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1   Can benthic foraminifera serve as proxies for changes in benthic macrofaunal community

2   structure? Implications for the definition of reference conditions

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26   **Abstract**

27   Benthic macrofauna is one of the most widely used biological groups to assess the ecological

28   status of marine systems. Lately, attention has been paid to similar use of benthic

29   foraminifera. In this study, distribution patterns of benthic foraminiferal and macrofaunal

30   species were investigated simultaneously in 11 fjords in southeastern Norway in order to

31   assess correlations and responses to environmental conditions. Selected fjords allowed to

32   investigate contrasted environmental conditions from low total organic carbon (TOC)

33   content (sediment TOC < 2.7%) in normoxia (bottom-water $[O_2]$ > 2 mL $O_2.L^{-1}$) up to high

34   TOC content (> 3.4%) in severe hypoxia (< 0.5 mL $O_2.L^{-1}$). Environmental parameters

35   comprised bottom-water dissolved oxygen, grain size, total organic carbon, total nitrogen

36   (TN), pigments and depth below threshold (DBT). Foraminiferal and macrofaunal community

37   data were significantly correlated (Procrustes analysis m^2 = 0.66, p = 0.001). Hence, benthic

38   foraminiferal distribution patterns mirror those of benthic macrofauna. However, as

39   opposed to the foraminifera, macrofauna was not recorded at the most oxygen-depleted

40   stations and, hence, was more sensitive to severe oxygen depletion. With regard to

41   assigning species to ecological groups for ecological quality status assessment, the results

42   suggest that species, *e.g. Spiroplectammina biformis* (foraminifera), *Scalibregma inflatum*

43   (macrofauna), may exhibit different ecological requirements depending on their habitat.

44   Considering the observed congruent patterns of benthic foraminifera and macrofauna,

45   palaeo-communities of benthic foraminifera could be used as indicators of reference

46   conditions for benthic macrofaunal community structure. This would however need further

47   developments of algorithms to perform such a translation.

1. Introduction

Most benthic macro-invertebrate species are sedentary, making them dependent on the local environmental conditions. Living at the sediment-water interface, they integrate aquatic as well as sediment conditions. Their communities show dramatic changes in their composition in response to organic matter loads (Pearson & Rosenberg 1978, Bouchet & Sauriau 2008), oxygen depletion (Rosenberg et al. 2002), oil spills (Gray et al. 1990), sewage (Glémarec & Hily 1981), heavy metals (Olsgard & Gray 1995) and physical disturbance (Lavesque et al. 2009). Tolerant species thrive at the early stages of the perturbation, followed by highly tolerant opportunistic species when the perturbation becomes severe (Glémarec & Hily 1981). Hence, macrofauna are routinely used in environmental bio-monitoring studies (e.g. Warwick 1986, Grall & Glémarec 1997, Borja et al. 2003, Bouchet & Sauriau 2008). In response to the implementation of marine legislation such as the Water Framework Directive (WFD), the Clean Water Act, and the Marine Strategy Framework Directive (MSFD), numerous indices based on macrofauna have been established for assessing the ecological quality status (EcoQ, see review in Pinto et al. 2009). Most of the indices developed to assess the EcoQ of marine systems are based on the indicative value of macrofaunal species. They have been classified into 5 ecological groups of sensitivity to disturbances from sensitive to first-order opportunistic species (Glémarec & Hily 1981, Borja 2000). Lately, concerns arose about these indices (see review in Spilmont 2013). One of the main concerns is the definition of reliable reference conditions for benthic macrofaunal communities. This is a crucial point since in the European Water Framework Directive (WFD), reference conditions are mandatory to assess the EcoQ. According to the WFD, the reference conditions (also called "high" status) are defined as "for any surface water body

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72 type reference conditions or high ecological status is a state in the present or in the past

73 where there are no, or only very minor, changes to the values of the hydromorphological,

74 physico-chemical, and biological quality elements which would be found in the absence of

75 anthropogenic disturbance" (Common implementation strategy for the Water Framework

76 Directive (2000/60/EC), Guidance Document No.5, transitional and coastal waters –

77 typology, reference conditions and classification systems p. 106). Assessment of

78 environmental quality is based on the extent of deviation from these reference conditions,

79 following the definitions in the WFD (www.ec.europa.eu/environment/water/marine.htm).

80 Most of the coastal areas are modified or have been modified by human activities (Diaz and

81 Rosenberg 2008). Hence, EcoQ assessment within the WFD is facing issues to determine

82 true reference condition (Nielsen et al. 2003, Elliott and Quintino 2007). As for benthic

83 macrofauna, since there is almost no data from pre-impact time, reference conditions have

84 to be determine using today's communities, which is an issue considering the

85 aforementioned degradation of coastal areas.

86   There is an increasing interest in the use of benthic foraminifera to characterize the

87 health of marine systems (e.g. Alve 1995, Scott et al. 2001, Mojtahid et al. 2006, Bouchet et

88 al. 2007, Frontalini et al. 2009). Lately, indices to use benthic foraminifera routinely to

89 assess EcoQs have been proposed (Hallock et al. 2003, Alve et al. 2009, Bouchet et al. 2012,

90 Barras et al. 2014, Dimiza et al. 2016). Specifically, benthic foraminiferal species were

91 assigned to ecological groups (EGs) according to their sensitivity/tolerance to increasing

92 organic matter enrichment (Alve et al. 2016, Jorissen et al. 2018), inspired by work on

93 benthic macrofauna to develop the AMBI index (Glémarec & Hily 1981, Borja et al. 2000). It

94 led to the development of the Foram-AMBI to assess the ecological quality status of marine

95 systems. In these studies, the response of species along a gradient of enrichment in organic

96   matter allowed their classification into groups of different sensitivity. Five ecological groups

97   were defined: sensitive (EG1), indifferent (EG2), tolerant (EG3), second-order opportunistic

98   (EG4) and first-order (most) opportunistic (EG5). The AMBI and the Foram-AMBI are

99   computed based on the proportion of the different ecological groups in the species

100   community, allowing assessment of ecological quality status.

101   Benthic foraminifera leave an easily accessible and abundant fossil record, which

102   allows reconstruction of the characteristics and timing of historical environmental variations

103   (e.g. Alve, 1991; Hayward et al., 2004, Dolven et al. 2013, Francescangeli et al. 2016).

104   Consequently, it is possible to trace the record of human-induced disturbance over decades

105   or centuries. Indeed, in a pilot study, Alve et al. (2009) suggested that *in situ* reference

106   conditions can be established using fossil benthic foraminiferal assemblages from dated

107   sediment cores. For example, by comparing the "background" fossil foraminiferal

108   assemblages to the modern living foraminiferal assemblages at the same site, it would be

109   possible to determine if a site is naturally anoxic or has become anoxic with recent human

110   influence. This kind of temporal, *in situ* monitoring is not possible with soft-bottom

111   sediment macrofauna because they do not leave abundant or, for most species, any fossil

112   records. Benthic foraminifera may thus provide a powerful tool for defining habitat-specific,

113   *in situ* reference conditions for soft-bottom coastal and transitional waters. Although the

114   response of macrofauna and foraminifera species to environmental gradients may partly

115   differ (Mojtahid et al. 2008), the few studies comparing the two groups have indicated that

116   their responses to environmental changes are basically similar (Schafer et al. 1975, Schafer

117   et al. 1995, Klitgaard-Kristensen & Buhl-Mortensen 1999, Bouchet 2007, Denoyelle et al.

118   2010, Dolven et al. 2013, Hess et al. 2013, Wlodarska-Kowalczuk et al. 2013). For instance,

119   benthic foraminiferal and macrofaunal communities showed similar response to oil-based

120   drill mud disposal with tolerant and opportunistic species dominating in the vicinity of the

121   disposal area (Denoyelle et al. 2010). Furthermore, calcareous foraminifera can be reliable

122   indicators for variability in density, diversity and species composition of benthic macrofauna

123   in the Artic at Svalbard (Wlodarska-Koawalczuk et al. 2013). Hence, it is reasonable to

124   suggest that macrofaunal and foraminiferal species with similar sensitivity to environmental

125   changes may show co-occurrence. This would be of great interest when it comes to the

126   definition of reference conditions. It is reasonable to think that fossil benthic foraminifera

127   could be used as proxies to define reference conditions for benthic macrofauna

128   communities. Further baseline studies are however necessary to validate such a hypothesis.

129   It is thus urgent to quantify the level of correlation between the distribution patterns of

130   these two groups in other environments.

