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1 **Short-term changes in nematode communities from an**
2 **abandoned intense sand extraction site on the**
3 **Kwintebank (Belgian Continental Shelf) two years post-**
4 **cessation.**

5

6

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19

20 **Abstract**

21

22 We investigated short-term changes (two years) in nematode communities (density,
23 diversity, biomass and community composition) in an area on the Kwintebank (Belgian
24 Continental Shelf) that was closed for sand extraction activities and compared these
25 patterns to nematode community characteristics from another area on the Kwintebank
26 where sand extraction was still ongoing. Six stations were sampled in 2003 and 2004 and
27 nematode community composition and univariate measures of diversity were compared
28 with values obtained during the extraction period and with a “pre-impact situation”
29 sampled in 1978.

30 Although nematode density, diversity and biomass did not change two years after
31 cessation of the exploitation, nematode community composition did and was more stable
32 than in the extracted site. This is attributed to the absence of continuous disturbances
33 associated with the extraction activities such as the creation and filling up of dredge
34 furrows. As a consequence of the typical life history traits of nematodes, recovery seems
35 to follow different pathways when compared to macrobenthic recovery from the same
36 impact.

37

38

39 Key words: benthos, nematodes, community composition, dredging, recovery,
40 Kwintebank

41

42 **1. Introduction**

43

44 Marine sand and gravel extraction has recently become a growing industry due to the
45 increasing demand for these resources in combination with the closing of land-based
46 extraction sites. Since these activities directly impact the seabed, many studies have been
47 conducted investigating the effect of mineral extraction on the benthos inhabiting the
48 seafloor. Most studies so far focused on the eventual changes in bottom topography,
49 sediment composition and macrobenthos (see reviews by Newell et al., 1998; Boyd, et
50 al., 2004). The effects on the macrobenthos seem to be site-specific and dependent on
51 local sedimentological and topographical characteristics of the extraction site in
52 combination with the ability of the local macrobenthic communities to cope with the
53 induced disturbance (Kenny and Rees, 1994; Desprez 2000, van Dalftsen et al., 2000;
54 Sardá et al., 2000; van Dalftsen and Essink, 2001; Guerra-Garcia et al., 2003; Newell et
55 al., 2004; Robinson et al., 2005; Simonini et al., 2005). Many studies also investigated the
56 possible recovery of extraction sites after cessation of the activities (Desprez 2000, Sardá
57 et al., 2000, Van Dalftsen et al., 2000, Van Dalftsen and Essink, 2001). Their results
58 suggest that substantial progress towards full restoration of the macrobenthic
59 communities can be expected within 2-4 years following cessation of the extraction
60 activities. However, their studies concerned cases where dredging operations lasted only
61 over a relatively short time scale (up to one year: Kenny et al., 1998, Sardá et al., 2000,
62 Van Dalftsen et al., 2000, Van Dalftsen and Essink, 2001). In a long-term (1971-1995)
63 extraction site (UK, Area 222) differences between macrobenthic assemblages from
64 reference sites and sites exposed to high and low levels of extraction persisted after a
65 period of 6 years (Boyd et al., 2005). Smith et al. (2006), investigating the epifaunal
66 communities (macrobenthos sampled with a dredge or trawl) of the same area, reached
67 the same conclusions. All this suggests that besides local characteristics and extraction
68 intensity, duration of the activities and associated disturbances and environmental
69 changes are important in determining restoration processes and timing.

70 In this paper, we report on the short-term (2 years) changes in nematode communities in
71 an abandoned extraction site on the Kwintebank on the Belgian Continental Shelf (BCS)
72 and we compare these communities with nematode communities from a site on the
73 Kwintebank where extraction is still ongoing. At the Kwintebank, extraction activities
74 started in 1976. Total amounts of sand extracted from the BCS increased from 29000 m³
75 y⁻¹ in 1976 to 1700000 m³ y⁻¹ in the mid 90's. Maximum exploitation was recorded in
76 2001 (1900000 m³ y⁻¹). Extraction activities were concentrated in the central and northern
77 part of the Kwintebank. Degrendele et al. (in press) observed the formation of a
78 depression in the central Kwintebank since 1992, which reached a depth of 5 m after 7
79 years. Since federal legislation prohibits further exploitation when a deepening of > 5m
80 with respect to the most recent hydrographical charts occurs, this area had to be closed
81 for extraction activities in February 2003. Nematode community composition at the
82 sandbank changed considerably since the start of the extraction activities, which was
83 attributed to long-term changes in sediment characteristics in combination with additional
84 short term disturbances by the creation and the filling of dredge furrows (Vanaverbeke et
85 al., 2007). Since nematode communities are generally accepted to be a good monitoring
86 tool for assessing changes in the benthic environment (Kennedy and Jacoby, 1999), we
87 sampled these communities to assess a possible restoration of the community
88 characteristics after cessation of the activities by comparing the post-extraction data with
89 (1) data obtained at the start of the extraction period (Vincx, 1986); (2) data obtained
90 from within the extraction period (Vanaverbeke et al., 2002) and (3) data obtained from
91 the northern part of the Kwintebank where high intensity sand extraction was still
92 ongoing. We investigated the hypotheses of no changes in nematode communities
93 (density diversity and community composition) between sampling events within the
94 different areas on the sandbank. In addition, we compared nematode biomass spectra
95 (Vanaverbeke et al., 2003) from the abandoned sites and the extraction sites in order to
96 further increase our understanding of the effects of sand extraction on nematode
97 communities.

98

99 2. Material and Methods

100

101 2.1. Collection and treatment of samples

102

103 Analyses in this paper are based on historical data from sampling campaigns conducted in
104 June – September 1978 (Vincx, 1986), February 1997 (Vanaverbeke et al., 2002),
105 December 2001 (Vanaverbeke et al., 2007), and new sampling campaigns in the central
106 and northern area of the Kwintebank in October 2003 and February 2004. The central
107 area was closed for extraction activities in February 2003, while extraction activities
108 continued in the northern part. Samples collected in 1978 are considered as samples from
109 the period before the intense sand extraction activities, while the samples obtained in
110 1997 and 2001 reflect the situation during intense extraction activities. Detailed
111 information about the location of the Kwintebank is given in Vanaverbeke et al. (2000)
112 and Vanaverbeke et al. (2002).

113 Collection and treatment of meiobenthic samples was identical during all sampling
114 campaigns. The long-term sampling stations Kw1 and Kw2 in the northern area and Kw5
115 and Kw6 in the central depression were visited in 2003 and 2004. In both areas, an
116 additional station was sampled as well: Kw14 in the northern area and Kw18 in the
117 central depression (Fig. 1). Samples collected in 2003 and 2004 in the central area are
118 considered to reflect post-extraction situations. All stations were sampled with a Reineck
119 box corer. The box corer was deployed three times at all stations, and from each box
120 corer, subsamples for meiobenthic and sediment analysis were obtained using a perspex
121 core (10cm²). Meiobenthic samples were fixed with a hot (70°C) neutral formaldehyde
122 tap-water solution (final concentration: 4%). Metazoan meiobenthic organisms were
123 extracted from the sediment by centrifugation with Ludox (Heip et al., 1985).
124 Macrofauna was excluded by means of a 1 mm sieve and all animals retained on a 38µm
125 sieve were stained with Rose Bengal, counted and classified to the taxon level. 200
126 nematodes (or all individuals if less than 200 were present) were picked at random,
127 transferred to glycerin and mounted on slides for species identification using the pictorial
128 keys of Platt & Warwick (1983, 1988), Warwick et al. (1998) and the NeMys online

