



Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat

Sköld, Mattias; Göransson, Peter; Jonsson, Patrik; Bastardie, Francois; Blomqvist, Mats; Agrenius, Stefan; Hiddink, Jan Geert; Nilsson, Hans C.; Bartolino, Valerio

Published in:
Marine Ecology - Progress Series

Link to article, DOI:
[10.3354/meps12434](https://doi.org/10.3354/meps12434)

Publication date:
2018

Document Version
Peer reviewed version

[Link back to DTU Orbit](#)

Citation (APA):
Sköld, M., Göransson, P., Jonsson, P., Bastardie, F., Blomqvist, M., Agrenius, S., Hiddink, J. G., Nilsson, H. C., & Bartolino, V. (2018). Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat. *Marine Ecology - Progress Series*, 586, 41-55. <https://doi.org/10.3354/meps12434>

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1 **Effects of chronic bottom trawling on soft seafloor macrofauna in the**
2 **Kattegat**

3

4 Running page head: Effects of trawling on macrofauna in the Kattegat

5

6 Authors: Mattias Sköld^{1*}, Peter Göransson², Patrik Jonsson¹, Francois Bastardie³, Mats
7 Blomqvist⁴, Stefan Agrenius⁵, Jan Geert Hiddink⁶, Hans C. Nilsson¹, Valerio Bartolino¹

8

9 ¹Department of Aquatic Resources, Institute of Marine Research, Swedish University of
10 Agricultural Sciences, SE453 30 Lysekil, Sweden

11 ²PAG Environmental Research, SE252 70 Råå, Sweden

12 ³National Institute of Aquatic Resources, DTU Aqua Technical University of Denmark, 2920
13 Charlottenlund, Denmark

14 ⁴Hafok AB, SE179 61 Stenhamra, Sweden

15 ⁵Department of Marine Sciences Kristineberg, University of Gothenburg, SE451 78
16 Fiskebäckskil, Sweden

17 ⁶School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, United
18 Kingdom

19

20 *corresponding author: mattias.skold@slu.se

21

22 Abstract: Chronic impact studies of bottom trawling aiming to reveal long term effects on
23 benthic organisms are often hampered by the lack of comparable untrawled conditions and the
24 difficulty to assess the spatial distribution of trawling intensity. We sampled soft sediment
25 macrofauna over a precise trawling gradient in the Kattegat using hourly vessel monitoring

26 systems and logbooks. The gradient accounted for the establishment of a marine protected
27 area where trawling intensity declined sharply. Our results show shifts in the macrofauna
28 assemblage and non-linear responses with decrease in number of species and diversity from
29 low to medium trawling intensities. The benthic community was dominated by burrowing
30 brittle stars, and one of the species *Amphiura chiajei* increased in abundance from low to
31 medium trawling intensities. We interpret the positive response to increasing trawling
32 intensities as a consequence of reduction in predation by benthivorous flatfish and *Nephrops*
33 *norvegicus* that are significant catches of the fishery. The response was supported by a
34 corresponding trend towards lower abundance of the dominating brittle stars following
35 enforcement of the MPA and presumably an increase in benthivore density and predation
36 pressure within the MPA. We conclude that chronic bottom trawling reduces diversity, and
37 may boost the abundances of species resistant to bottom trawling. The results emphasize the
38 need to consider food web effects when assessing the impact of bottom trawling.

39

40 Key words: Physical disturbance, *Amphiura filiformis*, Echinoderm, Otter trawling, Fishing
41 impact, Food web, Benthic habitats, *Nephrops norvegicus*, Anti-predator defenses