131   In the present study, living benthic foraminifera and macrofauna were investigated

132   in fjordic systems along the Norwegian Skagerrak coast to assess to which degree their

133   responses to major driving environmental factors correspond. This work is part of a

134   comprehensive project (PES), which includes both foraminifera and macrofauna collected at

135   the same sites at the same time. An understanding of the driving forces of the benthic

136   foraminifera communities, expressed as species diversity, was partly achieved in a previous

137   analysis of the same data set (Bouchet et al. 2012, 2013). The present paper aims (i) to

138   determine the driving environmental factors of both the benthic foraminiferal and

139   macrofaunal community structures, (ii) to identify indicator species of both normal and poor

140   environmental conditions, (iii) to compare species assignment in EG from this study to the

141   existing Foram-AMBI and AMBI species lists, and (iv) to assess the correlation between

142   benthic foraminiferal and macrofaunal communities patterns to identify the potential of

143   benthic foraminifera to serve as a proxy for benthic macrofauna in environmental

144   assessments.

145

146   **2. Material and methods**

147

148   **2.1 Study area and sampling sites**

149

150   In August 2008, 27 stations from 11 silled basins along the Norwegian Skagerrak

151   coast, NE North Sea (Figure 1), were sampled for bottom water, sedimentological,

152   biogeochemical and faunal analyses. Stations between 23 and 204 m water depth were

153   selected to provide an oxygen gradient with stable temperature (5-6°C; occasionally 8-9°C at

154   <40 m depth) and salinity (33-34) conditions (Table 1; see Bouchet et al. 2012 for further

155   details) using information from previous studies (Buhl-Mortensen et al. 2009 and

156   unpublished data from the Norwegian Institute for Water Research (NIVA) and Institute of

157   Marine Research (IMR)). The study basins commonly experience partial to complete deep-

158   water renewals during winter. In addition to measured variables, the depth below threshold

159   (DBT) *i.e.* the difference between the water depth at a station and the sill depth of the

160   fjord, has been characterized for stations. DBT is not a factor *sensu stricto*, but a measure

161   that reflects the degree or duration of water stagnation in the deep areas of the fjord.

162

163   **2.2 Field sampling**

164

165   Four sediment cores (8 cm diameter) were collected at each of the 27 stations with a

166   Gemini gravity corer, a modified Niemistö corer (Niemistö 1974). Three replicate cores were

167   used for benthic foraminifera and one for pigments, total organic carbon and total nitrogen

168   analyses. Once on deck, bottom water samples from just above the sediment-water

169   interface in two cores were immediately transferred to Winkler bottles for subsequent

170   dissolved oxygen analysis. All sediment cores were sectioned on board and, for the present

171   study, the top 0-1 and 1-2 cm slices were analysed. Sediment samples for pigments, total

172   organic carbon and total nitrogen analyses were frozen immediately after sectioning, and

173   kept away from the light. Foraminiferal samples were preserved in rose Bengal-stained 70%

174   ethanol (1 g l^{-1}) to avoid protoplasm degradation and to distinguish living (stained) from

175   dead specimens (Murray & Bowser 2000). At each station, macrofauna was sampled using a

176   0.1 m^2 van Veen grab (4 replicates) and a sub-sample of the top 0-1 cm from one grab per

177   station was collected for grain size analyses. The grab sediments were sieved on board

178   through 1 mm screens and fixed in 4% buffered formaldehyde in seawater to preserve

179   macrofauna specimens.

180

181   **2.3 Biogeochemical analyses**

182

183   Bottom-water dissolved oxygen concentrations at the time of sampling were

184   analysed using Winkler titration. Classification of stations as normoxic (bottom-water $[O_2]$ >

185   2 mL O_2.L^{-1}), hypoxic (0.5 - 2 mL O_2.L^{-1}) or severe hypoxic (< 0.5 mL O_2.L^{-1}) follows Diaz and

186   Rosenberg (1995). Sediments were freeze-dried prior to sedimentological and geochemical

187   analyses. For grain size analyses, the dried sediment was weighed, soaked in tap water, and

188   washed on a 63 μm Endecote-sieve. The >63 μm fraction was dried and weighed and the

189   <63 μm-fraction was calculated based on the dry mass. Total organic carbon (TOC) and total

190   nitrogen (TN) were analysed following acid treatment (10% HCl) to remove inorganic C using

191   a CHN analyser (Carlo Erba Elemental Analyzer 1106). Classification of stations as low

192   (<2.7%), medium (2.7-3.4%) and high (>3.4%) TOC content follows that of Molvaer et al.

193   (1997). For pigment analyses, homogenised freeze dried sediment (0.3-0.6 g) was extracted

194   in 5 ml 90% acetone in water. The mixture was sonicated for 30s before overnight

195   extraction. The extract was centrifuged (15 min. at 3500 rpm), and 100 µL of the

196   supernatant was injected on the HPLC for pigment analysis. The analytical system was based

197   on a method described earlier (Wright et al. 1991, Jeffrey et al. 1997). Pigments were

198   identified by comparison of retention time and absorption spectra of authentic standards

199   (DHI Water and Environment, Denmark) and the literature (Jeffrey et al. 1997). Individual

200   pigments were quantified at 436 nm for chlorophylls and pheopigments, and 450 nm for

201   carotenoids. Response factors (RF) for each pigment were obtained by single standard runs.

202   When no standard was available, RF for similar pigments was used with a correction for

203   differences in mass. Pigment concentrations were standardised by the total organic carbon

204   content (Reuss et al. 2010).

205

206   **2.4 Faunal analyses**

207

208   Foraminiferal samples were washed through 500 and 63 µm mesh sieves, and the

209   63-500 µm fraction was split into 8 using a modified Elmgren wet splitter (Elmgren 1973).

210   One eighth of each sample was re-sieved and all live (stained) foraminifera in the 63-125

211   and 125-500 µm fractions were identified to species level and counted in the wet state. The

212   number of individuals >500 µm relative to smaller ones was trivial (<0.1%) so including them

213   would not influence the results. Wet-sample analysis allows preservation of all species,

214   including fragile organic-walled and loosely cemented agglutinated foraminifera. This study

215   is based on the 63-500 µm fraction *i.e.* the sum of 63-125 and 125-500 µm fractions.

216   In the laboratory, macrofaunal samples were rinsed on 1 mm-mesh sieves and

217   transferred to 70% ethanol. All macrofaunal specimens were counted and identified to

218   species level, or the lowest identifiable taxonomic unit.

219   Assignments of foraminiferal and macrofaunal species into ecological groups (EG)

220   were made according to Alve et al. (2016) and Borja et al. (2000), respectively. The concept

221   is based on the classification of species (or groups of species) into five EGs (sensitive,

222   indifferent, tolerant, 2nd order opportunist and 1st order opportunist) representing specific

223   sensitivity levels to an increasing gradient of organic matter (Borja et al. 2000). The groups

224   allow the assessment of the ecological quality status of marine systems.

225

226   **2.5 Numerical analyses**

227

228   Principal components analysis (PCA) was applied on the set of environmental

229   variables to characterize the main natural gradients and describe relationships between

230   sediments, oxygen and fjord topography. For the species community data, initial detrended

231   correspondence analyses indicated that the gradient is short (1.6 SD) in the foraminiferal

232   data and long (3.3 SD) in the macrofaunal data. Consequently, redundancy analysis (RDA)

233   and canonical correspondence analysis (CCA), respectively, were applied to find which

234   environmental variables were most clearly related to the species communities. Analyses

235   were done on the subset of 15 stations with all chemistry data and at least 30 individuals

236   in the pooled macrofaunal sample (all pooled foraminiferal samples had many more than 30

237   individuals). Community data were log(x + 1) transformed prior to analysis; taxa occurring at

238   only one station were removed. Environmental variables were selected using forward

239   selection with 999 permutations. Procrustes analysis (Peres-Neto & Jackson 2001) was used

240   to compare unconstrained ordinations of the foraminiferal (PCA) and

241   macrofaunal (correspondence analysis) community data. The m^2 statistics, which is

242   analogous with the r^2 of a correlation, is reported. Co-correspondence analysis (Co-CA, Ter

243   Braak & Schaffers 2004) was used to relate the foraminiferal and the macrofaunal

244   communities in a direct way.

245   All calculations were performed using the statistical language R version 3.4.1 (R Core

246   Team, 2017). Ordinations were run with the vegan version 2.4-3 (Oksanen et al. 2010). R

247   code is archived at https://github.com/richardjtelford/PES.

248

249   **3. Results**

250

251   **3.1 Environmental conditions at sampling stations**

252

253   Depth-below threshold (DBT), bottom-water dissolved oxygen concentration,

254   sediment grain size and sediment organics were rather different among the stations (Table

255   1). Sandnesfjord, Eidangerfjord, Risørbassenget (R60), Topdalsfjord, Groosefjord, Frierfjord

256   (except F70) and Indre Hvaler have rather shallow DBT below 50 m, whereas the other

257   fjords have DBT up to 169 m. In Kristiansandsfjord there is no sill. High (normoxic) bottom-

258   water oxygen concentrations (>2 mL $O_2.L^{-1}$) characterized stations in the Indre Hvaler basin,

259   Kragerøfjord, Topdalsfjord, the shallower stations in Groosefjord, Frierfjord (F30 and F50),

260   Ærøydypet, Sandnesfjord, Eidangerfjord and Kristiansandsfjord as opposed to stations in

261   Risørbassenget (except R60), the deeper stations in Frierfjord (F70 and F90) and Håøyfjord

262   where hypoxic (0.5-2 mL $O_2.L^{-1}$) to severe hypoxic (<0.5 mL $O_2.L^{-1}$) conditions are recorded.