129 identification key (Steyaert et al. 2005). Nematodes from two replicates were identified
130 for the 1997 and 2001 sampling campaigns; in 1978 nematodes from only one replicate
131 were identified to species level. Nematode length and width from all nematodes from one
132 replicate per station were measured for the sampling campaign in 2004. Measurements
133 were done using the Quantimet 500+ image analyser. Nematode biomass was calculated
134 from Andrassy's formula (Andrassy 1956) and a dry-to-wet-weight ratio of 0.25 was
135 assumed. Nematode biomass spectra (NBS) were constructed following Vanaverbeke et
136 al. (2003). Kolmogorov-Smirnov two sample tests were used to compare NBS for 2004
137 with NBS from 1997 for the same area, recalculated from Vanaverbeke et al. (2003).
138 Grain size analyses were performed using the Coulter LS 100 Particle Size Analyser. For
139 the latter method, sediment fractions up to 1000 μm are expressed as volume percentages,
140 while the fraction between 1000 and 2000 μm and $> 2000 \mu\text{m}$ are mass percentages. For
141 all sampling years, sediment fractions are defined according to the Wentworth scale
142 (Buchanan, 1984).

143 **2.2 Data analysis**

144
145 Grain size variables per area were compared by Principal Component Analysis using
146 normalised Euclidean distance. Differences between stations and treatment (extraction vs.
147 no extraction) in the central depression were analysed using 2-Way crossed ANOSIM
148 Since sand extraction was ongoing in the northern area, differences between stations and
149 subsequent years were analysed using the same procedure.

150 Nematode densities from different years were compared using one-way ANOVA. When
151 assumptions for ANOVA were not met, data were root-root transformed. The non-
152 parametric Kruskal-Wallis Analysis by Ranks was used when transformation did not
153 result in suitable data for ANOVA. Data from October 2003 were excluded from this
154 analysis, since Vanaverbeke et al. (2000) described higher densities in October as a
155 consequence of seasonal dynamics. December and February are here considered as winter
156 months.

157 Multivariate patterns in nematode communities from the periods 1997-2001 and 2003-
158 2004 per area were investigated using non-metric multidimensional scaling (MDS) on

159 non-transformed species densities (all species from all replicates) based on the Bray-
160 Curtis similarity measure. This was followed by a 2-way crossed ANOSIM allowing to
161 test for differences between years while allowing for differences between stations and
162 vice versa. Species accounting for the similarity between samples within the different
163 years were identified using the SIMPER routine within the Primer package (Clarke and
164 Gorley 2001). A cut-off of 50% was applied. This allows for investigating short-term
165 changes in nematode community composition after cessation of the activities or further
166 changes when extraction is ongoing.

167 Temporal trends for Stations Kw5 and Kw6 in the central depression, and Kw1 and Kw2
168 in the northern area for the period 1997-2004, were evaluated using MDS based on non-
169 transformed species densities and the Bray-Curtis similarity measure. Spearman rank
170 correlations between these similarity matrices underlying their temporal development
171 were used as input for a 2nd stage MDS. This technique removes the site factor (site
172 differences at one time) and concentrates on the consistency of temporal patterns across
173 sites (Clarke et al., 2006).

174 In order to evaluate a possible recovery of the nematode communities in the central area,
175 MDS was applied on all available data from the central depression (including 1978). All
176 multivariate analyses were conducted using the Primer 5 package.

177 Nematode diversity was analysed by calculating a wide array of diversity indices
178 available in Primer 5, including total species (S), Margalef species richness (d), Pielou's
179 evenness (J), Shannon Wiener (H' , log e based), Simpson Index ($1-\lambda'$) and Hill numbers
180 N_1 , N_2 and N_∞ . In addition, Average Taxonomic Distinctness ($AvTD \lambda^+$) and Variation
181 in Taxonomic Distinctness ($VarTD \lambda^+$) based on presence/absence data were calculated
182 following Warwick and Clarke (2001). These indices differ from the previously
183 mentioned indices since they are not based on species richness but on taxonomic
184 relatedness of species in the samples. For the calculation of the taxonomic indices equal
185 step-lengths between each taxonomic level were assumed. In total 7 taxonomic levels
186 were used. All indices were calculated using Primer 5 (Clarke and Gorley, 2001)
187 Differences between years were analysed using 1-way ANOVA after testing for the
188 assumptions for ANOVA. Values were subjected to a double square root transformation
189 when needed to meet the assumptions. When the assumptions were not met, the non-

190 parametric Kruskal Wallis analysis by ranks was applied. When significant differences
191 were observed in the ANOVA approach, Tukey's HSD for unequal N was used to test for
192 pairwise differences between years. All ANOVA and Kruskal Wallis analysis were
193 performed using the Statistica 6 software package.

194

195 **3. Results**

196

197 **3.1 Sediment characteristics**

198

199 No clear patterns in sedimentological characteristics in the central depression could be
200 discerned (Fig 2A). The first two axes of the PCA explained 67.8% of the variation of the
201 dataset. 2-way crossed ANOSIM revealed no significant differences between stations
202 ($R=0.104$; $p=0.08$), but a significant difference between the sedimentological
203 characteristics before and after the cessation was observed ($R=0.208$; $p=0.047$). In the
204 northern area (Fig. 2B), significant differences between the different years ($R=0.256$;
205 $p=0.024$) and stations ($R=0.31$; $p=0.01$) were observed.

206

207 **3.2 Nematode densities and community composition**

208

209 Nematode densities ranged between 84 ± 14 ind. 10 cm^{-2} and $228.3 \pm 3.2\text{SE}$ ind. 10 cm^{-2}
210 in the central depression and between 76 ± 14.8 ind. 10 cm^{-2} and 1208 ± 460 ind. 10 cm^{-2}
211 in the northern area. There were no significant differences between densities observed
212 in the different years for both areas (central depression: ANOVA: $F_{2,18} = 0.483$; $p > 0.05$ –
213 northern area: Kruskal-Wallis Analysis by Ranks: $H = 3.21$; $p > 0.05$).

214 There were no differences (2-way crossed ANOSIM: $R=0.927$; $p=0.08$) in nematode
215 community composition from the different stations in the central area (Fig.3A). However,
216 differences between years were obvious (global $R=0.7019$; $p=0.001$). Pairwise
217 comparisons revealed that strongest differences occurred between communities sampled

218 in 1997 and all other years (all pairwise $R=1$) and between the communities encountered
219 in 2001 and 2003 (pairwise $R=0.875$). Smallest differences were found between the
220 nematode communities from 2003 and 2004 ($R=0.25$). SIMPER analysis revealed that a
221 large part ($>40\%$) of the within-group similarity is mainly due to different species during
222 the extraction era (*Neochromadora munita* and *Metadesmolaimus pandus* in 1997; *Onyx*
223 *perfectus* and *Viscosia franzii* in 2001), while after the cessation of the activities, the
224 contribution of *Onyx perfectus* and *Mesacanthion hirsutum* made up the bulk of the
225 within-group similarity ($>40\%$) in both 2003 and 2004 (Table 1).

