4. Coupling of sediment and water column chlorophyll a*

236

237 An archive of surface chlorophyll *a* concentration images, derived from MODIS-Aqua
238 satellite ocean colour data using a modified version of the case-II water algorithm ‘OC5’
239 (Gohin et al., 2002), was processed and supplied by Ifremer, France. This regional algorithm
240 differs from generic, global satellite chlorophyll products in that additional sensor bands are
241 used to correct for the presence of suspended sediments and the chromophoric (coloured)
242 fraction of dissolved organic matter (cDOM). The surface chlorophyll maps cover the north-
243 west Atlantic shelf at a resolution of 1 km² and were made available for the time period June
244 2002 to present by the EU/ESA project MarCoast (Marine and Coastal Environmental
245 Information Services; www.gmes-marcoast.com). Maps in the archive were queried with the
246 ‘Zonal Statistics’ function of ArcMap version 9.2 in order to extract discrete chlorophyll *a*
247 values for the surface waters of the sampling stations A, B and C (Fig. 1). This approach
248 provided a time-series of surface chlorophyll *a* estimates for each station. Valid, cloud-free
249 estimates of chlorophyll *a* were obtained on approximately 23 % of all days during the time
250 period of the study. The pelagic chlorophyll *a* values were then assembled, converted to
251 monthly means and compared with chlorophyll *a* concentrations in the sediment.

252

253 *2.5. Data processing*

254

255 *2.5.1. Univariate methods*

256 Spatial and temporal patterns of environmental variables were investigated using Kruskal-
257 Wallis one-way analysis by ranks where measures are transformed to ranks, ignoring group
258 membership. The ranks were used to test the null-hypothesis (H_0) that there was no significant

259 shift in the centre of the groups between stations and over time. There was no statistically
 260 significant co-variation between the environmental measures included in the analyses.

261 Total nematode abundance, species diversity of the entire community and diversity within the
 262 four feeding types (H') were calculated from the species abundance data (Shannon and
 263 Weaver, 1949):

264

$$265 \quad H' = \sum_{i=1}^S p_i (\ln p_i)$$

266

267 where p_i is the number of individuals in the i^{th} species (n_i) divided by the total number of
 268 individuals (N).

269

270 The Index of Trophic Diversity (ITD), based on the proportion of each of four feeding types
 271 was calculated following Heip et al. (1985). ITD values range from 0.25 (highest trophic
 272 diversity with the four trophic groups accounting for 25 % each) to 1.0 (lowest trophic
 273 diversity when a single feeding type is present):

274

$$275 \quad \text{ITD} = \sum \theta^2$$

276

277 where θ is the percentage contribution of each of four feeding types according to Wieser
 278 (1953).

279

280 Average individual body mass was calculated from the body dimensions across all species
 281 present in the total nematode community and for populations of *Spilophorella paradoxa*,
 282 *Sabatieria punctata* and *Leptolaimus elegans*.

283 Bartlett's and Cochran's tests were used to test for homogeneity of variance before spatio-
 284 temporal variations in all community attributes were analysed by two-way analysis of
 285 variance (ANOVA). Following the detection of significant 'station' and sampling 'month'

286 effects, the Tukey HSD multiple comparisons test was used in pair-wise comparisons of
287 samples. When the interaction term station x month was significant, the two-way ANOVA
288 was broken down to a one-way ANOVA.

289 All univariate statistical analyses were performed using the software package Statgraphics
290 Plus version 3.3.

291

292 *2.5.2. Multivariate methods*

293 Non-metric multi-dimensional scaling (MDS) ordination using the Bray-Curtis similarity
294 measure (Clarke et al., 2006) was applied to the relative abundance (i.e. proportion) of
295 species, feeding types and geometric size classes (Clarke and Warwick, 2001). The statistical
296 significance of spatial differences (averaged over the 12-month study period) and changes in
297 distribution patterns over time (averaged over the three stations) were assessed by two-way
298 crossed analysis of similarities (ANOSIM; Clarke, 1993), a non-parametric analogue of the
299 univariate ANOVA.

300 BIO-ENV (Clarke and Ainsworth, 1993) and BVSTEP (Clarke and Warwick, 1998) were
301 used to investigate relationships between environmental variables and the species, feeding
302 type and size composition of nematode communities. Spearman rank correlations (R) between
303 resemblance matrices derived from faunal data (based on Bray-Curtis similarity) and matrices
304 derived from various sub-sets of environmental data (based on normalised Euclidean
305 Distance) were used to identify suites of variables that best explained observed community
306 patterns. The significance of the correlations was determined using a permutation procedure
307 (Stoffels et al., 2005).

308 All multivariate statistical analyses were performed using Primer version 6.1.5 (Clarke and
309 Gorley, 2006).

310

311 **3. Results**

312

313 *3.1. Benthic habitat in the Silver Pit*

314

315 All stations comprised soft bottom, muddy habitat. Stations were comparable with respect to
316 water depth (A: 63 m, B: 64 m, C: 55 m) and sediment granulometry, although grain size at
317 station C was slightly smaller than at station A and B (Table 1). The silt-clay content of the
318 sediment did not differ significantly between stations and seasons, nor did the content of total
319 organic carbon (Table 2). A temporal trend in chlorophyll *a* and phaeopigment concentrations
320 in the sediment was apparent with a distinct peak in May 2005 and to a lesser extent in
321 September 2005 (Tables 1 and 2, Fig. 2).

322

323 *3.2. Coupling of sediment and water chlorophyll a*

324

325 Pelagic chlorophyll *a* concentrations were typically higher to the north and to the south of the
326 Silver Pit than over the central Silver Pit (see Fig. 1 for a monthly composite image of April
327 2005). Time series analysis showed that the spring bloom started in the first week of April in
328 both 2005 and 2006. Water chlorophyll *a* concentration was low in summer in both years,
329 especially at station C (Fig. 3). It is likely that a deep chlorophyll maximum is present during
330 this period of strongly stratified conditions (Olesen, 1995; Richardson et al., 2000), but this
331 cannot be detected by the satellite. There was an autumn bloom in both years peaking during
332 late September and early October. The spring bloom of 2006 was more pronounced than in
333 2005.

334 The most productive station was station A with a mean water chlorophyll *a* concentration of
335 $0.75 (\pm 0.60) \text{ mg m}^{-3}$ over the study period. Station B was intermediate with $0.64 (\pm 0.44) \text{ mg}$
336 m^{-3} and station C was lowest with a mean value of $0.55 (\pm 0.37) \text{ mg m}^{-3}$. Hence there was a
337 gradient in pelagic productivity through the Silver Pit from west (high) to east (low), with
338 station A being closest to the areas of high primary production to the north and south of the
339 Silver Pit (Fig. 1). Higher phytoplankton abundance at the surface was reflected in higher
340 pigment concentrations in the upper layers of the sediment, particularly during the spring

341 bloom of both years (Fig. 3). However, the relationship between surface production and
342 benthic deposition differed considerably between 2005 and 2006 (Fig. 3). It is unknown to
343 what extent the settling particles are buried in the sediment at the place they arrive on the
344 seafloor and how much is lost to other areas by advection near the sediment surface.