263   Sediments at stations in Risørbassenget (except R160 and R180) and Kristiansandsfjord, as

264   well as station G50 were sandier than the others, with less than 90% of the sediment mass <

265   63 µm (Table 1). Total organic carbon concentrations were higher than 3.4% in Ærøydypet,

266   Kragerøfjord, Sandnesfjord, Eidangerfjord, Risøbassenget, Topdalsfjord, Frierfjord (F90) and

267   Groosefjord (Table 1).

268   In the PCA of environmental variables, the first two axes explained 75.2% of the

269   variance (Fig. 2). Two main gradients appear; one related to sediment components (particle

270   fine fraction, TOC) and one to oxygen and fjord basin topography (O_2, DBT). The sediment

271   gradient separates stations with very high fine fraction and moderate organic content

272   (lower left: Indre Hvaler IH, Frierfjord F) from stations with lower fine fraction and high

273   organic contents (upper right: Groosefjord G, Risørbassenget R). The oxygen – fjord

274   topography gradient separates stations in deep fjord basins with shallow sill and low oxygen

275   content (lower right: Risør basin R, Håøyfjord 102, deep Frierfjord F) from stations with

276   either shallow water depths or in fjords with deep sills (upper left). The pigments correlate

277   with DBT and characterized the deep basins, particularly the Risør basin. Most pigments

278   were intercorrelated, except allo-xanthin that appeared to be related also to the sediment

279   fine fraction.

280

281   **3.2 Environmental variables and fauna**

282

283   In total, 116 foraminiferal taxa and 290 macrofaunal taxa were identified. Benthic

284   foraminifera occurred in all samples, whereas macrofauna were absent from station F90

285   (replicate 1 and 2), station R120 (replicate 4), station R160 (all replicates) and station R180

286   (all but replicate 1). Based on RDA and CCA, respectively, benthic foraminifera and

287   macrofauna species were significantly related to the same subset of environmental

288   parameters, viz. TOC and DBT (Figs 3 and 4). Together, the selected parameters explained

289   43% and 29% of the variation for foraminiferal and macrofaunal species assemblages,

290   respectively.

291   The distribution of foraminiferal taxa in relation to TOC and oxygen, the latter being

292   related to DBT (Fig. 2), is illustrated in Fig. 5. The species *Micrometula hyalostriata*,

293   *Phainogullmia aurata* and *Spiroplectammina biformis* mainly occur at low TOC (<2.7%) and

294   high bottom-water oxygen concentrations. Highest abundances of *Cassidulina laevigata* and

295   *Bulimina marginata* were observed at stations with low to high TOC (0.8-9%) and high

296   bottom-water oxygen concentrations. *Cylindrogullmia alba* and *Leptohalysis scottii* occur at

297   similar TOC levels but at stations with high to low bottom-water oxygen concentrations.

298   *Liebusella goësi*, *Textularia earlandi* and *Recurvoides trochamminiforme* show highest

299   abundances under TOC concentrations between 3.0 and 4.3% and well-oxygenated

300   conditions. *Stainforthia fusiformis*, *Discorbinella bertheloti, Fissurina* sp. and *Bolivinellina*

301   *pseudopunctata* thrive under high TOC concentrations (>3.4%) and hypoxic to severe

302   hypoxic conditions.

303   Compared to the assignments of foraminifera in Alve et al. (2016) four new species

304   (*Micrometula hyalostriata, Phainogullmia aurata, Cylindrogullmia alba, Leptohalysis scottii*)

305   were assigned and three (*Cassidulina laevigata, Liebusella goësi, Bolivinellina*

306   *pseudopunctata*) were re-assigned based on their abundance relative to sediment TOC in

307   this new data set (Table 2).

308   The distribution of dominant macrofaunal species on TOC and oxygen is illustrated in

309   Fig. 6. *Pseupopolydora* sp., *Chaetozone setosa*, *Capitella capitata*, *Thyasira* cf. *sarsii* occurred

310   at hypoxic stations with high TOC. *Mediomastus fragilis* was overabundant in

311   Kristiansandfjord that is contaminated from trace elements*. Thyasira equalis* and

312   *Spiophanes kroeyeri* occurred at well-oxygenated stations with medium TOC content.

313   *Amphiura chiajei*, *A. filiformis* and *Scalibregma inflatum* occurred at normoxic stations (Fig.

314   6B) with low organic matter concentrations (Fig. 6A).

315   Compared to the assignments of the AMBI list (Borja et al. 2000, last update: June

316   2017), two species (*Scalibregma inflatum* and *Thyasira* cf. *sarsi*) were re-assigned based on

317   their abundance relative to sediment TOC in this new data set (Table 2).

318

319

320   **3.3 Foraminiferal and macrofaunal community relationships**

321

322   Foraminiferal and macrofaunal community data were significantly correlated

323   (Procrustes analysis m^2 = 0.66, p = 0.001). Using a co-correspondence analysis on

324   foraminiferal and macrofaunal community, 24% of the variance in the macrofaunal

325   community was explained by the foraminiferal community (Fig. 7).

326

327   **4. Discussion**

328

329   In the present study, patterns of distribution of foraminiferal and macrofaunal

330   species are best explained by the variables of TOC and DBT. Along the same lines, deep-

331   water renewal and oxygenation in a fjord depend on DBT as well as on the supply of organic

332   matter (*i.e.*, impacts oxygen consumption). DBT will, however, also represent the influence

333   of other variables, e.g. pigments, different organic components and temperature, that

334   increase or decrease due to the gradually changing conditions with depth. In the following

335   discussion, however, it will be made reference to oxygen rather than of DBT *sensu stricto*

336   that may incorporate several unknown factors. This is further supported by Bouchet et al.

337   (2012) who showed on the same dataset that benthic foraminiferal diversity is correlated to

338   bottom-water dissolved water oxygen. These two variables (oxygen and TOC) are indeed

339   known to be drivers of both diversity and species composition of benthic foraminifera and

340   macrofaunal communities (Alve 1990, Riera et al. 1999, Gustafsson & Nordberg 2000,

341   Rosenberg et al. 2002, Bouchet et al. 2012). In the studied Norwegian fjords, benthic

342   foraminiferal and macrofaunal species responded in the same way to different

343   environmental conditions (Procrustes analysis), except that macrofauna was less tolerant to

344   the oxygen depleted conditions. This is because, unlike macrofauna, some foraminiferal

345   species can perform anaerobic metabolism (e.g., Risgaard-Petersen et al. 2006). Our findings

346   confirmed the results from the few studies assessing and comparing the response of benthic

347   foraminifera and macrofauna to different environmental conditions, mentioned in the

348   introduction.

349

350   **4.1 Foraminiferal indicator species**

351

352   In this study, *Micrometula hyalostriata*, *Phainogullmia aurata* and *Spiroplectammina*

353   *biformis* are sensitive (EG1) to organic enrichment, occurring primarily in normoxic

354   conditions. *Phainogullmia aurata* has been described as a pioneer species showing

355   maximum abundance in the colonization phase on uncontaminated clay and almost

356   disappearing with time as the amount of sediment organic material increased (Hess et al.

357   2014). The ecology of the soft-walled species *M. hyalostriata* is poorly known. In this study,

358   it was common only at normoxic, low-TOC sites (Fig. 5). *Spiroplectammina biformis* was the

359   second-most common species in the most hypoxic parts of the organic matter enriched

360   Drammensfjord, southern Norway (Alve 1995) but it was not able to survive persistent

361   severe hypoxia below 0.5 mL $O_2.L^{-1}$ (Alve 1991, 1995). It was also reported to tolerate

362   organic enrichment in several eastern Canadian estuaries and embayments and in the

363   North-east Atlantic (Alve et al. 2016, Schafer et al. 1991). In the present study, its highest

364   abundance was at a low-TOC site. It was also sensitive to TOC in the Saguenay fjord and in a

365   study in Canadian fish aquaculture sites (Schafer et al. 1991, 1995).

366   *Cassidulina laevigata* and *Cylindrogullmia alba* show the same distribution pattern

367   along the TOC gradient as for species from the indifferent EG2. *Cassidulina laevigata* is a

368   typical species of the Skagerrak-Kattegat fauna (*sensu* Nordberg et al. 2000), which used to

369   flourish in several Scandinavian fjords until it was replaced by species associated with

370   frequent coastal hypoxia (e.g., Alve 1991, Polovodova Asteman & Nordberg 2013,

371   Polovodova Asteman et al. 2015). In the present study, *C. laevigata* is never abundant, it

372   only occurs at stations with normoxic conditions and mainly, but not solely, where TOC is

373   low to moderate (Fig. 5). Hence, *C. laevigata* may belong in the indifferent group EG2,

374   although it has been classified as a sensitive species (Alve et al.2016). The present results

375   show that *C. alba* can survive under a wide range of TOC concentrations.