226 In the northern area (Fig. 3B), significant differences in nematode community
227 composition were observed between stations (2-way crossed ANOSIM: global $R=0.78$;
228 $p=0.02$) and years (global $R=0.67$; $p=0.001$). Pairwise comparisons between the
229 nematode communities sampled in subsequent years all showed strong differences (All
230 pairwise $R > 0.625$). A SIMPER analysis (Table 2) revealed that within group similarity
231 was due to different species in the different years. Only *Theristus bastiani* was found
232 among the species contributing to 50% within group similarity in three years, while *Onyx*
233 *perfectus* was important for within-group similarity in both 2003 and 2004.

234 The nematode communities from the individual stations of the central depression and the
235 northern area revealed temporal differences since 1997 (Fig. 4) which was confirmed by
236 the respective ANOSIM analyses (all $p<0.02$). The 2nd stage MDS (Fig. 4) indicates that
237 the temporal patterns in the stations of the central depression were similar and very
238 different from the evolution of the communities at the stations at the northern area.

239

240 3.3 Nematode diversity

241 From the wide array of diversity indices calculated (Table 3), none were found to be
242 significantly different between years in the central depression (1-way ANOVA or
243 Kruskal-Wallis analysis by ranks, all $p>0.05$). Only in the northern part, significant
244 differences between years were observed for J' ($F_{3,14}=3.93$; $p<0.05$) and A^+ ($F_{3,14}=3.96$;
245 $p<0.05$) (Table 3). Tukey HSD for unequal N showed that significantly ($p<0.05$) higher
246 values were observed in 2004 in comparison with 1997. All other pairwise comparisons

247 showed no significant differences. Concerning A^+ , no significant differences were
248 detected in the pairwise comparisons.

249

250 **3.4 Nematode Biomass Spectra**

251

252 Nematode biomass spectra in both the central depression and the northern area showed
253 the same irregular pattern already described by Vanaverbeke et al. (2003). In 2004, a
254 more traditional pattern is visible, with peak biomass values located in size class 0 (Fig.
255 5). In the lower size classes, highest biomass values are found in the northern part of the
256 Kwintebank, while in the higher ranges the opposite trend emerges. However, differences
257 between spectra were not statistically different (Kolmogorov-Smirnov two sample test,
258 all $p > 0.05$).

259

260 **4. Discussion**

261

262 **4.1 Environmental changes**

263

264 Although a detailed discussion of the sedimentological and morphological changes on the
265 Kwintebank is beyond the scope of this paper, some trends merit attention. Our results
266 indicate a change in sedimentological variables in the central depression after cessation of
267 the extraction activities. In a more detailed study, using a sampling grid of 100 m during
268 4 sampling campaigns between September 2003 and February 2005, B ellec et al.
269 (unpublished) reached the same conclusions. However, this does not indicate a
270 morphological and sedimentological recovery of the central depression (Degrendele et al.
271 in press) since a general filling up of the depression or a restoration of the height of the
272 large sand waves in the depression was not observed in the two years after the closing of
273 this area for extraction activities. On a smaller scale, the dredge furrows created by the
274 suction hoppers have disappeared in the central depression (Degrendele et al. in press).

275 Since the closing of the central area for exploitation, extraction was very concentrated in
276 the northern area of the sandbank where a new depression is being formed (Degrendele et
277 al. in press). Our results indeed indicate a continuous change in the sedimentological
278 environment which can be caused by long-term changes associated with sand extraction
279 in combination with additional short-term disturbances by the creation and the filling of
280 dredge furrows.

281

282 **4.2 Changes in the nematode communities**

283

284 Our results indicate changes in the nematode communities both in the central depression
285 of the Kwintebank and in the northern area where extraction is still ongoing. However, the
286 nature of change in both areas is different. In the northern area, nematode community
287 composition seems to be unstable and changing even on a short term scale: pairwise
288 ANOSIM showed large R-values when comparing the nematode communities sampled in
289 October 2003 and February 2004.

290 The observed changes in the nematode communities in both areas can have several
291 causes: (1) seasonal changes and/or (2) cessation or continuation of the extraction
292 activities and/or (3) changes due to unmeasured non-seasonal, non-cessation factors.
293 Although seasonal changes and changes due to unmeasured factors cannot be ruled out
294 completely, we believe that this has a minor impact on the composition of the nematode
295 communities. A first reason is given by Vanaverbeke et al. (2002) who found no
296 differences in nematode communities from sandbanks on the BCS when sampled in
297 different seasons. In addition, seasonal differences should be visible both in the northern
298 part of the Kwintebank and in the central depression of the Kwintebank. This is clearly
299 not the case: nematode communities in the central depression change from 1997 to 2001
300 and from 2001 to 2003, while differences between 2003 and 2004 were the smallest
301 observed between subsequent years, which is confirmed by the SIMPER analyses for
302 both areas.

303 The 2nd stage MDS confirms that the temporal development of the stations in the central
304 depression is different from the stations in the northern area. This again suggests that
305 seasonal changes and changes due to unmeasured factors had a minor impact on the

306 observed differences between the central area and the northern area after cessation of the
307 extraction activities. In the northern area, the temporal evolution of stations Kw1 and
308 Kw2 is different as well, which reflects the local impact of sand extraction activities on
309 the nematode communities (Vanaverbeke et al., 2007).

310 From this, we conclude that the continuous alteration of the nematode communities in the
311 northern area is caused by the extraction activities whereas the establishment of a more
312 stable community in the central depression is possible as a consequence of the absence of
313 the exploitation.

314 Long-term changes (1978 – 2001) in the nematode communities from the Kwintebank
315 were attributed to long-term changes in the sedimentological environment in combination
316 with the extra dynamics imposed by the creation and filling up of dredge furrows
317 (Vanaverbeke et al., 2007). Our results show that on a relatively short time scale, the
318 absence of the creation and filling of dredge furrows can lead to the establishment of a
319 more stable nematode community. Dredge furrows at the edge of the depression of the
320 Kwintebank remained visible for 6 months (Degrendele et al., in press). There are no data
321 available for the central parts of the depression, but we assume that regeneration of
322 dredge furrows in the absence of sand extraction was completed before our sampling in
323 October 2003. Hence, two major changes occurred in benthic environment of the central
324 depression within the first year after closing: the daily creation of the furrows by the
325 suction hoppers and the slow filling up of the furrows. This leads to a new and more
326 stable nematode community which is able to cope with the daily ebb-flood related
327 dynamics of the area.

328 Nematode diversity did not change, both in the depression and the northern area during
329 our sampling period. These results are based on a low number of replicates and should be
330 interpreted with care. However, our results are in accordance with Vanaverbeke et al.
331 (2007) who did not observe a decrease in diversity during the long-term extraction period
332 at the Kwintebank. Nematodes are indeed highly diverse, and there is a wide range of
333 species, from those that are very sensitive to disturbances to very tolerant species
334 (Kennedy and Jacoby, 1999). Therefore, nematode community composition can be
335 different while diversity remains unaffected (Bolam et al., 2006). In our case, we suggest

336 that sensitive species are replaced by tolerant species without a significant loss/gain of
337 species in the presence/absence of disturbance.