345 The temporal variability of pulses of primary production reaching the seafloor along the
346 gradient of pelagic productivity allowed us to investigate the relationship between nematode
347 taxonomic, trophic and size structure and changes in food quality and quantity.

348

349 3.3. Nematode species and feeding types

350

351 The analysis of spatio-temporal differences in community-related measures (Table 3) showed
352 that density, species diversity and trophic diversity were higher at station A and B than at
353 station C. Similar trends were recorded for species diversity within the four feeding types
354 (data not shown). Spatial differences in univariate community attributes were generally more
355 pronounced than temporal trends. With the exception of trophic diversity (ITD), the
356 magnitude and direction of spatial differences were maintained throughout the 12-month
357 study period. ITD did not change significantly over time at station A and B and decreased
358 within the first 9 months at station C ($p = 0.059$). Communities at station C were most
359 trophically diverse in February 2006.

360 Across all three stations, proportions of the epigrowth feeder *Spilophorella paradoxa* were
361 consistently lower in winter (November 2005) than in spring (May 2005 and April 2006,
362 Table 3, Fig. 4). The non-selective deposit feeder *Sabatieria punctata* dominated nematode
363 communities at station B. Spatial distributions of *Leptolaimus elegans* were not consistent
364 over time nor were temporal dynamics of this species consistent among stations. While
365 relative abundance remained temporally stable at station B and C, values at station A were
366 significantly increased in November 2005 following the autumn bloom (Table 3).

367 As shown in Table 4, the relative abundance of selective deposit feeders ($F = 78.56$, $p <$
368 0.001) and predators ($F = 15.43$, $p < 0.001$) were lowest at station C whereas communities at

369 station A were characterised by relatively low proportions of epigrowth feeders ($F = 26.75$, p
370 < 0.001). Lowest proportions of non-selective deposit feeders were recorded at station B ($F =$
371 6.12 , $p = 0.004$). Temporal patterns of nematode feeding types were inconsistent amongst
372 stations and generally not statistically significant at $p > 0.05$.

373 There were significant spatial differences in distribution patterns of nematode species ($R =$
374 0.583 , $p = 0.001$) and feeding guilds ($R = 0.492$, $p = 0.001$) and these generally dominated
375 temporal dissimilarities (species assemblages: $R = 0.213$, $p = 0.001$, trophic groups $R = 0.065$,
376 $p = 0.089$; Fig. 5).

377 Distribution patterns of nematode species were correlated with grain size, total organic carbon
378 content in the sediment and sedimentary chlorophyll *a*:phaeopigment ratios ($R = 0.533$, $p =$
379 0.010). Spatial differences in species distribution patterns were most marked in May 2005
380 when station-specific differences in chlorophyll *a*:phaeopigment ratios were highest (Table 1).

381 A combination of grain size and total organic carbon content in the sediment best explained
382 the trophic structure of assemblages ($R = 0.424$, $p = 0.010$). Spatial differences in the trophic
383 structure of nematode assemblages were most pronounced in April 2006 and coincided with
384 low levels of total organic carbon in the sediment (Table 1).

385

386 3.4. Nematode body size

387

388 Spatially significant differences in individual body mass across the entire community
389 included a higher average individual body mass at station C than at station A and B whereas
390 the opposite trend was observed for populations of the epigrowth feeder *Spilophorella*
391 *paradoxa* and the non-selective deposit feeder *Sabatieria punctata* (Table 5). Average
392 individual body mass remained stable over the 12-month study period for the total community
393 and for *Sabatieria punctata* and *Leptolaimus elegans* populations. Individual body mass of
394 *Spilophorella paradoxa*, in contrast, peaked in September 2005 at all stations (Fig. 6).

395 In contrast to functional analyses, the investigation of the distribution of both absolute (not
396 shown) and relative nematode abundance across body size classes revealed significant

397 temporal differences. Conversely, spatial differences were less pronounced when the total
398 community was taken into account (Table 6). We observed a shift from larger to smaller
399 individuals over the 12-month production cycle but this could not be linked to any of the
400 measured environmental variables ($p > 0.05$).

401 At all three sampling stations, populations of the epigrowth feeder *Spilophorella paradoxa*
402 were dominated by mature adults, as indicated by an abundance peak in size class -1 (Fig. 7).
403 Significant spatial and temporal dissimilarities in the body size distribution (Table 6) were
404 clearly related to differences in the total organic carbon content and the progression of
405 chlorophyll *a* decomposition (i.e. chlorophyll *a*:phaeopigment ratio) in the sediment
406 throughout the annual production cycle ($R = 0.368$, $p = 0.040$). There was a clear temporal
407 succession in the size distribution of individuals in the population of *Spilophorella paradoxa*
408 (Fig. 8) following deposition of the spring phytoplankton bloom in May 2005 and its
409 decomposition over the following 11 months. Relatively high levels of both fresh (i.e. high
410 chlorophyll *a*:phaeopigment ratios) and refractory (i.e. total organic carbon content) organic
411 material in the sediment in May 2005 coincided with approximately equal proportions of
412 juveniles and adults in the population, indicating continuous asynchronous breeding. Adults
413 clearly dominated in July and September 2005 when sub-surface temperatures peaked and
414 food availability was still high. The abundance of small individuals increased and that of
415 larger individuals decreased over the winter months (November 2005 to February 2006) as
416 both sub-surface temperatures and carbon resources in the sediment declined. The distribution
417 of individuals among size classes was most homogeneous in April 2006, prior to the
418 deposition of material from the next spring bloom.

419

420 **4. Discussion**

421

422 It has been estimated that sedimentation of organic matter accounts for approximately half of
423 net primary production in stratified parts of UK shelf seas (Jago et al., 2007). Here we show
424 from paired observations of pelagic and benthic pigment concentration that the degree of

425 transfer between surface and sediment is not constant, and can differ greatly between
426 locations and years. The approximately two-fold higher concentration of phytoplankton in the
427 water column over the Silver Pit during April 2006 did not result in enhanced benthic
428 chlorophyll or carbon concentrations. This could be due to the combined effects of
429 differences in (1) the rate of pelagic consumption (e.g. grazing), (2) local hydrodynamics,
430 resulting in sedimentation of the phytoplankton at other locations and (3) the timing of
431 benthic sample collection (i.e. time elapsed following the pelagic phytoplankton bloom). In
432 the absence of light measurements and live observation of microalgal cells, *in situ* benthic
433 primary production in the Silver Pit cannot be ruled out (McGee et al., 2008). However,
434 investigating sediments from the Dogger Bank in the central North Sea, Reiss et al. (2007)
435 showed that stations below 40 m water depth were characterised by a phytopigment
436 composition originating from pelagic phytoplankton settled on the sea floor.