376   *Bulimina marginata*, *Recurvoides trochamminiforme*, *Liebusella goësi* and *Textularia*

377   *earlandi* are all tolerant species (EG3) to organic enrichment in the studied fjords, occurring

378   in normoxic conditions. *Bulimina marginata* is tolerant to oxygen-depleted conditions (Alve

379   1991, Barmawidjaja et al. 1992). However, it is not able to survive persistent severe hypoxia

380   below 0.5 mL $O_2.L^{-1}$ (Filipsson & Nordberg 2004). In this study, it occurred over a broad

17

381   range of TOC concentrations, but only under normoxic conditions. As for *R.*

382   *trochamminiforme*, Alve et al. (2016) mentioned it as a tolerant species. *Liebusella goësi* is

383   known not to survive severe hypoxia (Nordberg et al. 2000, Filipsson & Nordberg 2004).

384   Tolerance to TOC enrichment under appropriate oxygen concentrations has already been

385   observed for *T. earlandi* (Schafer et al 1995). It is however sensitive to oxygen depletion

386   (Gustafsson & Nordberg 2000, Polovodova Asteman et al. 2015). Its abundance decreased at

387   dissolved-oxygen concentrations below 1.0 ml $O_2.L^{-1}$ (Gustafsson & Nordberg 2000).

388   *Bolivinellina pseudopunctata, Stainforthia fusiformis*, *Leptohalysis scottii* and

389   *Fissurina* sp. are assigned in the opportunistics EG4/5, thriving well in sediment with high

390   TOC content based on this study results, occurring at hypoxic to severe hypoxic stations. The

391   two first species are known to be able to survive at high TOC and hypoxic to severe hypoxic

392   conditions (Alve 1994, Gustafsson & Nordberg 2000, Alve 2003). These species

393   outcompeted the typical Skagerrak-Kattegat species throughout the degradation of the

394   environmental conditions in the area during the 1900s (Gustafsson & Nordberg 2001, Alve

395   et al. 2009, Dolven et al. 2013). *Bolivinellina pseudopunctata* is an opportunistic species able

396   to tolerate low oxygen conditions (Gustafsson & Nordberg 2001), although it has been

397   reported to disappear after periodic severe hypoxia or anoxia (Gustafsson & Nordberg

398   2000). The observation of this species in the most organic rich stations supports that it is an

399   opportunistic species, which is not in agreement with the classification of Alve et al. (2016)

400   in the indifferent EG2. Our results suggest that *L. scottii* is able to survive under hypoxic

401   conditions as opposed to what has been reported in Havstensfjord in Sweden (Gustafsson &

402   Nordberg 2000). Furthermore, it occurs in this study in fjords with a wide range of TOC

403   concentrations from 2 to 9%. It is a species known to tolerate environmental disturbances

404   such as paper mill and fish farming effluents (Alve & Nagy 1986, Scott et al. 2001,

405 Polovodova Asteman et al. 2015) and it is common in eutrophic environments (Scott et al.,

406 2005; Sabbatini et al., 2012). *Stainforthia fusiformis* is a characteristic species of heavily

407 disturbed environments (see review in Alve 2003). Except that species of *Fissurina* seem to

408 be ectoparasites on *Discorbis vilardeboanus* (d'Orbigny) and *Rosalina bradyi* (Cushman) (see

409 Collen & Newell, 1999, and references therein), little is known about the ecology of

410 *Fissurina* spp. In the present material, *Fissurina* sp always co-occurs with *Discorbinella*

411 *bertheloti*, perhaps as a parasite?

412   *Discorbinella bertheloti* (also found under the name *Cibicides bertheloti*) was found

413 alive (stained) at hypoxic and severe hypoxic stations. With their epifaunal mode of life

414 (Murray 2006), *Cibicides* spp. have been considered as sensitive species not directly linked

415 to sedimentary TOC (Alve et al. 2016). They rather reflect the impact of bottom-near

416 currents (Linke & Lutze 1993). Hence, occurrence of *D. bertheloti* at the most oxygen-

417 depleted stations with high TOC content was probably due to recent transport of living

418 specimens. It is thus difficult to conclude on the indicative value of this species.

419

420 **4.2 Macrofaunal indicator species**

421

422   In this study, *Amphiura chiajei*, *A. filiformis*, *Scalibregma inflatum* are sensitive

423 species (EG1) to TOC*,* occurring at normoxic stations. They are known to not tolerate

424 oxygen-depleted conditions (Aschan & Skullerud 1990, Nilsson & Rosenberg 1994, 2000,

425 Rosenberg et al. 2001). The three species have been reported to solely occur at unpolluted

426 sites in the Oslofjord (Mirza & Gray 1981). A high abundance and biomass of *A. filiformis* and

427 *A. chiajei* has been observed at well oxygenated sites in the Skagerrak (Josefson 1990).

428 According to AMBI's ecological groups (EG) of sensitivity to disturbances (Borja et al. 2000),

429   *A. chiajei* and *A. filiformis* are indifferent species (EG2) and *S. inflatum* is a tolerant species

430   (EG3). *Amphiura filiformis* has been reported to be sensitive to severe disturbances around

431   oil platforms (Olsgard & Gray 1995). Note that the tolerance level of *S. inflatum* is rather

432   uncertain since it has been reported to be either sensitive (Mirza & Gray 1981, Rygg 1985b,

433   Nilsson & Rosenberg 1994, 2000, Rosenberg et al. 2001, Pabis & Sobczyk 2015) or tolerant

434   (Rygg 1985a, Aschan & Skullerud 1990, Borja et al. 2000, Levin et al. 2009) to disturbances.

435   *Thyasira equalis* and *Spiophanes kroeyeri* dominate at well-oxygenated stations

436   moderately rich in organic matter. They are not present at the hypoxic/severe hypoxic

437   stations, suggesting that neither of the species would tolerate low oxygen concentrations.

438   This contradicts other works on these species (see review in Levin et al. 2009). For instance,

439   *T. equalis* has been reported to survive low-oxygen concentrations (Josefson & Widbom

440   1988, Nilsson & Rosenberg 2000). It usually occurs in moderately disturbed areas (Pearson

441   1975, Mirza & Gray 1981, Rygg 1985a), although it has been reported not to tolerate copper

442   pollution (Rygg 1985b). The results of the present study are in accordance with the

443   classification of *T. equalis* in the tolerant EG 3 (Borja et al. 2000). Conversely, *S. kroeyeri* has

444   been mostly reported to disappear in the early stage along a gradient of increasing

445   disturbances *i.e.* oil platform activities, sewage outfall, copper, organic enrichment, oxygen

446   depletion (Mirza & Gray 1981, Rygg 1985b, Aschan & Skullerud 1990, Nilsson & Rosenberg

447   2000, Mojtahid et al. 2008, Oug et al. 2012). Few studies nevertheless reported the

448   presence of this species in low disturbed sites (Pearson 1975, Gray & Pearson 1982, Rygg

449   1985a, Moore & Rodger 1991). The classification of *S. kroeyeri* in the tolerant EG3 (Borja et

450   al. 2000) is at least questionable.

451   *Pseupopolydora* sp., *Chaetozone setosa*, *Capitella capitata* and *Thyasira* cf. *sarsii*

452   occur at stations with hypoxic conditions and high TOC contents. *Mediomastus fragilis*

453   dominates in the heavily polluted with trace metals Kristiansandfjord. It belongs together

454   with *T.* cf. *sarsii* to the tolerant EG3, *C. setosa* and *P.* sp. belong to the second-order

455   opportunistic EG4 and *C. capitata* to the first-order opportunistic EG5 (AMBI-list, Borja et al.

456   2000). They are all characterizing low-oxygenated environments (Levin et al. 2009).

457   *Mediomastus fragilis* can tolerate pollution such as oil spills, disturbances associated to oil

458   platforms, metals and high level of organic enrichment (Pearson & Rosenberg 1978, Mirza &

459   Gray 1981, Dauvin 2000, Mojtahid et al. 2008, Oug et al. 2012). *Thyasira* cf. *sarsii* is sensitive

460   to low oxygen concentrations (Josefson & Widbom 1988, Nilsson & Rosenberg 2000) but it

461   can colonize sediments polluted by copper, organic matter, and dredging materials from oil

462   platform activities (Pearson 1975, Rygg 1985b, a, Olsgard & Gray 1995). *Capitella capitata*

463   and *P.* spp. are known colonizers of completely anoxic sediments in fjord systems

464   (Rosenberg et al. 2001). They are often the last species to survive these depleted conditions

465   (Pearson & Rosenberg 1978, Mirza & Gray 1981, Oug et al. 2012). *Chaetozone setosa* and *C.*

466   *capitata* are typical indicators of severe effects around oil platforms of the Norwegian

467   continental shelf (Olsgard & Gray 1995). *Chaetozone setosa* usually thrives in depleted

468   conditions (Rygg 1985a, Olsgard & Hasle 1993, Pabis & Sobczyk 2015). It is a common

469   species in organic enriched areas (Gray et al. 1990).