338

339 **4.3 Recovery of nematode communities**

340

341 Boyd et al. (2003) described 'recovery' as a two-step process. In a first step,
342 recolonisation (the settlement of new recruits from the plankton or immigration of adults
343 from outside the area) occurs, followed by restoration (the return of the community
344 structure). An indication of the restoration can then be gained by comparing the attributes
345 of the community (eg. species richness, abundance, biomass) with a reference community
346 obtained from a reference site or pre-dredging communities (see Boyd et al., 2003 and
347 references therein). These definitions are commonly applied in studies focusing on
348 macrobenthos. Nematodes do not have planktonic life stages but in intertidal areas, adults
349 do disperse through the water column after passive resuspension (Schratzberger et al.,
350 2006). Passive resuspension should be no problem in a hydrodynamically stressed
351 sandbank environment (Palmer and Brandt, 1981; Palmer and Gust, 1985; Thistle and
352 Levin, 1998) and is most probably the main reason for the introduction of new nematode
353 species in the central depression. However, introduction of new species should be
354 considered a continuous process and ongoing while the exploitation still occurred.
355 Therefore, the emergence of different communities after the cessation of sand extraction
356 are most probably due to the fact that certain nematode species (already present in low
357 numbers or introduced through pelagic dispersal) have better survival chances in the
358 absence of the disturbances (eg. extra dynamics as a consequence of creating and filling
359 up dredge furrows).

360 In order to assess the full recovery (return of community structure) we performed a MDS
361 analysis (Fig. 6) in which the communities sampled in 1978 (Vincx, 1986) were included
362 as well. Although the exploitation of the Kwintebank started already in 1976, extraction
363 intensity was low in that period and therefore we are comparing the recently sampled
364 communities with communities subjected to a very limited disturbance rather than
365 comparing with a reference situation *sensu strictu*. However, it is very obvious that there
366 is no return to the community structure of 1978, which is confirmed by ANOSIM

367 (R=0.595; p=0.001). All pairwise comparisons, except 2003-2004 were significantly
368 different in the pairwise comparison.

369 A second way of assessing the rate of recovery was indirectly through comparing the
370 biomass spectra of the extracted sites with the abandoned sites. Vanaverbeke et al. (2003)
371 showed peak biomass values in size classes -3 to 0 in the intensely extracted areas on the
372 Kwintebank, while in unexploited sandbanks on the BCS and areas on the Kwintebank
373 with low sand extraction intensity, highest biomass values were observed in size class -1
374 or 0. This indicates that nematode communities shift towards smaller individuals in areas
375 with high physical disturbance. In the long term, Vanaverbeke et al. (2007) reported a
376 loss of large species in the heavily exploited areas on the Kwintebank. Similar
377 observations were made by Lampadariou et al. (2005) in the Aegean Sea where larger
378 nematodes disappeared as a consequence of intense trawling. Although reference size
379 distribution data of nematode populations on the Kwintebank are not available, we
380 expected that nematode size spectra would reveal higher biomass in the larger size classes
381 in the absence of extraction activities, which was clearly not the case. This can have two
382 reasons: either the larger nematodes have not colonized the depression yet, or the
383 environment is not suitable for these organisms and colonizing large nematodes will not
384 survive. At the moment, there is no evidence underpinning a preference for one of the
385 possible explanations.

386 Using the definition of Boyd et al. (2003), no recovery of the nematode communities
387 occurred. However, there is no evidence that the original community would not have
388 changed in the course of 26 years due to naturally occurring processes. Since even small
389 differences in the median grain size and the fractions of medium sand and fine sand
390 content are reflected in differences in the nematode communities (Vanaverbeke et al.,
391 2002), it seems unlikely that nematode communities would remain unchanged during
392 such a long period in this very dynamic environment. Bolam et al. (2006) summarised
393 earlier discussions (see Bolam and Whomersley 2003, 2005 and Schratzberger et al.,
394 2006) on reference sites, defined as pre-impact situations or a non-impacted reference
395 site. Although they studied the recolonisation of dredged material deposited in intertidal
396 systems, their remarks are valid for the central depression as well: pre-impact situations
397 are very different from the impacted situations (eg. the creation of a depression of more

398 than 5 m depth) and this imposed difficulties when comparing impact and reference sites
399 which will always show small differences in physical properties. Especially in the case of
400 nematodes, which are very dependent on grain size characteristics (Vanaverbeke et al.,
401 2002), finding a suitable reference site for sandbanks systems is very problematic.
402 Therefore, we suggest to use the rate of change in nematode communities as a measure of
403 recovery of the benthic system. In the central depression, nematode communities were
404 not changing significantly anymore after 1.5 -2 years of cessation of exploitation, while
405 there was an ongoing change in areas where extraction still occurred.

406 **4.4 Trends in nematode communities versus macrobenthic** 407 **communities**

408

409 Boyd et al. (2005) summarise the observed patterns in recovery of the macrobenthic
410 communities in sites subjected to sand and gravel extraction. In a first phase, abundance
411 and species numbers increase as a consequence of the colonisation of the area by larvae
412 and adults of opportunistic species from surrounding areas. In a second phase,
413 community biomass will be reduced since colonizers have to grow on to maturity
414 comparable with the pre-dredging situation. In gravelly areas, abrasive effects of
415 increased sediments can limit growth and survivorship of epifauna, which is an extra
416 factor inhibiting the re-establishment of the original communities. However, there is no
417 clear picture if the latter holds for sandy areas as well. When bedload transport eventually
418 returns to pre-dredging levels, there is the possibility for the communities to fully return
419 to the original state. In sandy muds, Hily (1983) adds a third phase, during which
420 opportunistic species are replaced by a greater number of species as a consequence of
421 interspecific competition.

422 Our results indicate that recovery of nematode communities follows a different path. We
423 have no evidence of increased densities in the year following cessation of dredging.
424 Moreover, densities in the abandoned area were not higher than densities in the exploited
425 area. This can be explained by the life history traits of nematodes and their ability to cope
426 with physical disturbance. Nematodes reproduce constantly, hence there is a constant
427 presence of juveniles facilitating the recolonisation of the impacted area (Vanaverbeke et

428 al., 2002) even during the exploitation period. Macrobenthic reproduction on the other
429 hand is limited to certain periods in the year. A disturbance event during the recruitment
430 period therefore can destroy the population until the next recruitment. These mechanisms
431 also explain the absence of a shift in species diversity in the nematode communities after
432 cessation of extraction activities. The constant reproduction, in combination with the high
433 diversity, ensures the presence of community with a constant level of diversity, consisting
434 of species well adapted to the extra disturbance induced by the exploitation of the seabed.
435 These species are then gradually replaced by species preferring a more stable
436 environment who can outcompete the species present during the extraction period.
437 However, it is still unclear how the different phases of the recolonisation/restoration
438 processes of the macrobenthic and meiobenthic communities match in time. More
439 studies, incorporating both meiobenthic and macrobenthic data are needed to fully
440 understand this process. This will most probably increase our understanding of
441 recolonisation processes by fine-tuning the different phases in the very early (based on
442 the nematode communities) and later (based on the macrobenthic communities) phases of
443 these processes.

444

445 **5. Conclusions**

446

447 We showed that nematode communities in sites closed for sand extraction activities
448 evolved differently from nematode communities inhabiting area that are still exploited.
449 Diversity and density did not change, however nematode community composition was
450 more stable due to the absence of the creation and filling of dredge furrows. In addition,
451 we hypothesise that recovery of nematode communities follows different pathways than
452 macrobenthic recovery as a consequence of the typical nematode life history traits.

453

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455

456

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470

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Figure Captions

633

634

635 Figure 1. Map of the Belgian Continental Shelf and detailed location of the sampling
636 stations on the Kwintebank (Maps redrawn from UGent – RCMG and Federal Public
637 Service Economy, SMEs, Self employed and energy – Fund for Sand Extraction). Full
638 circle: area with ongoing sand extraction; Dotted circle: area closed for sand extraction.