437 Nematode assemblages were studied at three stations in the Silver Pit area of the central North
438 Sea during a 12-month production cycle to identify the relative importance of different
439 environmental factors (including the quality and quantity of organic material reaching the
440 seafloor) in controlling their taxonomic, trophic and biomass distribution patterns. Our data
441 suggest that spatio-temporal differences in nematode species composition were partly a
442 response to the sedimentation of pelagic production and appeared to reflect species-specific
443 responses to its nutritional quality. These correlative relationships provide valuable pointers
444 to the mechanisms potentially causing the observed variation.

445

446 *4.1. Does a local increase in food promote consistent temporal changes in the taxonomic,*
447 *trophic and size structure of nematode communities?*

448

449 The taxonomic and trophic structure of nematode communities differed significantly among
450 stations over relatively short distances, potentially masking some of the temporal dynamics.
451 Nematode assemblages appeared to respond to spatial gradients of declining grain size and
452 pelagic productivity in the Silver Pit from west to east as evidenced by decreasing density,

453 species diversity and trophic diversity. Taking the entire community into account, average
454 individual body size increased with decreasing grain size and pelagic productivity. This result
455 was counter to the analysis of Udalov et al. (2005) who investigated the relationship between
456 mean nematode individual weight, sediment granulometry and food availability from 120
457 worldwide locations in the depth range 0 – 8260 m. In their analysis, nematode size increased
458 with particle diameter and the concentration of sediment-bound chloroplastic pigments.
459 However, the overall relationships masked more complex patterns within habitat types.
460 Variability of generally more diverse, coarser sediments at shallower depths compared to
461 fluid clays and oozes in the deep sea were mainly responsible for the changes in the nematode
462 size structure from shelf to slope. Thus, the relationships between sediment granulometry and
463 nematode size were strong for intertidal and shallow subtidal habitats but weaker for deeper
464 subtidal areas. Equally, although Udalov et al. (2005) found evidence for decreases in the size
465 of nematodes with decreasing food availability, the correlation with nematode size was
466 significant for oligotrophic areas only and weakened when organic input was sufficient to
467 cover the higher energy consumption rates of larger species (Warwick and Price, 1979). Low
468 pelagic productivity and small grain size at the easternmost station in the Silver Pit resulted in
469 high proportions of large-bodied non-selective deposit and epigrowth feeders in the nematode
470 community whereas the density and diversity of their smaller-sized bacteria feeding
471 congeners was reduced.

472 Although spatial differences in species composition dominated temporal dynamics,
473 significant temporal changes were recorded over the 12-month production cycle. These were
474 linked to changes in the quality and quantity of organic material reaching the seabed, as
475 indicated by the chlorophyll *a*:phaeopigment ratio and the total organic carbon content.
476 Davies and Payne (1984) provided evidence of a large settlement of diatoms immediately
477 after the spring bloom in the northern North Sea, based on changes in the biochemical
478 composition of material collected in moored sediment traps. The significant relationship
479 between species distribution patterns and the state of phytoplankton remineralisation might
480 thus point towards a species-specific response to the nutritional quality of sedimenting

481 organic material and the biochemical changes in the sediment associated with its
482 decomposition (e.g. oxygenation, alterations in decomposer communities such as bacteria
483 etc.).

484 There was no consistent temporal relationship between the trophic composition of nematode
485 communities and spring chlorophyll *a* or carbon sedimentation, most likely a result of the
486 trophic plasticity of most feeding types. Thus different species belonging to one trophic guild
487 may be able to forage on different food sources and/or exploit their food at different rates (De
488 Mesel et al., 2004; Postma-Blaauw et al., 2005). Investigating the uptake of a radio-labelled
489 diatom by meiofauna species in a laboratory experiment, Ólafsson et al. (1999) found that
490 nematodes with similar buccal cavities and of similar size showed surprisingly large
491 differences in uptake, suggesting a strong selection both for and against the diatom among
492 epigrowth and non-selective deposit feeders. Likewise, also in a laboratory study, Moens et
493 al. (1999) demonstrated a highly species-specific response of bacteria feeding nematodes to
494 different types, densities and age structures of bacterial strains.

495

496 *4.2. Do selected nematode species, representing the main taxonomic and trophic categories*
497 *available to the phylum, respond in a differential way to a pulsed food supply?*

498

499 Phytoplankton sedimentation in stratified temperate marine waters is distinctly seasonal, but
500 the majority of studies in subtidal environments found no unequivocal influence of
501 sedimentation on the density and biomass of meiofaunal nematodes (Heip et al., 1985;
502 Ólafsson et al., 1999). However, the apparent absence of a community response may be
503 misleading. Phytoplankton during and after bloom conditions may settle quickly to the
504 seafloor and these fresh cells may be largely intact and rich in nutrients (Graf, 1992;
505 Richardson et al., 2000). Sedimented phytoplankton might be directly ingested or contribute
506 to the microbial loop, ultimately increasing meiofaunal food supply. Fleeger et al. (1989)
507 hypothesised that this variation in phytoplankton settlement might affect meiofaunal
508 survivorship and reproductive success. Our results suggest that populations of species,

509 assumed to feed on fresh organic material such as *Spilophorella paradoxa*, can exhibit
510 temporal patterns in their abundance and size distribution. Given the seasonal cycle of detrital
511 sedimentation, the balance of benthic food input and demand may shift seasonally, with
512 spring surpluses followed by deficits later in the year. Across all three stations, relative
513 abundance of *Spilophorella paradoxa* declined following the spring phytoplankton bloom in
514 May 2005 and reached the lowest values the following November. This suggests that food
515 deficits may be particularly acute for those species that feed at the sediment-water interface
516 and depend on fresh inputs, although other unmeasured factors, such as competition for food,
517 are also likely to influence population dynamics.