470

471   **4.3 Concerns about the indicative value of classified species**

472

473   The use of the presence of certain species to assess the state of marine systems has

474   a long history. The concept is based on an *a priori* apprehension that some species have

475   narrow ecological requirements. Hence, species are meant to be indicative of the prevailing

476   conditions where they are found. Based on numerous works (e.g., Pearson & Rosenberg

477 1978, Glémarec & Hily 1981, Hily 1983), lists of benthic macrofaunal species, assigned into

478 groups of sensitivity to disturbances, have been established; the most widely used being the

479 species associated to the AMBI index (Borja et al. 2000). Lately, following the suggestions of

480 the FOBIMO working group, the same approach was used to assign benthic foraminiferal

481 species to EGs of sensitivity/tolerance to conditions along an increasing stress (organic

482 matter enrichment) gradient (Alve et al. 2016, Jorissen et al. 2018). So far, assignment of

483 foraminiferal species has only been done for the North-East Atlantic and Arctic fjords,

484 continental shelves, and slopes and for the Mediterranean (Alve et al. 2016, Jorissen et al.

485 2018). The use of a single species list classification means that the indicative value of a

486 species is a static concept *i.e.* a species is expected to have a similar sensitivity or tolerance

487 wherever it occurs and regardless of the adaptation ability of this species. However, it is

488 known that some species are plastic enough to adapt to their environment and could

489 change their autecology requirements along environmental gradients (see review in Zettler

490 et al. 2013 and references therein). Hence, a species tolerance spectrum might be wider

491 than a single category, *i.e.* "sensitive species" or "tolerant species". Species even exhibit

492 different responses to disturbance depending on their habitat and the source of

493 disturbances; they behave as sensitive species while they can be tolerant or opportunistic

494 somewhere else or against a different pollution source (Zettler et al. 2013). The

495 biogeographical/ecosystem-type restricted approach chosen to assign foraminiferal species

496 tend to support the ability of species to adapt their sensitivity/tolerance level to their

497 environment.

498   In this study, we reported discrepancies in the assignment in EG with the study of

499 Alve et al. (2016) for *S. biformis*, *C. laevigata*, *L. goësi* and *B. pseudopunctata*. For *C.*

500 *laevigata*, our study results suggest a classification in the indifferent EG2 instead of the

501   sensitive EG1 (Alve et al. 2016). These two EGs are rather close conceptually since they

502   include species that cannot tolerate any excess in organic matter. Some biotic indices, *i.e.*

503   Bentix (Simboura & Zenetos 2002), group these two EGs in one EG. This might be something

504   to consider in a further implementation of the Foram-AMBI list. *Spiroplectammina biformis*

505   was assigned to the tolerant EG in the Foram-AMBI list of species from the North-East

506   Atlantic (Alve et al. 2016). In several eastern Canadian estuaries and embayments, *S.*

507   *biformis* has been reported in moderately polluted local environments (Schafer et al. 1991).

508   This study results however suggest that it is a sensitive species to TOC enrichment. In the

509   Saguenay fjord, *S. biformis* abundances have also been reported to decrease with increasing

510   organic matter load from a pulp mill effluent (Schafer et al. 1991). In a study in four

511   Canadian aquaculture sites, it showed a significant negative correlation to TOC enrichment

512   due to the presence of fish cages (Schafer et al. 1995). These evidences suggest that it is

513   thus not sure whether this species belongs to the sensitive EG1 or the tolerant EG3.

514   Discrepancies in the response of species to TOC enrichment have been found between this

515   study results and previous work for both benthic foraminifera and macrofauna. As for

516   benthic macrofauna, there are eight studies, including this one, reporting a sensitive

517   behavior of the polychaete *S. inflatum* towards disturbances and at least four reporting a

518   tolerant one (see aforementioned references). In the AMBI species list, this species is

519   assigned to the tolerant EG. The assignment of *S. inflatum* within the AMBI list is rather

520   uncertain. The same concerns arose about *T.* cf. *sarsii* which behave like an opportunistic

521   species in this study and is assigned to tolerant EG in the AMBI-list. Occurrences of *T.*

522   *equalis, S. kroeyeri* and *S. inflatum* in several Norwegian fjords and coastal areas (Rygg &

523   Norling 2013) showed tolerance levels corresponding to EG3 (tolerant), thus supporting the

524   classification in the AMBI system. These discrepancies may be due to the fact that indices'

525 scores come from large dataset collections covering large geographical regions and

526 subregions and not local scales (Borja et al. 2000, Rosenberg et al. 2004). Hence, they

527 integrate the "experience" from a species behavior over a large span of data or literature

528 data. Local adapation of species ecological requirement may lead to wrong interpetation of

529 the species indicative value (Dauvin et al. 2010, Zettler et al. 2013).

530   Zettler et al. (2013) reported that the response of macrofaunal species towards

531 organic enrichment would change along a gradient of salinity. They concluded that the

532 interaction between environmental variables should not be neglected when using static

533 indicative value of a species. This study results tend to confirm the latest concerns about the

534 concept of species lists of tolerance/sensitivity. Furthermore, this study shows that these

535 concerns may apply to benthic foraminifera. At a large biogeographical scale, the indicative

536 value may be reliable, but it is rather uncertain at a local geographical scale. This study

537 results definitively support cautions (Dauvin et al. 2010, Zettler et al. 2013) when it comes to

538 the use of indicator species lists. It seems obvious that more studies are needed to constrain

539 these biases. Supplementary approaches should be considered, for instance rank-frequency

540 diagrams (Frontier 1976, Bouchet et al. 2007, Seuront 2013) and diversity indices (Bouchet

541 et al. 2012, Dolven et al. 2013, Francescangeli et al. 2016, Bouchet et al. 2018).

542

543 **4.4 Benthic foraminifera as indicator of macrofaunal community structure**

544

545   The assessment and quantification of cross-taxon congruence *i.e.* similar response

546 along an environmental gradient of species belonging to different taxa, in space and time,

547 represents a critical step in the identification of suitable indicator taxa for biodiversity. In

548 this study, Procrustes rotation and co-correspondence analysis (Co-CA) were used to

549 quantify the strength of the congruence between foraminiferal and macrofaunal

550 communities along the studied environmental parameters gradient. Procrustes rotation and

551 Co-CA are powerful and robust methods to evaluate the degree of congruence between two

552 community datasets (Peres-Neto & Jackson 2001, Gioria et al. 2011). Patterns of

553 foraminiferal species distribution closely resembled those of the macrofauna, as is showed

554 by significant correlation between the groups. The strength of the congruence in species

555 composition between benthic foraminifera and macrofauna along the environmental

556 gradient reflects the similarity in their response to TOC enrichment. Interactions can explain

557 congruence in species between these two groups. First, there may be a trophic link between

558 the two groups; benthic macrofauna species being able to feed on benthic foraminifera

559 (Lipps 1983). Secondly, benthic macrofauna bioturbating activities enhance the vertical

560 distribution of foraminifera in deeper sedimentary layers (Bouchet et al. 2009). Last but not

561 least, there is an evident similarity in the patterns of distribution of species of both groups in

562 response to environmental gradients.

563   In this study, benthic foraminiferal and macrofaunal species composition appear to

564 respond to the same environmental factors, in particular bottom-water dissolved oxygen

565 and organic matter content. Changes in the composition of foraminiferal and macrofaunal

566 assemblages are expressed in increased dominance of tolerant/opportunistic species and

567 the progressive disappearance of sensitive species under degraded conditions *i.e.* increasing

568 TOC content and decreasing bottom-water oxygen concentrations. It supports other studies,

569 although there are few, showing similar response of the two groups to adverse

570 environmental conditions. Patterns of foraminiferal species distribution closely resembled

571 those of macrofauna in response to disturbances of a glacier (Wlodarska-Kowalczuk et al.

572 2013). Similar succession from sensitive to tolerant species has been reported for both

573 groups in response to different pollution sources such as sewage outfalls, industry, oil-based

574 drill mud disposal and aquaculture (Schafer et al. 1975, Schafer et al. 1995, Mojtahid et al.