639

640 Figure 2. PCA ordination plots of grain size variables. A: Central depression. B: northern
641 area of the Kwintebank. Grain size variables included % clay, % silt, % very fine sand, %
642 fine sand, % medium sand, % coarse sand; % between 1000-2000 μm , %>2000 μm ,
643 median grain size

644

645 Figure 3. Results of MDS analyses on non-transformed nematode species densities. A:
646 Central depression. B: northern area of the Kwintebank

647

648 Figure 4: Temporal development of nematode communities from Sts Kw1 (panel A),
649 Kw2 (panel B), Kw5 (panel C) and Kw6 (panel D).. Panel E: 2nd stage ordination based
650 on the Spearman Rank Correlations between similarity matrices of original MDS
651 analyses. Each symbol represents the patterns of community change at a site through
652 time.

653

654 Figure 5. Nematode biomass spectra of the central depression and northern area of the
655 Kwintebank per year.

656

657

658 Figure 6. Result of MDS plot on non-transformed nematode species densities from the
659 central depression. All sampling years combined

660

661

662

663

664 **Tables**

665

666 Table 1. Results of SIMPER analysis of the nematode data from the central depression,
667 listing the main discriminating species and their abundance (Ab, ind 10 cm⁻²) and
668 contribution (Contr) to within group similarity (Av. Sim.).

669

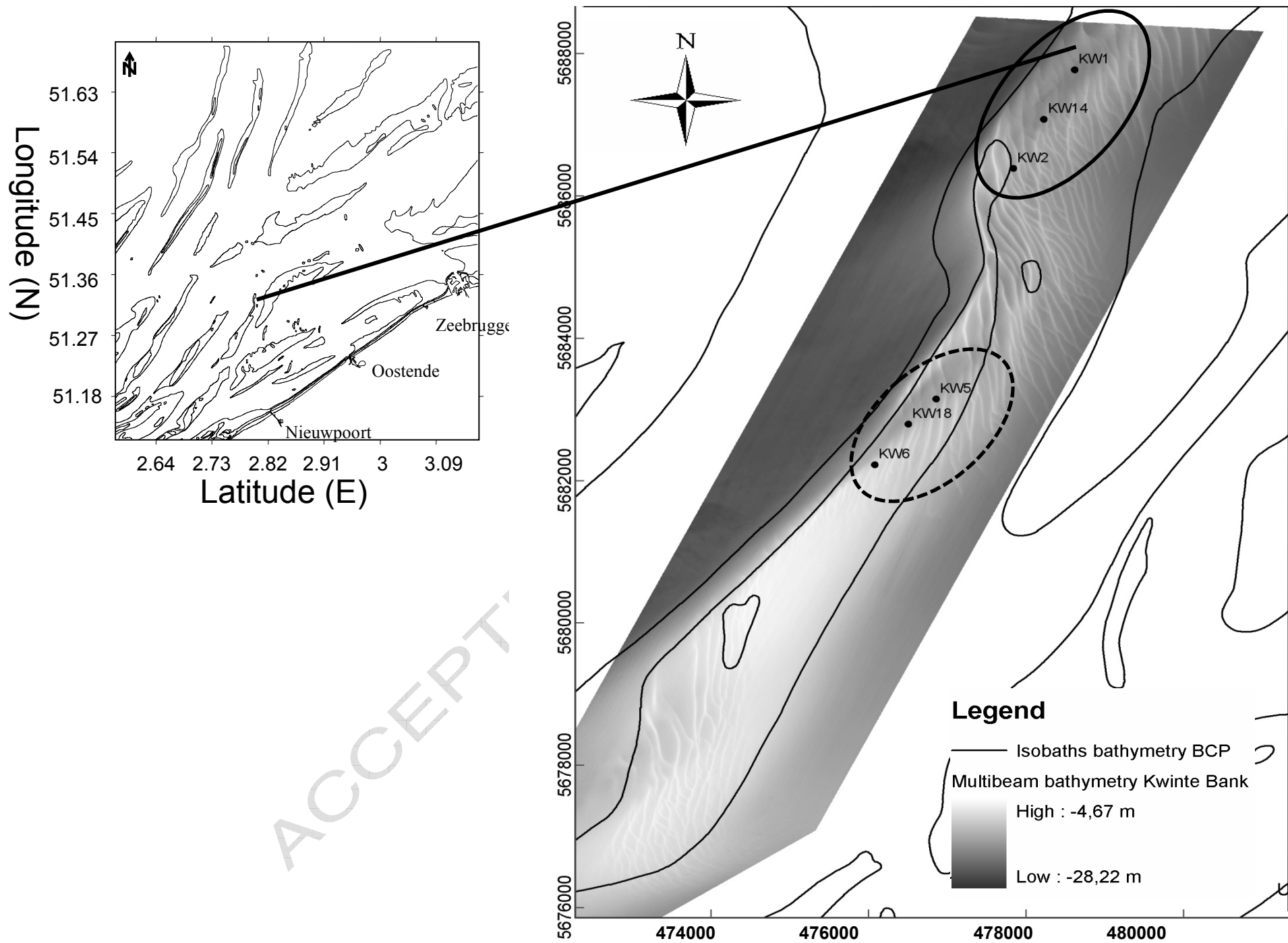
670 Table 2. Results of SIMPER analysis of the nematode data from the northern area of the
671 Kwintebank, listing the main discriminating species and their abundance (Ab, ind 10 cm⁻²)
672 and contribution (Contr) to within group similarity (Av. Sim.).