518 Temporal dynamics of *Spilophorella paradoxa* populations were clearly linked to the quality
519 and quantity of organic material present in the sediment throughout an annual production
520 cycle, confounded by annual fluctuations in sub-surface temperature. Temperature may
521 trigger or terminate reproductive activities of nematodes and determine the development time
522 of juveniles. Generally, higher ambient temperatures result in shorter development times;
523 however, little is known of the development time of most species (Warwick and Price, 1979
524 and references therein; Moens and Vincx, 2000a). High concentrations of fresh and refractory
525 organic material in the sediment and rising sub-surface temperatures in the Silver Pit in May
526 2005 resulted in approximately equal proportions of juveniles and adults in the population.
527 Developmental time decreased as ambient temperatures increased, leading to adult-dominated
528 populations in July and September 2005 when food availability was still sufficient to cover
529 their metabolic demands. Declining food availability and temperatures slowed growth and,
530 potentially, reproduction in subsequent months, leading to low numbers of individuals across
531 the entire size spectrum in November 2005. The abundance peak of adults in summer 2005
532 was followed by an increase of juveniles between February and April 2006 when
533 temperatures in the sediment began to increase prior to the deposition of the spring
534 phytoplankton bloom.

535 Many deeper dwelling, deposit-feeding nematodes, including populations of *Sabatieria*
536 *punctata* and *Leptolaimus elegans* may not be able to use sedimenting phytoplankton as food

537 directly and they may rely on the microbial loop to stimulate bacterial production from
538 sedimented material. Results from experimental studies, investigating the importance of
539 freshly produced phytoplankton detritus in the diet of meiofauna are conflicting. Rudnick
540 (1989) hypothesised that, in contrast to surface-dwelling nematodes, the food resources of
541 sub-surface deposit feeders are more stable because they have access to and assimilate a
542 portion of the buried pool of older organic matter. Consequently, one might not expect
543 consistent temporal changes in their density and size distribution. Ólafsson et al. (1999)
544 contradicted this hypothesis by revealing that sub-surface dwelling nematode species can
545 assimilate as much phytoplankton carbon per unit biomass as surface dwellers. Recently,
546 Franco et al. (2008) showed that *Sabatieria*-species can benefit from sedimenting
547 phytoplankton by moving to the sediment surface.

548 Patterns of food availability for deposit feeding organisms can be spatially and temporally
549 complex and total organic carbon measurements might be inadequate to elucidate the
550 mechanisms by which food abundance and variety regulate the organisation of deposit-
551 feeding assemblages (Whitlatch, 1981). Whilst such measures provide information on the total
552 standing stock of organic carbon, they generally overestimate its labile, readily utilisable
553 fraction. At the same time, all living components (e.g. bacteria, microphytobenthos,
554 protozoans) represent a high-quality food source but generally account for a minor fraction of
555 the sediment organic carbon pools (Fabiano and Danovaro, 1994; Danovaro and Gambi,
556 2002).

557

558 **5. Conclusions**

559

560 Biomass-size distributions showed the most consistent temporal patterns in nematode
561 assemblages. When applied to the whole community, the size-based approach has significant
562 advantages over taxon-based and functional approaches through its simplicity, since it avoids
563 distinguishing between taxonomic groups or defining distinct trophic guilds (Soetaert et al.,
564 2002). Our results from the central North Sea show that the relationship between

565 phytoplankton sedimentation and meiofaunal response is complex and that community
566 responses are weaker than those of some of the component species. Hence, size-based
567 analyses provided the most insightful results when performed on selected species.

568 The differential responses within communities reflect different life histories and feeding
569 modes and the changes in the resources available during the seasonal production cycle. The
570 rate of response indicates that the life histories of meiofauna allow their populations to track
571 the availability of suitable food resources. Since the feeding habits of most meiofauna species
572 are not well known, the majority of previous studies on the structure and connectedness of
573 aquatic food webs have ignored meiofaunal taxa or aggregated them into broad functional
574 groups. Existing food web data are therefore strongly biased towards trophically higher
575 organisms. Our findings suggest that future investigations of the relationship between size-
576 structure of meiofauna populations (Vanaverbeke et al., 2004b) and potential food sources
577 (Dauwe and Middelburg, 1998), factors regulating meiofauna fecundity (e.g. food,
578 temperature; Moens and Vincx, 2000b) as well as novel information on species-specific
579 feeding habits and preferences (Moens and Vincx, 1999) are crucial to the understanding of
580 their role in food webs.

581

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583

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589

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775 Table 1

776 Sediment properties (mean \pm SE) at the three stations in the Silver Pit over a 12-month production cycle. TOC = total organic carbon, Chl *a* = chlorophyll *a*,

777 Phaeo = phaeopigment

Station	Date	Grain size [μm]	Silt-clay [%]	TOC [%]	Chl <i>a</i> [mg m^{-2}]	Phaeo [mg m^{-2}]	Chl <i>a</i> :Phaeo
A	21 – 26 May 2005	106	21	0.38	89 \pm 16	111 \pm 40	1.2 \pm 0.5
	12 – 16 Jul 2005	98	24	0.49	21 \pm 10	46 \pm 2	0.5 \pm 0.2
	29 Sep – 4 Oct 2005	99	26	0.56	31 \pm 7	73 \pm 3	0.4 \pm 0.1
	5 – 10 Nov 2005	104	22	0.44	7 \pm 1	22 \pm 2	0.3 \pm 0.1
	13 – 17 Feb 2006	86	28	0.51	21 \pm 2	51 \pm 8	0.5 \pm 0.1
	26 Apr – 5 May 2006	84	29	0.20	16 \pm 5	67 \pm 13	0.2 \pm 0.1
B	21 – 26 May 2005	99	21	0.31	26 \pm 4	113 \pm 10	0.2 \pm 0.1
	12 – 16 Jul 2005	83	29	0.36	9 \pm 4	25 \pm 8	0.3 \pm 0.1
	29 Sep – 4 Oct 2005	85	28	0.39	29 \pm 4	67 \pm 13	0.5 \pm 0.1
	5 – 10 Nov 2005	90	26	0.36	8 \pm 1	29 \pm 2	0.3 \pm 0.1
	13 – 17 Feb 2006	92	22	0.33	12 \pm 1	46 \pm 2	0.3 \pm 0.0
	26 Apr – 5 May 2006	97	24	0.33	12 \pm 3	53 \pm 4	0.2 \pm 0.0
C	21 – 26 May 2005	71	26	0.47	72 \pm 38	54 \pm 27	2.5 \pm 1.6
	12 – 16 Jul 2005	78	25	0.34	11 \pm 1	37 \pm 6	0.3 \pm 0.0
	29 Sep – 4 Oct 2005	69	28	0.34	18 \pm 6	54 \pm 4	0.3 \pm 0.1
	5 – 10 Nov 2005	67	29	0.35	11 \pm 1	25 \pm 3	0.4 \pm 0.0
	13 – 17 Feb 2006	73	24	0.44	6 \pm 1	32 \pm 2	0.2 \pm 0.0
	26 Apr – 5 May 2006	74	25	0.33	8 \pm 3	42 \pm 20	0.2 \pm 0.1