575 2008, Denoyelle et al. 2010). However, some studies suggested that benthic foraminifera

576 could be more indicative than benthic macrofauna along a gradient of disturbances

577 (Mojtahid et al. 2008, Denoyelle et al. 2010). In this study, benthic foraminifera exhibited

578 more tolerance to the most depleted conditions (high TOC and anoxic conditions), by

579 maintaining higher densities than did the macrofauna. This confirms previous results

580 showing that benthic macrofauna is more sensitive than benthic foraminifera to depleted

581 oxygen conditions (Josefson & Widbom 1988) and, as previously mentioned, is directly

582 linked to the fact that some foraminiferal species perform anaerobic metabolism (*e.g.*,

583 Risgaard-Petersen et al. 2006). It implies that benthic foraminifera are able to occur along

584 the whole environmental gradient, which is an asset compared to benthic macrofauna in

585 monitoring studies when approaching the "bad" end of the environmental gradient. The

586 strength of the congruence between benthic foraminifera and macrofauna suggests that

587 foraminifera could be reliable indicators of benthic macrofauna community structure. This

588 has interesting implications, in particular with regard to defining reference conditions for

589 areas where the environmental conditions may have changed over time, as suggested by

590 Alve et al. (2009). Defining reference conditions are mandatory according to the WFD and

591 complying to MSFD when it comes to assessing the health of marine systems. Hindcasting is

592 one method that can be used to determine previous conditions. This is hardly possible with

593 benthic macrofauna since historical data are scarce. Mostly the molluscs can fossilise and

594 allow a reconstruction of palaeo-environments (Poirier et al. 2009), meaning that most of

595 the biological signal is lost in the fossil sediment. Conversely, most of the foraminiferal

596 community can fossilise and be preserved in the fossil sediment. It allows reconstruction of

597   palaeo-environments (e.g., Alve 1991, Alve et al. 2009, Dolven et al. 2013, Polovodova

598   Asteman et al. 2015, Francescangeli et al. 2016). Using fossil benthic foraminifera, it is

599   possible to determine objective and reliable reference conditions. Hence, fossil benthic

600   foraminifera could be used as proxies to assess the deviation from reference conditions for

601   benthic macrofauna communities. However, this requires an algorithm for translating

602   foraminiferal community data into macrofaunal community data (specified macrofaunal

603   species and their abundances). More conceivably, the ecological quality status has to be

604   estimated directly from the foraminiferal data. This requires an environmental classification

605   system using foraminiferal indices. The development of Foram-AMBI (Alve et al. 2016,

606   Jorissen et al. 2018) is one step towards such a system.

607

608   **Acknowledgment**

609

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Figure Captions

Figure 1: Map of the sampling stations

Figure 2: Principal components analysis (PCA) of environmental variables: biplot of stations and variables for axes 1 and 2 (75 % of variation). Stations with one or more missing values have been omitted from analysis.

Figure 3: Redundancy analysis (RDA) of foraminiferal species assemblages: triplot of species (crosses), stations (dots) and significant environmental variables (vectors). Most dominant species are indicated by abbreviated names. Stations with missing data for environmental variables or strongly impoverished fauna have been omitted from analysis.

Figure 4: Canonical correspondence analysis (CCA) of macrofaunal species assemblages: triplot of species (crosses), stations (dots) and significant environmental variables (vectors). Most dominant species are indicated by abbreviated names. Stations with missing data for environmental variables or strongly impoverished fauna have been omitted from analysis.

Figure 5: Abundances (ind.m^{-2}) of the main foraminiferal species at stations along (A) the TOC-gradient (%) and (B) the bottom-water dissolved oxygen concentration-gradient (mL O$_2$.L^{-1}). Definition of low (<2.7%), medium (2.7-3.4%) and high (>3.4%) level of TOC follows Molvaer et al. (1997). Definition of normoxia (bottom-water [O$_2$] > 2 mL O$_2$.L^{-1}), hypoxia (0.5 - 2 mL O$_2$.L^{-1}), severe hypoxia (< 0.5 mL O$_2$.L^{-1}) follows Diaz & Rosenberg (1995). Please note: different scales on the x-axes.

922

923   Figure 6: Abundances (ind.m^{-2}) of the main macrofaunal species at stations along (A) the

924   TOC-gradient (%) and (B) the bottom-water dissolved oxygen concentration-gradient (mL

925    $O_2.L^{-1}$). Definition of low (<2.7%), medium (2.7-3.4%) and high (>3.4%) level of TOC follows

926   Molvaer et al. (1997). Definition of normoxia (bottom-water $[O_2]$ > 2 mL $O_2.L^{-1}$), hypoxia (0.5

927   - 2 mL $O_2.L^{-1}$) and severe hypoxia (< 0.5 mL $O_2.L^{-1}$) follows Diaz & Rosenberg (1995). Please

928   note: different scales on the x-axes.

929

930   Figure 7: Biplot based on predictive co-correspondence analysis (CoCA) of foraminifera (left)

931   against macrofauna (right) showing 49% and 24% of the total variance in the foraminiferal

932   and macrofaunal data, respectively.

933

934   **Table captions**

935

936   Table 1: Characteristics of sampling stations (nd: no data): water depth, depth below

937   threshold (Norwegian Hydrographic Service), bottom-water dissolved O_2-concentration at

938   the time of sampling ($[O_2]_{tos}$, mL $O_2.L^{-1}$), sediment grain size (%<63µm), total organic carbon

939   (TOC, %), Total nitrogen (TN, %) and C/N ratio of sampling stations. For location of areas, see