42

43 INTRODUCTION

44

45 Bottom trawls are designed to catch fish and shellfish that live on and close to the seabed and
46 are therefore by design in contact with the seabed. As a result, bottom trawling can lead to
47 disturbance of benthic habitats, and changes in the abundance, biomass and diversity of
48 communities and species (Collie et al. 2000; Kaiser et al. 2006). Sensitivity of benthic
49 habitats tends to be lower in shallow high energy areas with high levels of natural
50 disturbance, than in deeper areas where physical disturbance by waves caused by wind driven
51 energy, i.e. storms may not reach the seabed (van Denderen et al. 2015). Sensitivity of the
52 fauna also differs between species depending on their biological traits and the mechanism of
53 disturbance. Direct mortality of organisms and longer-term modification of habitats by mobile
54 demersal fishing gear are most severe in vulnerable areas such as deep-water coral reefs and
55 sponge communities where fragile species that build three-dimensional structures make up a
56 significant component of the habitats (Fosså et al. 2002, Greathead et al. 2007, Jørgensen et
57 al. 2016). Other components of the fauna, like sediment dwelling infauna may be less
58 sensitive to the direct physical impact because they are partly protected by burying in the
59 substrate (Tillin et al. 2006). For such species, indirect effects such as changes in particle
60 dynamics of the sediment (Dounas et al, 2007, Tjensvoll et al. 2013), or changes in the
61 balance between predators and prey (Hiddink et al. 2016) and their interactions, or whether
62 the abundance of benthos is top-down or bottom-up controlled (van Denderen et al. 2013),
63 may have larger impacts.

64

65 The effects of bottom trawling impact on seafloor species, communities and habitats have
66 been widely studied, and although some general patterns are emerging, there remains a lot of
67 unexplained variation in the findings of individual studies (discussed in e.g. Collie et al. 2000,

68 Løkkeborg 2005, Kaiser et al. 2006). The variation in outcomes of studies may relate to
69 variations in fishing pressures as well variations in the sensitivity of the system studied or
70 other environmental factors that may interact with fishing. In a recent global analysis of
71 depletion and recovery of benthic fauna based on gradient studies only 5 of 24 studies
72 included unfished conditions in their gradient of trawling (Hiddink et al. 2017). Observational
73 studies that sample over existing gradients in trawling intensity may thus suffer from a lack of
74 appropriate reference conditions, i.e. comparable sites without or with low bottom trawling
75 intensity

76

77 Fishing activities are patchy and concentrated on specific fishing grounds due to accumulated
78 knowledge by the fishers on catchability of target species, and accessibility by the gears used
79 (e.g. Bastardie et al, 2010, Eigaard et al. 2016a). Likewise, benthic communities are patchy
80 due to the spatial heterogeneity of factors structuring the communities such as the sediment
81 composition, depth, hydrodynamic regime and food availability (e.g. Rosenberg and Möller
82 1979; Gogina et al.2016). With the introduction of satellite monitoring of fishing vessels and
83 developed techniques to analyse and reconstruct fishing activities it has been increasingly
84 clear how certain areas and habitats periodically are fished intensively, while other areas are
85 fished in low intensities or not at all (Eigaard et al. 2016b, ICES 2016). These large spatial
86 and temporal differences occur both on the wide scale between and within sea areas and on
87 much finer scales of about 100 meters. It is crucial to assess the spatial distribution of bottom
88 trawling intensity at a fine resolution if the aim of impact studies is to cover long term impact
89 and effects of direct disturbance of the seafloor. This is because relationships between
90 trawling and responses might otherwise be confounded by misclassification of the pressure at
91 the site where the impact is studied. A universal problem for observational studies of trawling
92 gradients is that trawling intensity, for practical and data access reasons is aggregated within

93 grid cells much larger than the sampled site, usually 1 X 1 nm or larger (e.g. Hiddink et al.
94 2006, Reiss et al. 2009, Eigaard et al. 2016b, ICES 2016, Pommer et al. 2016). This may lead
95 to unreliable estimations of the trawling intensity because large areas are likely to
96 overestimate the trawling intensity in lightly trawled sites and underestimate the trawling
97 intensity in heavily trawled sites. To our knowledge, no bottom trawling gradient study of
98 benthic fauna communities have assessed the trawling intensity on a fine scale directly on the
99 sampled position using a Euclidian radial distance approach.