778

779 Table 2

780 Results from Kruskal-Wallis one-way analysis by ranks: Spatio-temporal differences in

781 sediment properties

Source	Test statistic	<i>p</i> -value
Grain size		
Station	11.94	0.003
Month	1.09	0.950
Silt-clay		
Station	0.92	0.630
Month	4.13	0.530
Total organic carbon		
Station	3.82	0.148
Month	5.88	0.318
Chlorophyll <i>a</i>		
Station	3.43	0.180
Month	27.41	< 0.001
Phaeopigment		
Station	4.95	0.084
Month	25.80	< 0.001
Chlorophyll <i>a</i> :Phaeopigment		
Station	2.53	0.282
Month	8.72	0.121

782

783 Table 3
 784 Results from two-way analysis of variance (ANOVA): Spatio-temporal differences in
 785 nematode community-related measures and the relative abundance of discriminating species

Source	Sum of squares	Df	Mean square	F-Ratio	p-value
Total abundance (Log)					
Station	0.2681	2	0.1341	8.90	0.001
Month	0.1532	5	0.0306	2.03	0.088
Station x Month	0.1523	10	0.0152	1.01	0.446
Species diversity (H')					
Station	2.9267	2	1.4634	40.36	< 0.001
Month	0.1543	5	0.0309	0.85	0.520
Station x Month	0.4608	10	0.0461	0.05	0.270
Trophic diversity (ITD)					
Station	0.0627	2	0.0331	90.93	< 0.001
Month	0.0034	5	0.0008	2.28	0.059
Station x Month	0.0084	10	0.00084	2.42	0.018
<i>Spilophorella paradoxa</i> [%]					
Station	8.7173	2	4.3587	1.41	0.253
Month	47.5376	5	9.5075	3.08	0.016
Station x Month	38.3231	10	3.8323	1.24	0.288
<i>Sabatieria punctata</i> [%]					
Station	406.4300	2	203.2150	8.97	< 0.001
Month	121.2810	5	24.2562	1.07	0.387
Station x Month	256.3180	10	25.6318	1.13	0.357
<i>Leptolaimus elegans</i> [%]					
Station	452.2720	2	226.1360	33.76	< 0.001
Month	150.2450	5	30.0491	4.49	0.002
Station x Month	137.5660	10	13.7566	2.05	0.045

786

787 Table 4

788 Mean (\pm SE) relative abundance of nematode feeding types (sensu Wieser, 1953) at the three
 789 stations in the Silver Pit over a 12-month production cycle

Station	Date	Selective deposit feeders [%]	Non- selective deposit feeders [%]	Epigrowth feeders [%]	Predators [%]
A	21 – 26 May 2005	21 \pm 1	43 \pm 1	29 \pm 1	6 \pm 0
	12 – 16 Jul 2005	18 \pm 1	38 \pm 2	37 \pm 3	7 \pm 1
	29 Sep – 4 Oct 2005	22 \pm 1	42 \pm 2	31 \pm 0	5 \pm 1
	5 – 10 Nov 2005	29 \pm 2	37 \pm 1	28 \pm 4	7 \pm 2
	13 – 17 Feb 2006	24 \pm 1	42 \pm 2	28 \pm 2	6 \pm 1
	26 Apr – 5 May 2006	20 \pm 2	41 \pm 2	32 \pm 1	7 \pm 1
B	21 – 26 May 2005	17 \pm 2	35 \pm 4	40 \pm 5	8 \pm 1
	12 – 16 Jul 2005	15 \pm 2	35 \pm 1	46 \pm 2	5 \pm 1
	29 Sep – 4 Oct 2005	18 \pm 2	37 \pm 6	42 \pm 5	4 \pm 0
	5 – 10 Nov 2005	15 \pm 2	44 \pm 1	36 \pm 3	5 \pm 1
	13 – 17 Feb 2006	17 \pm 1	34 \pm 3	44 \pm 3	5 \pm 1
	26 Apr – 5 May 2006	18 \pm 1	33 \pm 3	45 \pm 4	4 \pm 1
C	21 – 26 May 2005	8 \pm 2	44 \pm 4	45 \pm 4	2 \pm 1
	12 – 16 Jul 2005	10 \pm 1	46 \pm 2	42 \pm 3	2 \pm 0
	29 Sep – 4 Oct 2005	11 \pm 1	43 \pm 4	44 \pm 4	2 \pm 1
	5 – 10 Nov 2005	11 \pm 0	39 \pm 4	45 \pm 4	5 \pm 0
	13 – 17 Feb 2006	15 \pm 3	40 \pm 4	40 \pm 2	5 \pm 1
	26 Apr – 5 May 2006	11 \pm 2	41 \pm 5	42 \pm 5	6 \pm 1

790

791 Table 5

792 Results from two-way analysis of variance (ANOVA): Spatio-temporal differences in average

793 individual body mass in the total nematode community and for populations of discriminating

794 species

Source	Sum of squares	Df	Mean square	F-Ratio	p-value
<i>Total community</i>					
Station	0.280737	2	0.140369	3.45	0.043
Month	0.320326	5	0.0640652	1.57	0.193
Station x Month	0.490307	10	0.0490307	1.2	0.321
<i>Spilophorella paradoxa</i>					
Station	0.322737	2	0.161369	4.15	0.024
Month	0.481504	5	0.0963007	2.48	0.050
Station x Month	0.339041	10	0.0339041	0.87	0.566
<i>Sabatieria punctata</i>					
Station	0.271078	2	0.135539	4.23	0.022
Month	0.105911	5	0.0211822	0.66	0.656
Station x Month	0.316011	10	0.0316011	0.99	0.473
<i>Leptolaimus elegans</i>					
Station	0.00149259	2	0.000746296	0.41	0.667
Month	0.0101259	5	0.00202519	1.11	0.372
Station x Month	0.0280407	10	0.00280407	1.54	0.166

795

796 Table 6

797 Results from two-way crossed analysis of similarities (ANOSIM): Spatio-temporal
 798 differences in the size distribution of the total nematode community and populations of
 799 discriminating species

	Station		Month	
	Spearman R	<i>p</i> -value	Spearman R	<i>p</i> -value
Total community	0.111	0.074	0.123	0.032
<i>Spilophorella paradoxa</i>	0.159	0.009	0.282	0.001
<i>Sabatieria punctata</i>	0.126	0.060	0.033	0.312
<i>Leptolaimus elegans</i>	0.050	0.221	0.001	0.471

800

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801 **Figure captions**

802

803 Fig. 1. Sampling stations in the Silver Pit (A, B and C), with background showing the mean
804 monthly water chlorophyll *a* concentration for April 2005. The 25 m depth contour is shown
805 as a solid white line, and the 50 m contour as a solid black line.