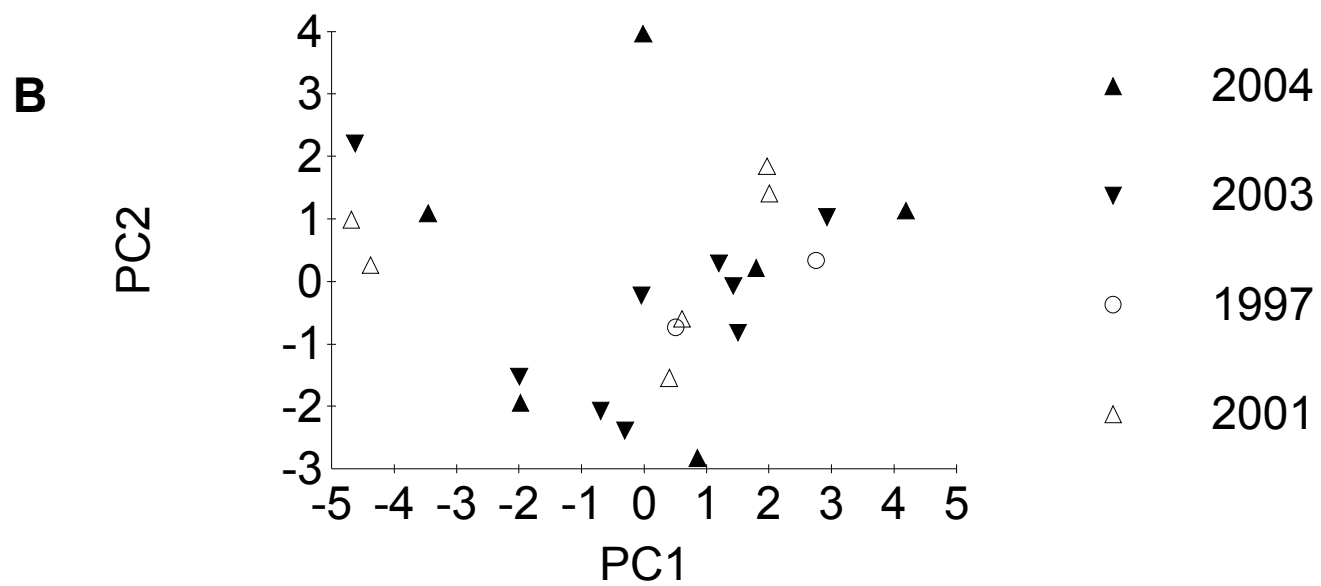
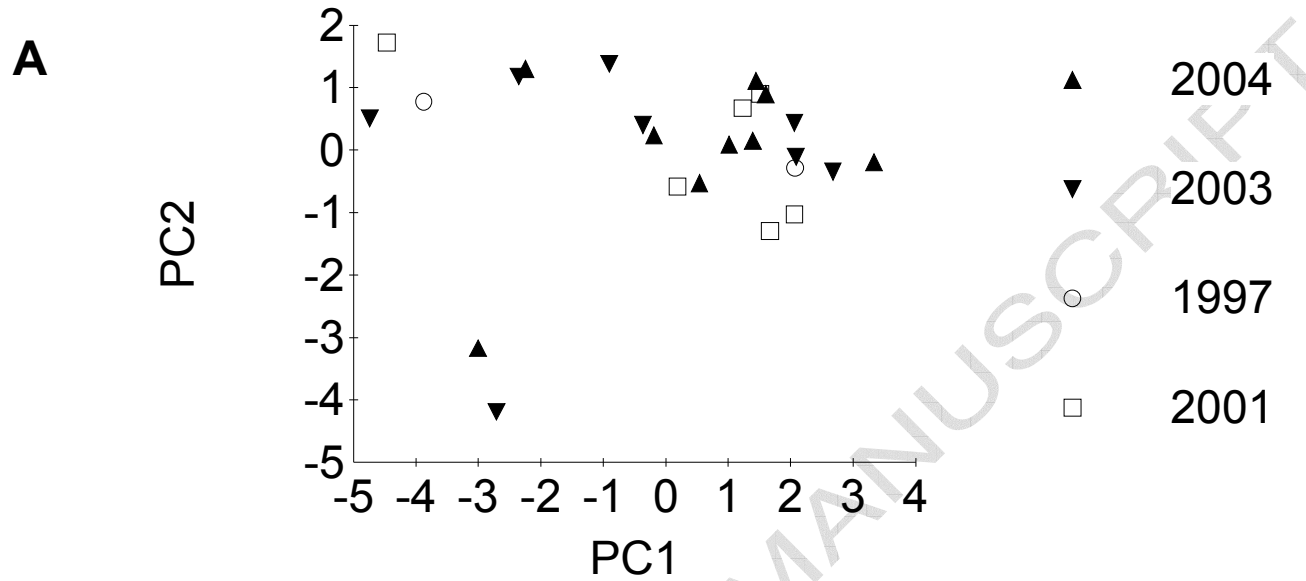
673

674 Table 3: Average univariate diversity values per year in the Northern and Central Area of
675 the Kwintebank and results of the statistical tests for difference between years. **p**
676 values indicate statistical differences at p<0.05. For abbreviations of diversity indices: see
677 Material and Methods Section.

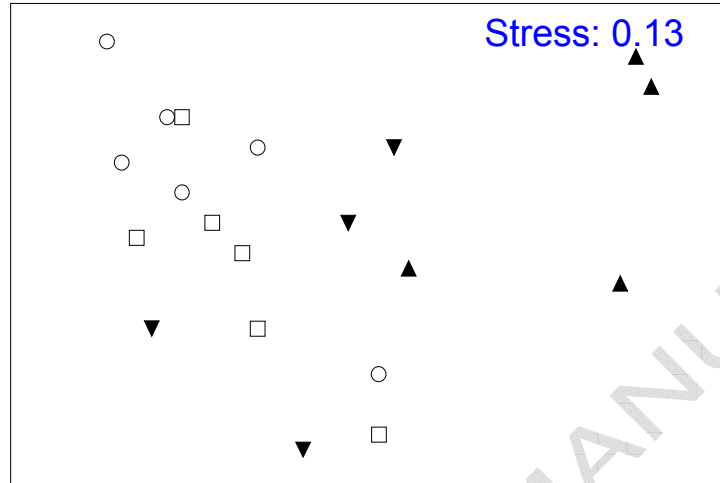
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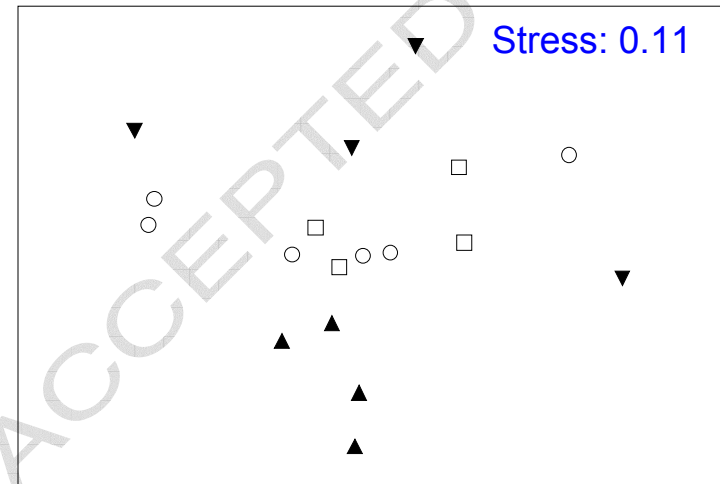