100

101 The aim of this study was to evaluate the effects of bottom trawling on benthic macrofaunal
102 assemblages using fine resolution trawling distribution data and untrawled reference
103 conditions. We hypothesize that benthic macrofauna will be influenced by trawling intensity
104 and evaluate this by stratifying a sampling programme in relation to a known bottom trawling
105 gradient in the Kattegat. The power to detect effects was maximized by precisely assessing
106 the trawling pressure to the sites where the sampling was carried out. The stratification took
107 into account the establishment of a marine protected area (MPA) where bottom trawling was
108 stopped to ensure as far as possible the inclusion of comparable untrawled conditions. We
109 also study the effect on the macrofauna following the enforcement of the MPA, and
110 hypothesize that temporal changes in the assemblage within the MPA will deviate from
111 changes outside the MPA where trawling continues.

112

113 **MATERIAL AND METHODS**

114

115 **Study area**

116

117 Kattegat is a shallow (mean depth 27 m) sea area between Sweden and Denmark and connects
118 to the Skagerrak in the north and to the Baltic Sea via narrow straits in the south. The
119 influence from the Baltic Sea by low saline surface waters creates a typical estuarine
120 circulation pattern and strongly stratified water masses separated by a halocline that persists
121 all year round at around 15 m depth but may extend down to 20 m (Granéli 1992). The
122 outflow from the Baltic, the so called Baltic current is mostly concentrated along the Swedish
123 coast where the halocline is deeper and stratification stronger than in the western parts. The
124 water beneath the halocline, originating from Skagerrak and the North Sea is more stable and
125 marine conditions prevail with salinity conditions usually above 32 PSU (Andersson and
126 Rydberg 1988). Depths and substrate vary with shallow areas with sandy sediments in the
127 west and deeper soft mud sediments in the east (Hallberg et al. 2010). Benthic fauna in the
128 soft mud habitats are today dominated by brittle stars of the *Amphiura*-community (Gogina et
129 al. 2016), but especially the south-eastern part was earlier dominated by amphipods of the
130 *Haploops* community (Petersen 1913).

131
132 Fishing by bottom trawling in the Kattegat has been ongoing since early 1900 and target
133 gadoid fish and flatfish in the south-eastern part of the Kattegat mainly using otter trawls
134 (Bartolino et al. 2012). Off cod spawning season, and today all year round, the fishery is
135 dominated by otter trawling targeting Norway lobster *Nephrops norvegicus* or *Nephrops* and
136 a mixture of fish, mainly plaice *Pleuronectes platessa*, sole *Solea solea* and cod *Gadus*
137 *morhua* (Hornborg et al. 2016). Denmark has the largest share (67%) of the Total Allowable
138 Catch (TAC) of *Nephrops*, Sweden has the second largest share (31%), while Germany has
139 the smallest share of demersal fish and *Nephrops* (ICES 2015).

140

141 In 2009 a large (653 km²) marine protected area, (MPA), was closed for all fishing activities
142 in the southeast Kattegat to protect spawning grounds for cod *G. morhua*. The MPA was one
143 of the core spawning areas that was fished by otter trawls historically for about 100 years
144 targeting aggregated cod during spawning season and *Nephrops* and mixture of fish the rest of
145 the year (Vitale et al. 2008). Some illegal fishing activities was documented the first year after
146 establishment of the MPA but seem to have decreased following actions taken by the Swedish
147 and Danish enforcement agencies (Bergström et al. 2016).

148

149 **Assessment of trawling intensity**

150

151 Trawling intensity was estimated as precisely as possible for each sampling site in relation to
152 the spatial resolution of the trawl path of the vessels within a radius of 250m around the
153 location benthic macrofauna were sampled. The method of using the Euclidian radial distance
154 to a sampling station and interpolated trawl tracks has been shown to be consistent and
155 accurate when compared to true distributions of trawl tracks for otter trawls (Lambert et al.
156 2012). The Swedish and Danish fleets equipped with vessel monitoring systems (VMS) were
157 analysed using the VMStools R package (Hintzen et al. 2012) and protocols developed and
158 described in Eigaard et al. (2016a). VMS covers hourly updated GPS positions for vessels of
159 15 m length and larger over the period 2006 - 2011, and all vessels of 12 m length and larger
160 during 2012 - 2014. Based on logbook information of the total effort in the Kattegat, we
161 estimated that the fleet coverage of vessels with VMS increased over the period studied from
162 50 – 60 % in 2006 - 2011 to > 75 % in 2012 - 2014. The VMS data set was interpolated into
163 positional data with 12 minutes' temporal resolution (Hintzen et al, 2010). The spread
164 between the trawl doors was estimated for each logbook trip based on the gear used and the
165 vessel's engine power (Eigaard et al. 2016a). This estimate was combined with interpolated