806

807 Fig. 2. Temporal changes in the mean (\pm SE) sediment chlorophyll *a* and phaeopigment
808 concentrations across the three stations in the Silver Pit.

809

810 Fig. 3. Comparison of mean pelagic and benthic chlorophyll *a* concentrations in each of the
811 sampling months during 2005 and 2006 coded by sampling station. Shaded areas identify the
812 spring bloom period showing the gradient in pelagic primary production throughout the Silver
813 Pit from west (station A) to east (station C).

814

815 Fig. 4. Temporal changes in the mean (\pm SE) relative abundance of *Spilophorella paradoxa*
816 across the three stations in the Silver Pit.

817

818 Fig. 5. Non-metric multi-dimensional scaling (MDS) ordination of mean relative abundance
819 of nematode species and feeding types (sensu Wieser 1953) at the three stations in the Silver
820 Pit over a 12-month production cycle. Day of year in parentheses.

821

822 Fig. 6. Temporal changes in the mean (\pm SE) individual body mass of *Spilophorella paradoxa*
823 across the three stations in the Silver Pit.

824

825 Fig. 7. Spatial differences in the mean (\pm SE) absolute abundance of *Spilophorella paradoxa*
826 over a 12-month production cycle plotted against geometric size class.

827

828 Fig. 8. Temporal changes in the mean (\pm SE) absolute abundance of *Spilophorella paradoxa*
829 in geometric size class -4 to class 0 across the three stations in the Silver Pit.