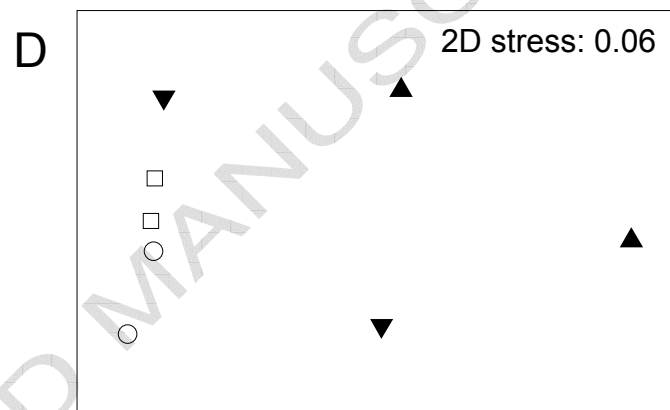
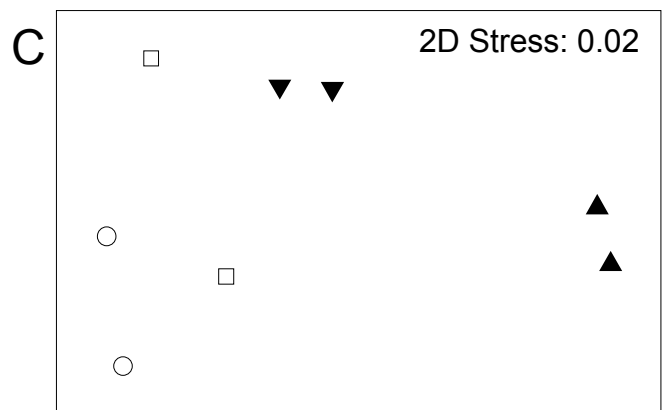
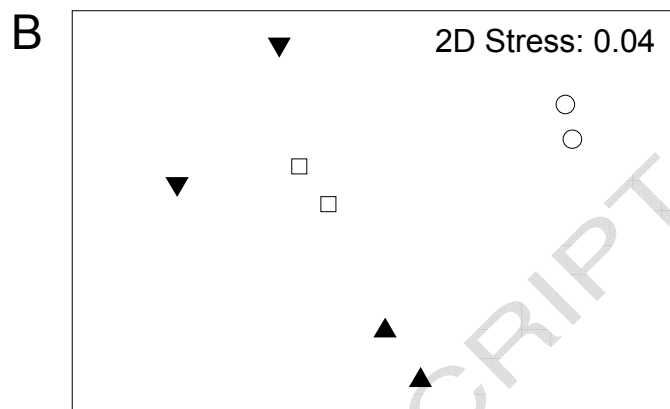
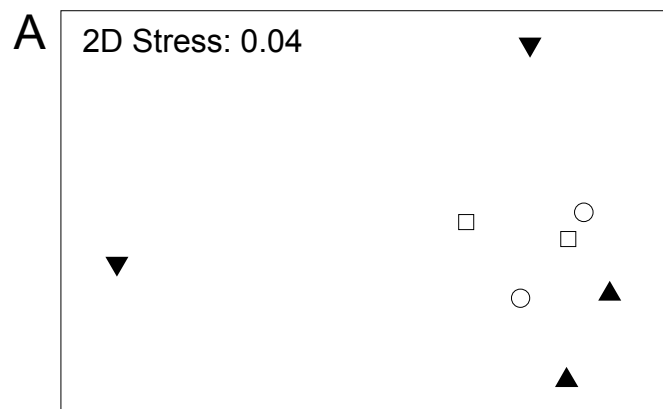


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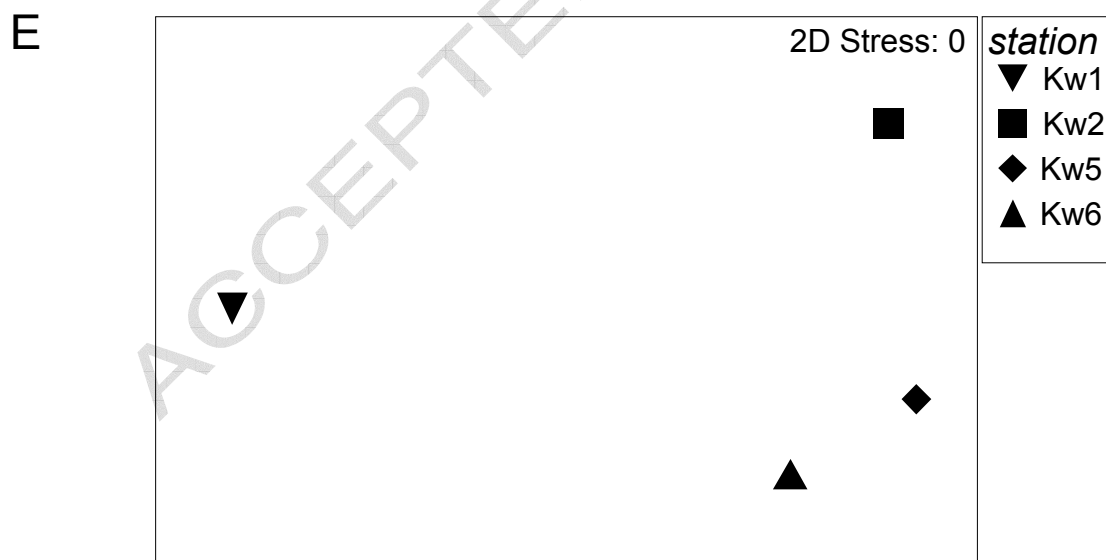


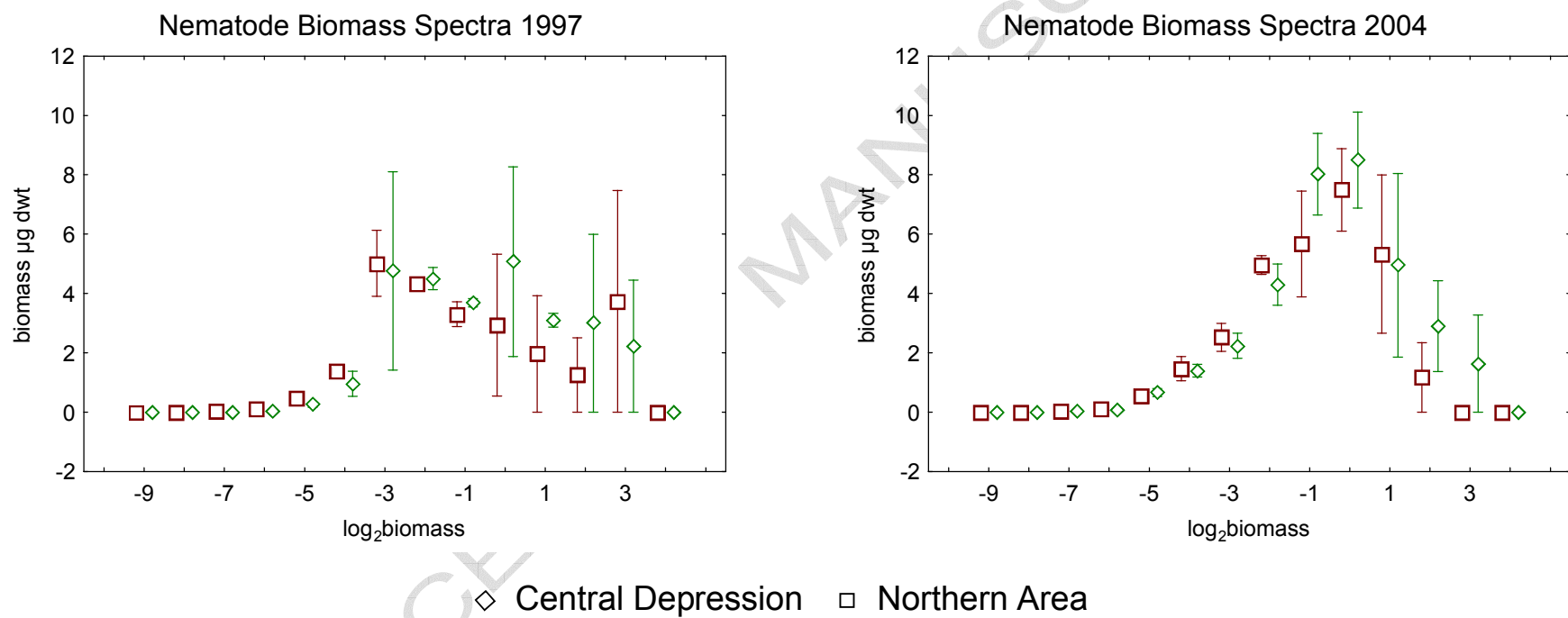
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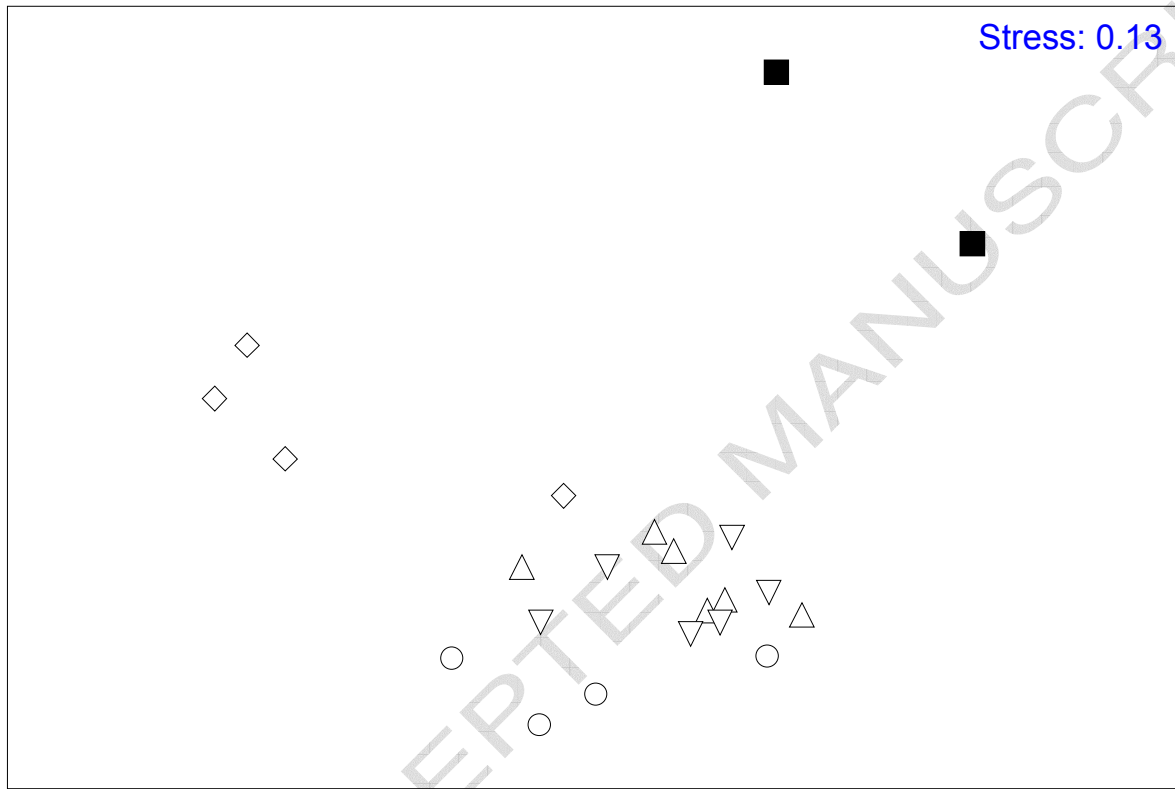