940   Fig. 1.

941

942   Table 2: Suggested new assignments into EGs for foraminifera and macrofauna species

943   according to Alve et al (2016) and Borja et al. (2000), respectively (na: not assigned).
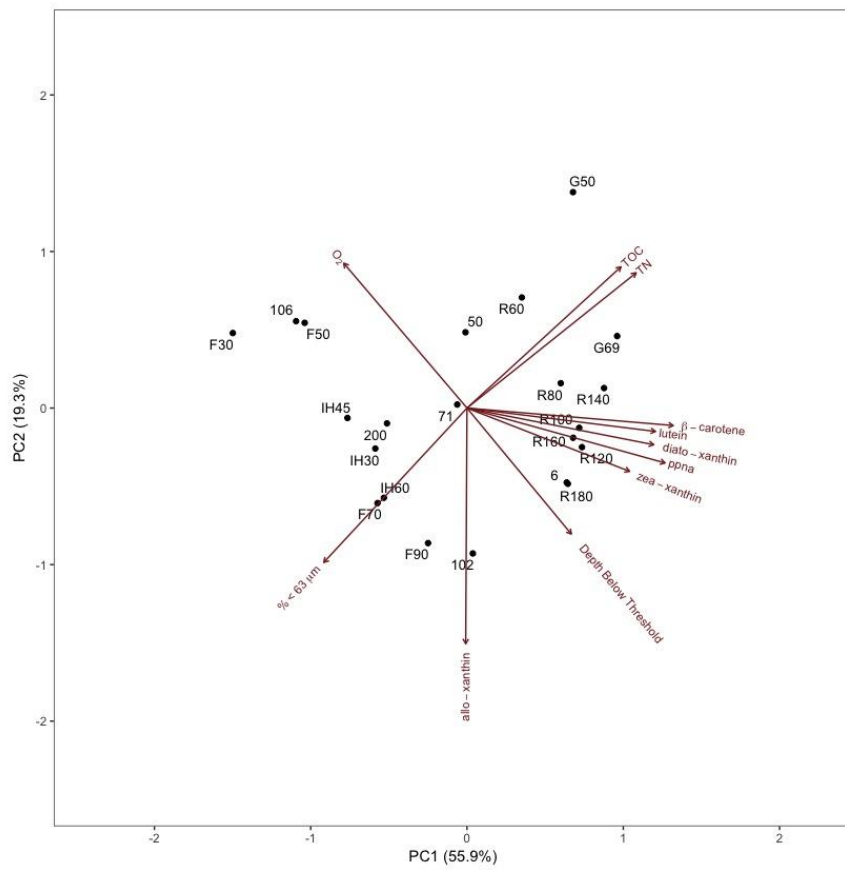
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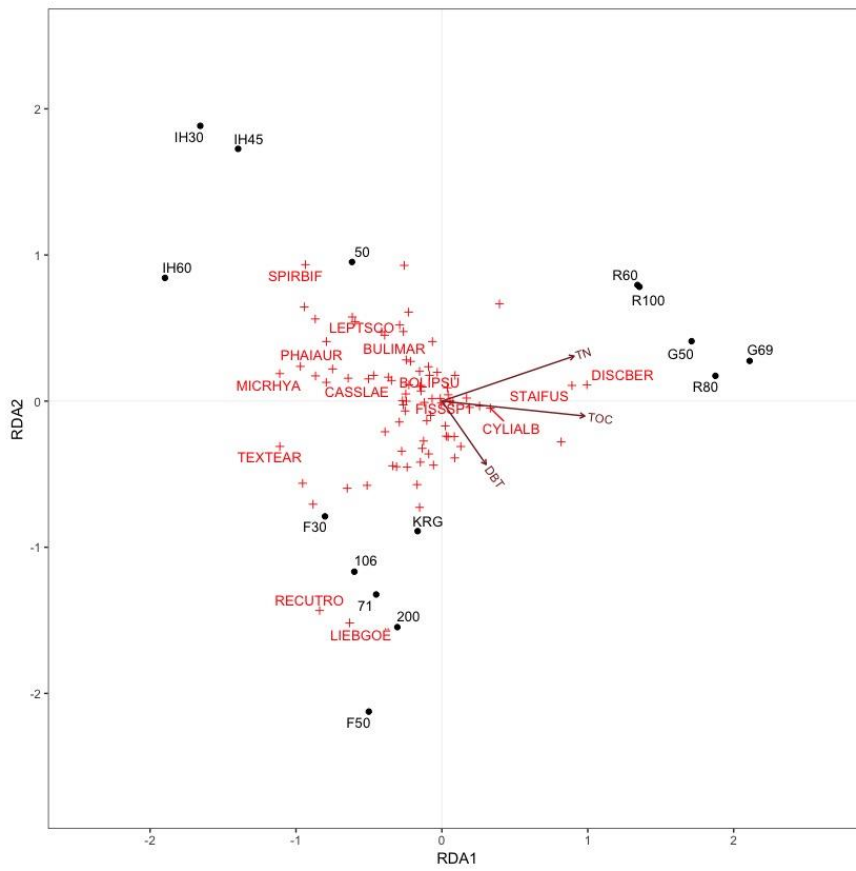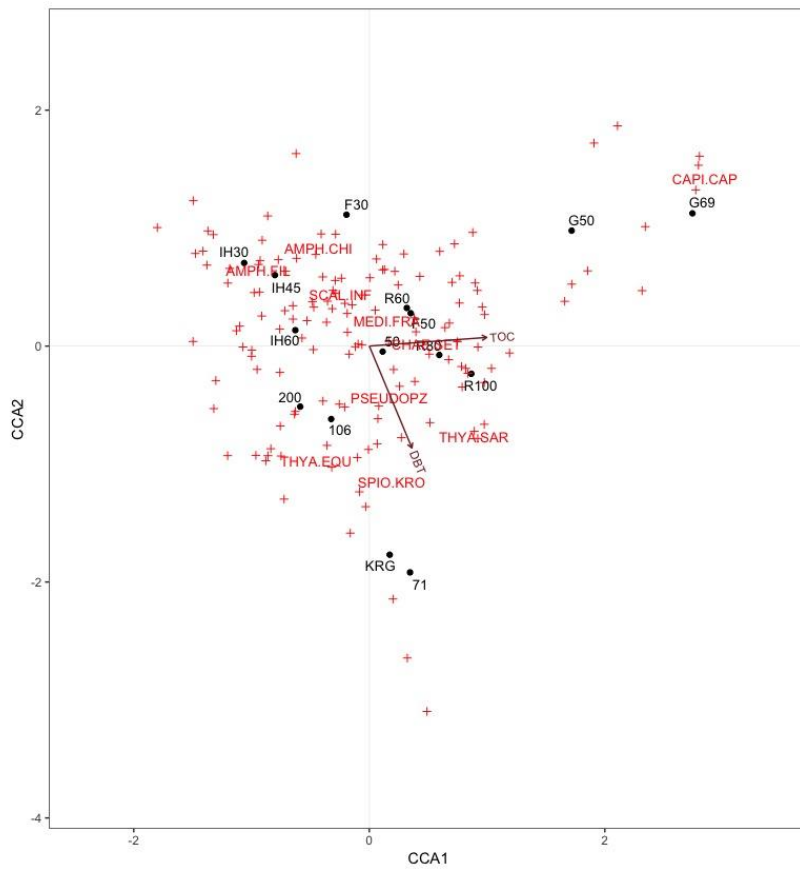945   Figure1
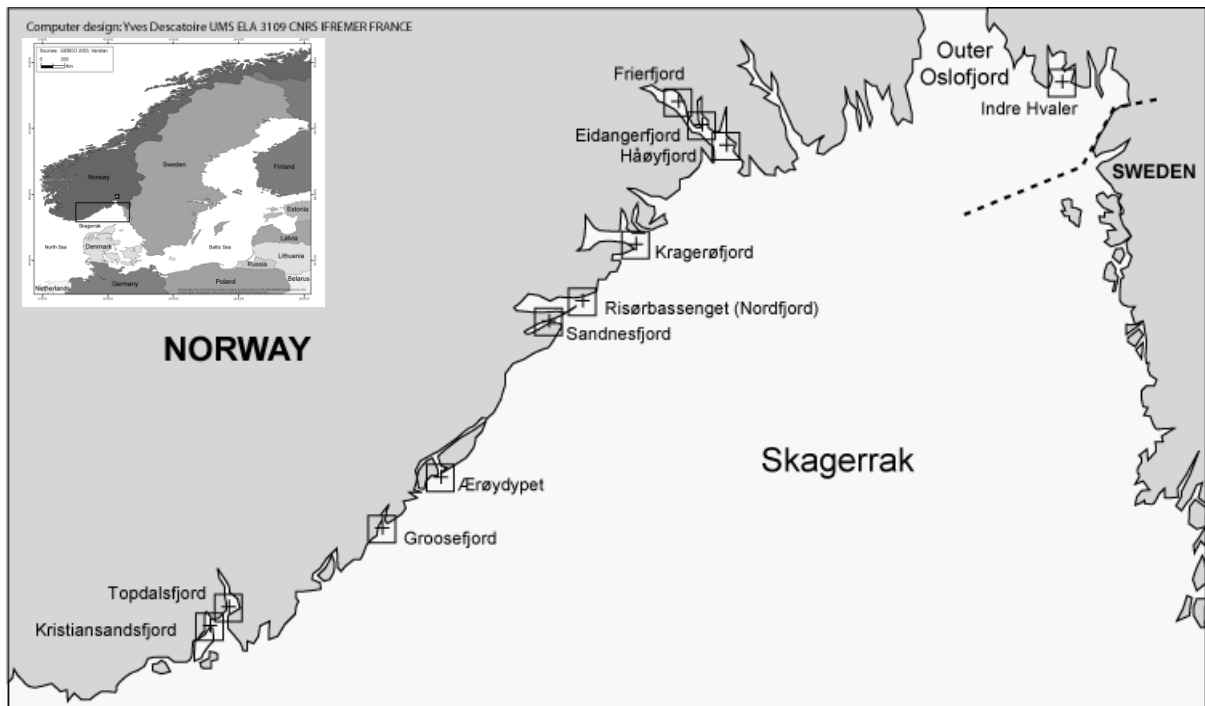
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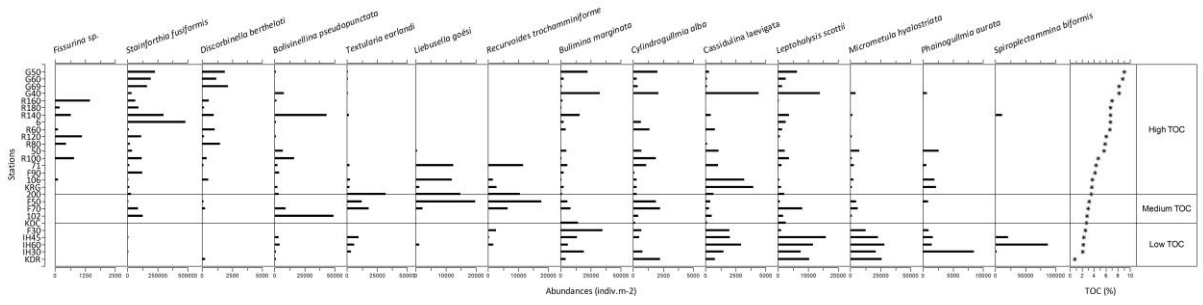948