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Fig. 1

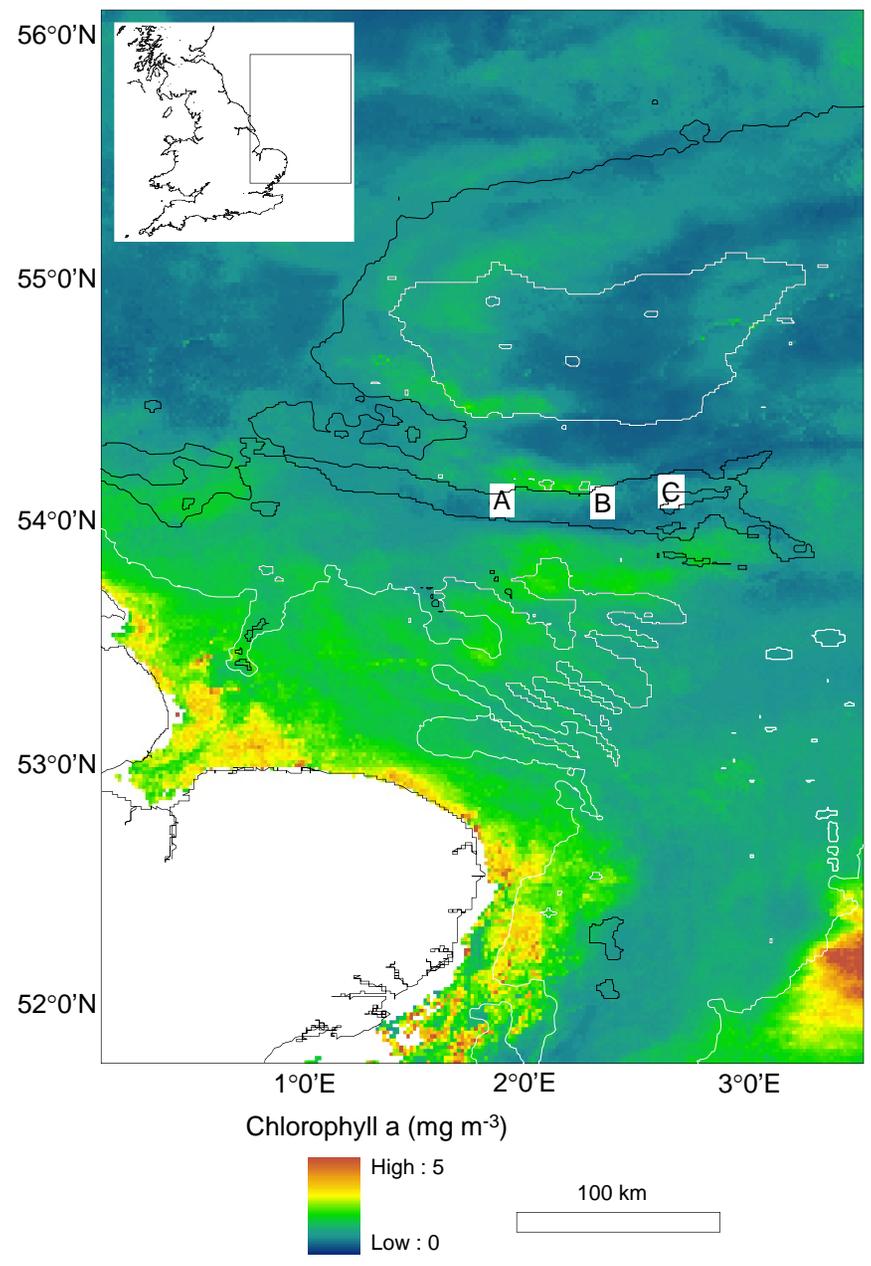


Fig. 2

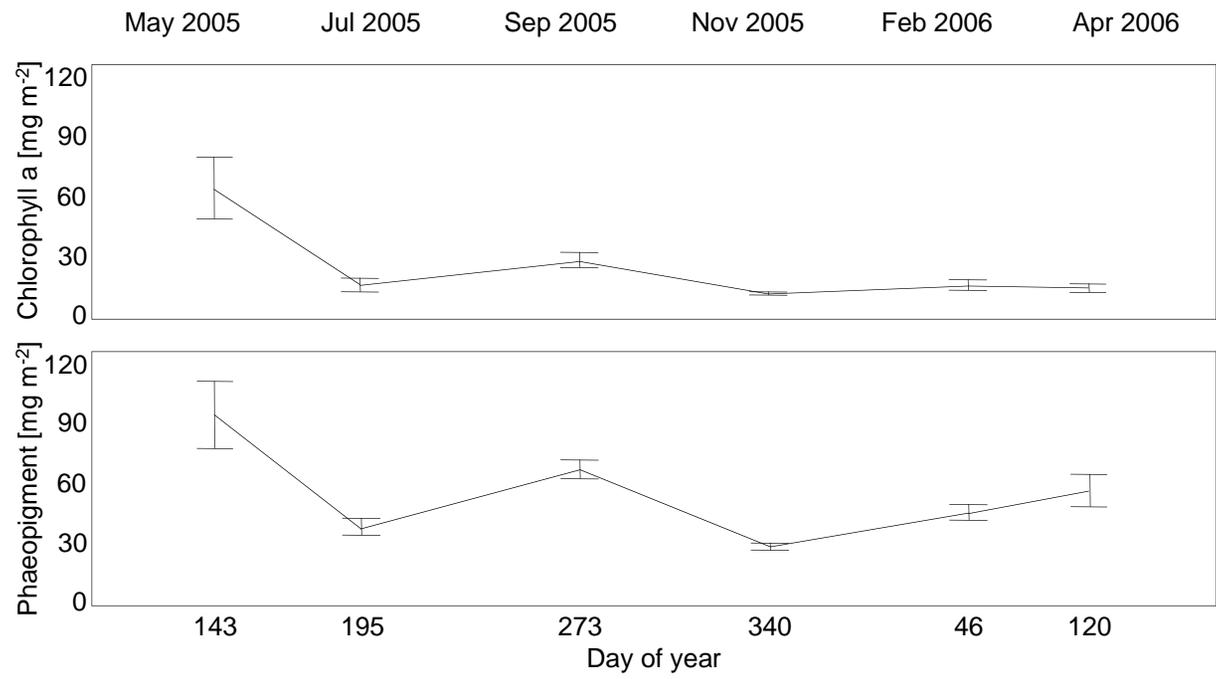


Fig. 3

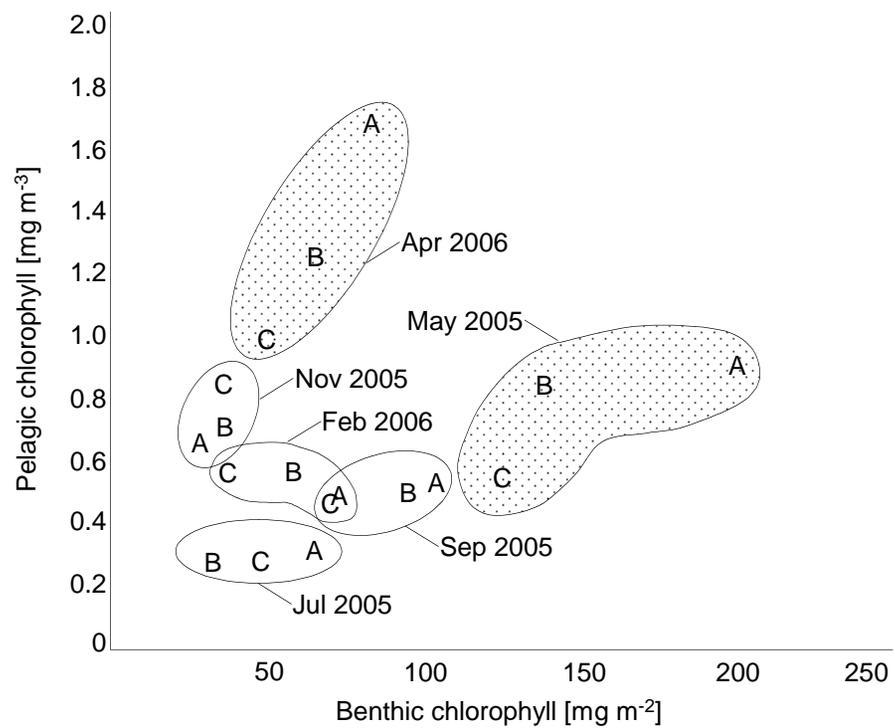