- ▲ 1997
- ▼ 2001
- 2003
- 2004







Stress: 0.13

■ 1978

◇ 1997

○ 2001

△ 2003

△ 2004

Table 1

1997 (Av. Sim.: 39.22)			2001 (Av. Sim.: 35.12)			2003 (Av. Sim.: 41.40)			2004 (Av. Sim.: 39.59)		
Species	Ab.	Contr (%)	Species	Ab.	Contr (%)	Species	Ab.	Contr (%)	Species	Ab.	Contr (%)
<i>Neochromadora munita</i>	42.36	29.84	<i>Onyx perfectus</i>	19.79	23.49	<i>Onyx perfectus</i>	62.69	35.84	<i>Onyx perfectus</i>	48.15	35.05
<i>Metadesmolaimus pandus</i>	18.95	11.43	<i>Viscosia franzii</i>	11.70	13.22	<i>Mesacanthion hirsutum</i>	14.98	6.36	<i>Mesacanthion hirsutum</i>	8.49	5.71
<i>Enoploides spiculohamatus</i>	6.93	7.49	<i>Xyala striata</i>	5.10	8.05	<i>Enoploides spiculohamatus</i>	10.80	5.25	<i>Xyala striata</i>	7.42	5.59
<i>Viscosia franzii</i>	5.56	6.09	<i>Neochromadora munita</i>	5.19	6.11	<i>Chromaspirina pellita</i>	8.51	4.54	<i>Dichromadora cucculata</i>	4.53	4.26

Table 2

1997 (Av. Sim.: 37.63)			2001 (Av. Sim.: 8.33)			2003 (Av. Sim.: 19.66)			2004 (Av. Sim.: 26.07)		
Species	Ab.	Contr (%)	Species	Ab.	Contr (%)	Species	Ab.	Contr (%)	Species	Ab.	Contr (%)
<i>Neochromadora munita</i>	49.10	27.88	<i>Sabatieria celtica</i>	50.49	25.72	<i>Onyx perfectus</i>	41.81	17.11	<i>Onyx perfectus</i>	18.06	16.84
<i>Theristus maior</i>	27.93	11.45	<i>Microlaimus arenicola</i>	99.95	10.05	<i>Microlaimus marinus</i>	105.21	13.03	<i>Theristus bastiani</i>	9.33	10.59
<i>Theristus bastiani</i>	55.22	7.37	<i>Actinonema celtica</i>	12.65	9.44	<i>Theristus bastiani</i>	31.02	12.53	<i>Dichromadora cucullata</i>	5.28	6.19
<i>Onyx perfectus</i>	16.30	6.45	<i>Leptonemella aphanothecae</i>	15.8	9.41	<i>Theristus longicollis</i>	6.14	4.20	<i>Richtersia inaequalis</i>	3.06	4.96
						<i>Dichromadora cucullata</i>	23.19	3.67	<i>Daptonema stylosum</i>	2.92	4.78
									<i>Odontophora sp. 3</i>	2.68	3.76
									<i>Prochromadorella ditlevensi</i>	1.65	3.37

Table

Northern Area of the Kwintebank

	1997	2001	2003	2004	F	p	H (Kruskal Wallis)	p
S	37	39.25	41.83	50.25			1.1	0.78
D	6.26	7.14	7.17	9.35	0.32	0.81		
J'	0.81	0.89	0.86	0.90	3.93	0.03		
H'(log_e)	2.91	3.12	3.167	3.41			3.42	0.33
1-A'	0.97	0.94	0.94	0.95	2.62	0.09		
N₁	18.75	25.40	24.06	33.54			3.47	0.33
N₂	11.46	16.78	14.59	20.38			2.69	0.44
N_∞	5.16	6.58	6.09	6.46			1.76	0.63
A⁺	39.08	39.79	38.76	39.27			5.18	0.16
A⁺	64.86	67.77	53.87	60.97	3.96	0.03		

Central Area of the Kwintebank

	1997	2001	2003	2004	F	p	H (Kruskal Wallis)	p
S	34.5	42	40.33	45.33			2.20	0.53
D	6.80	8.37	7.30	8.76	2.06	0.14		
J'	0.82	0.85	0.83	0.83	0.068	0.97		
H'(log_e)	2.92	3.14	3.06	3.17	0.60	0.62		
1-A'	0.90	0.92	0.91	0.91	0.12	0.95		
N₁	19.08	24.22	22.17	24.88	0.62	0.6		
N₂	11.31	14.77	13.45	13.74	0.2	0.89		
N_∞	4.26	5.87	5.42	4.85	0.34	0.79		
A⁺	39.24	39.07	39.54	38.35			4.15	0.25
A⁺	63.02	67.36	61.70	60.07			2.28	