949   Figure2

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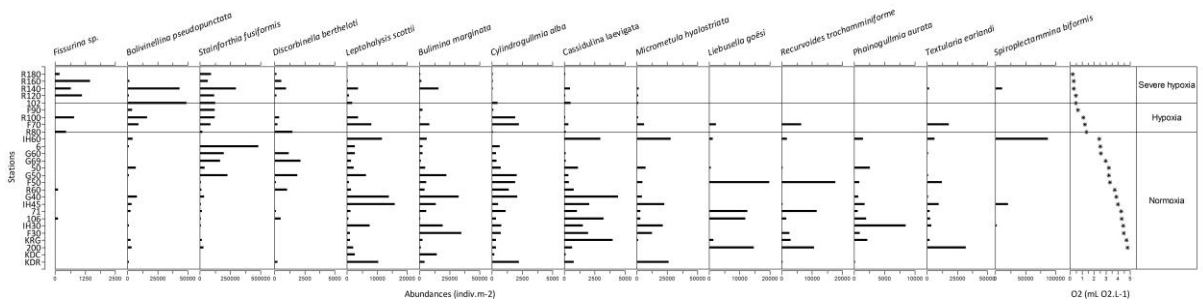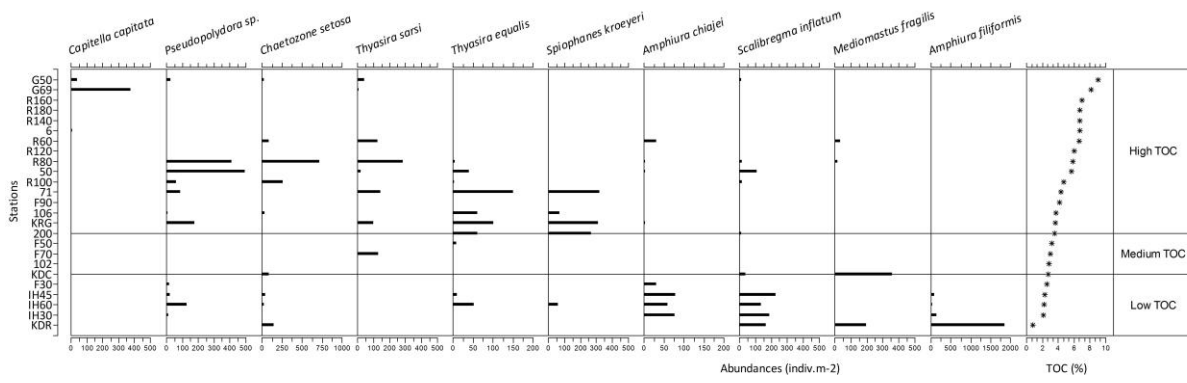954

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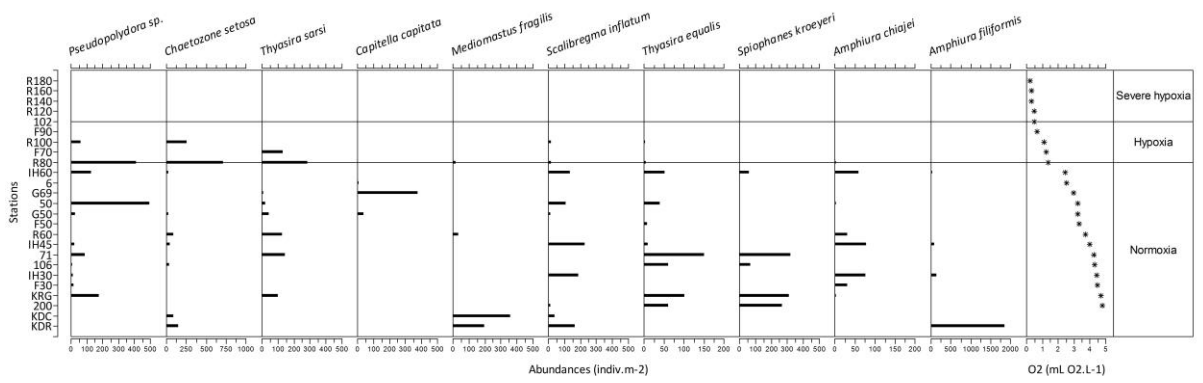

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958   Figure5A

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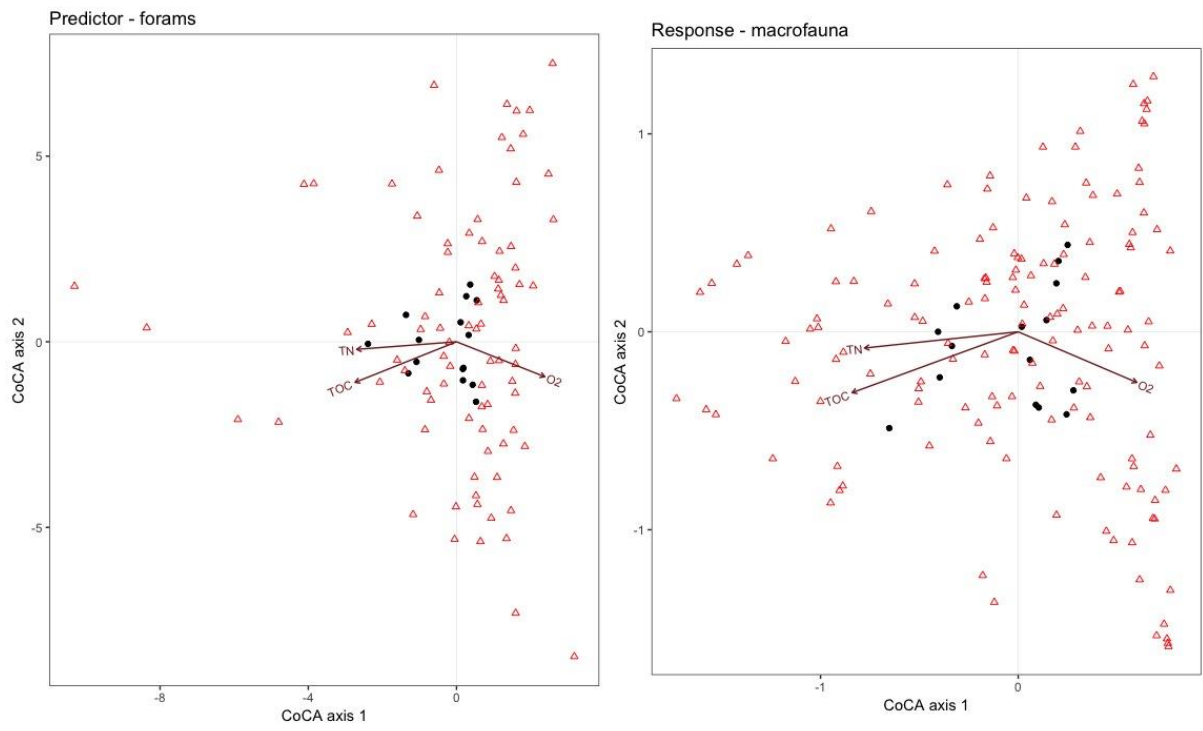
962   Figure5B

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965   Figure6A

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967   Figure6B

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970 Figure7

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972

973   Table1

	Station	Water depth (m) at stations	Depth below threshold (m)	$[O_2]_{tos}$	Grain size	TOC	TN	C/N
Ærøydypet	200	111	59	4.76	93	3.5	0.4	9.7
Kragerøfjord	71	138	118	4.25	98	4.3	0.5	7.9
	KRG	102	79	4.67	94	3.6	0.5	7.2
Sandnesfjord	50	65	42	3.21	92	5.7	0.4	12.6
Eidangerfjord	106	103	43	4.31	96	3.7	0.2	15.5
Risørbassenget	R60	60	35	3.73	83	6.6	0.9	7.4
	R80	80	56	1.36	89	5.8	0.6	10.1
	R100	104	75	1.09	87	4.7	0.6	8.1
	R120	124	99	0.47	90	6.0	0.6	10.5
	R140	142	118	0.33	83	6.7	0.6	10.7
	R160	157	134	0.29	91	7.0	0.7	10.4
	R180	182	157	0.20	91	6.7	0.7	10.1
Håøyfjord	102	204	169	0.49	98	2.8	0.3	9.7
Topdalsfjord	6	74	42	2.52	94	6.7	0.5	12.5
Groosefjord	G40	40	17	3.85	nd	8.1	0.6	12,9
	G50	54	31	3.25	84	9.0	0.7	12.5
	G60	60	37	2.58	nd	8.8	0.7	11.7
	G69	69	47	2.95	93	8.1	0.7	10.7
Frierfjord	F30	28	8	4.48	98	2.6	0.1	32.2
	F50	52	32	3.30	92	3.2	0.2	13.3
	F70	70	50	1.25	98	3.0	0.1	21.1
	F90	91	70	0.67	98	4.2	0.2	17.8
Indre Hvaler	IH30	30	6	4.44	98	2.1	0.1	14.2
	IH45	45	20	3.98	98	2.3	0.2	14.3
	IH60	62	37	2.42	98	2.2	0.2	13.2
Kristiansandsfjord	KDR	23	nd	nd	58	0.8	0.1	14.6
	KDC	31		nd	52	2.7	0.2	14.6

974

975 Table2

	This study EG	Foram-AMBI EG
FORAMINIFERA		
Micrometula hyalostriata	1	na
Phainogullmia aurata	1	na
Cylindrogullmia alba	2	na
Leptohalysis scottii	4	na
Cassidulina laevigata	2	1
Liebusella goësi	3	2
Bolivinellina pseudopunctata	4	2
MACROFAUNA	This study EG	AMBI-list EG
Scalibregma inflatum	1	3
Thyasira cf. *sarsii*	4 or 5	3

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