Fig. 4

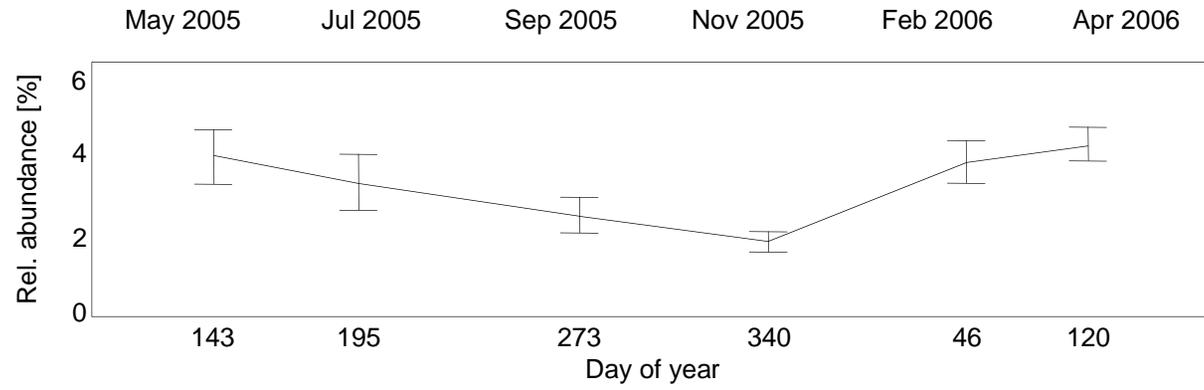


Fig. 5

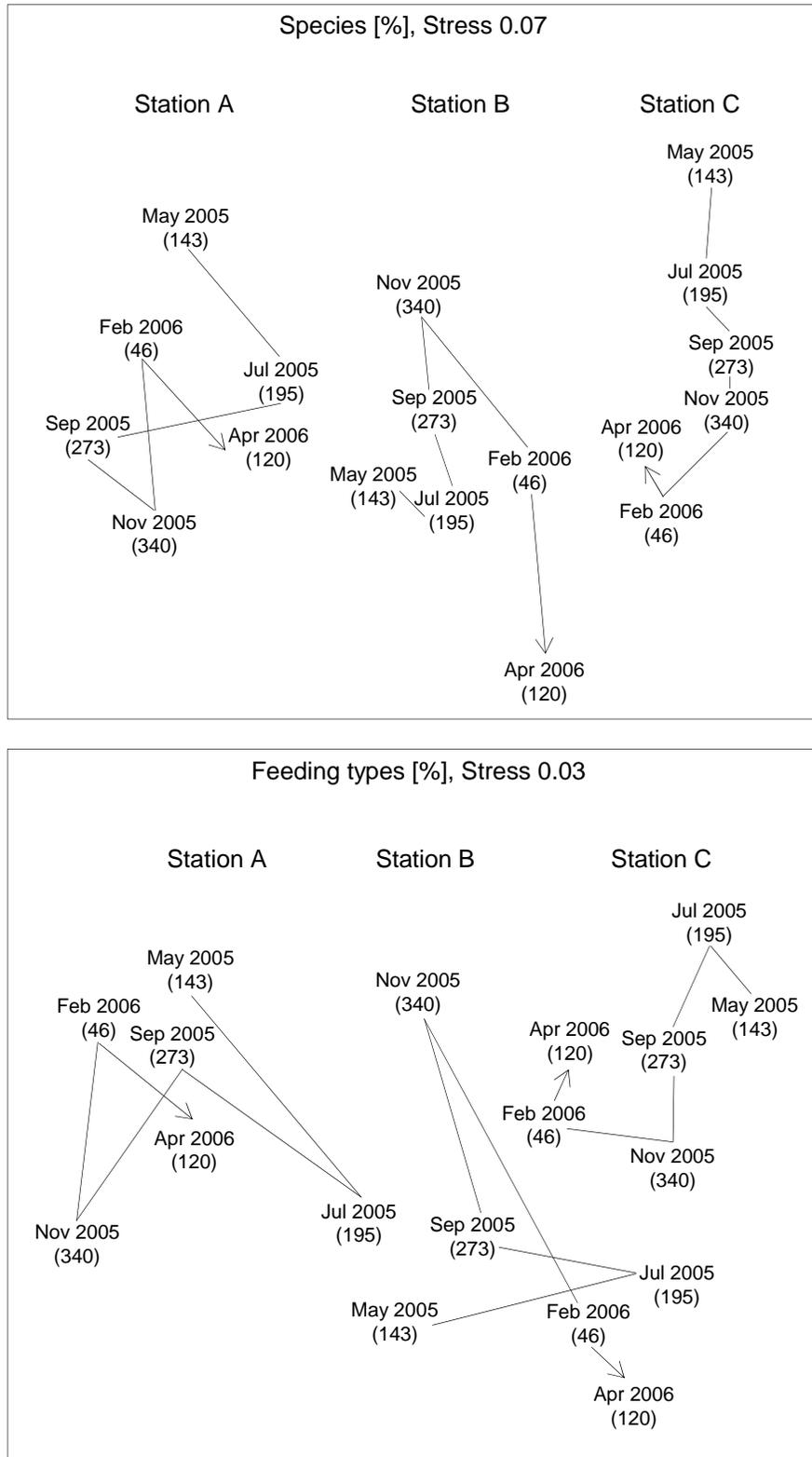


Fig. 6

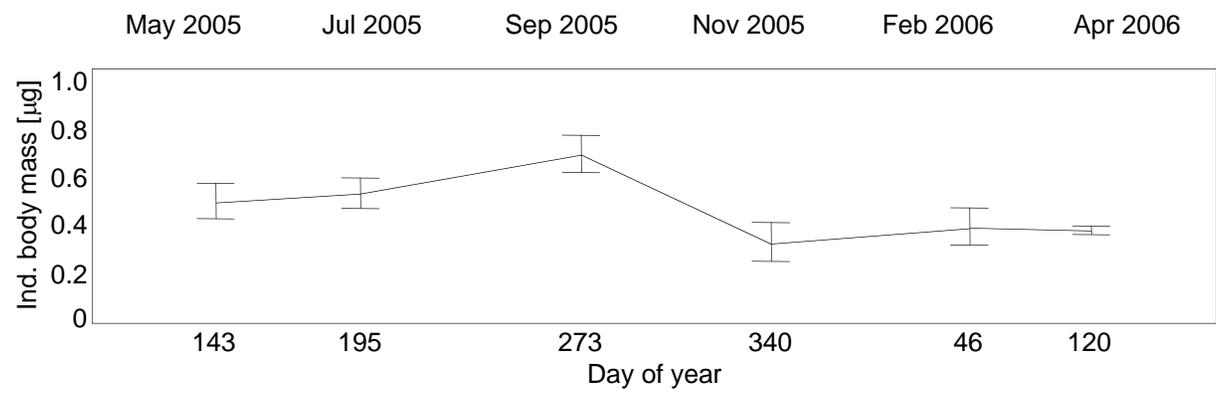


Fig. 7

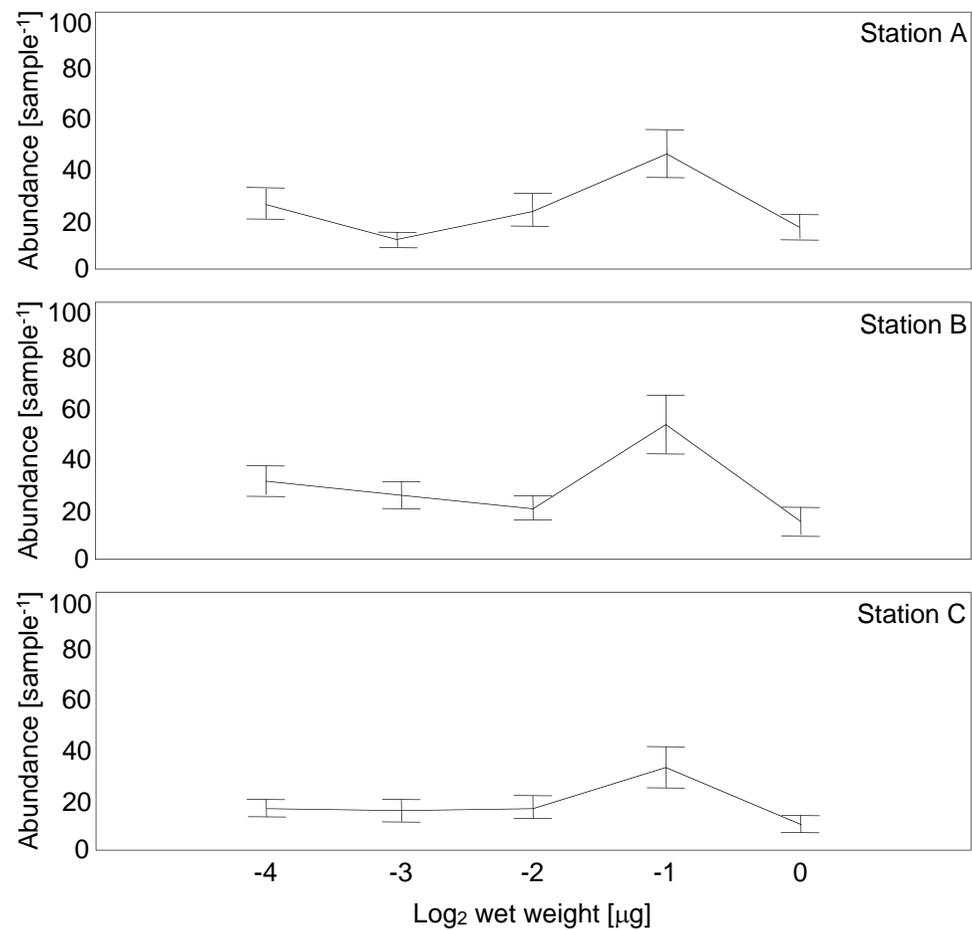


Fig. 8