166 VMS data to reconstruct individual trawl paths. Trawling intensity was then calculated around
167 the sampled position for benthic fauna as the area swept by trawls within the 250 m radius at
168 each station and summed over 32 months prior to the sampling date. The time scale of
169 accumulating trawling over 32 months was chosen to achieve a wide gradient ($0 - 15 \text{ yr}^{-1}$) of
170 the bottom trawl history, accumulate the index to cover more than one benthos recruitment
171 event at a sampling station, and as a reasonable match to recovery time of the long living and
172 presumably more sensitive part of the macrofauna species. To ensure that the gradient was
173 consistent and comparable over time, data on trawling intensity was standardised to vessels \geq
174 15 m in all the analyses.

175

176 **Benthic macrofauna sampling**

177

178 Sampling of benthic macrofauna was carried out in May - June in 2009, 2010, 2011 and 2014
179 using a modified Smith-McIntyre grab (0.1 m^2) at 58 stations (Fig. 1). One sample was taken
180 per station and sieved (1.0 mm mesh size) for macrofauna. Sediment properties mapped by
181 Hallberg et al. (2010) was inspected by eye and fingers for each sample and for all stations
182 verified as soft mud sediments sometimes mixed with fine sand –silt. Samples were stored in
183 4% borax buffered formaldehyde prior to sorting, counting and weighing. With few
184 exceptions, e.g. species belonging to the genus *Edwardsia* and the amphipod family Aoridae,
185 all taxa were identified to species level.

186

187 All statistical analyses on biomass were tested without large bodied species, i.e. the heart
188 urchins *Brissopsis lyrifera* and *Echinocardium cordatum*, and the ocean quahog *Arctica*
189 *islandica* that due to their individual weight in some samples may strongly influence the
190 outcome of the results. The distance based test for homogeneity of multivariate dispersions

191 PERMDISP (for statistical methods see below) was significant when including large bodied
192 species (Group factor Trawling intensity: $F = 5.60$, $df_1 = 3$, $df_2 = 228$, $p = 0.0034$). Removing
193 these species thus improved the statistical results by reducing heterogeneity of biomass.

194

195 A total of 29864 specimens belonging to 261 different taxa of benthic fauna were present in
196 the samples.

197

198 **Multivariate analysis of macrofauna structure along the trawling intensity gradient**

199

200 Taking into consideration that the bottom trawling activities would be removed from the
201 MPA, benthic fauna sampling stations was established inside and outside the MPA with the
202 aim to cover a wide gradient in bottom trawling intensity (Fig. 1). The sampled stations were
203 situated to cover the habitat and depths explored by the dominant demersal bottom trawl
204 fisheries, and thus chosen within the depth interval 23 - 65 m where 95% of the trawled
205 positions from the VMS of the dominant fisheries were located. Sampling stations were
206 placed to reduce natural variation between habitats by limiting the stations to post glacial soft
207 mud sediments according to sediment mapping of the Kattegat (Hallberg et al. 2010). In this
208 design, we expect to identify macrofauna community shifts in the benthic community along
209 the identified trawling intensity gradient.

210

211 All multivariate analyses were performed using the statistical package PERMANOVA + for
212 PRIMER (Anderson et al. 2008). The effect of trawling intensity on the macrofauna
213 community was analysed with PERMANOVA with trawling intensity at sampling station
214 categorised into statistical quartiles (≤ 0.4 , $>0.4 \leq 2.1$, $>2.5 \leq 4.6$, $>4.6 \text{ yr}^{-1}$) as fixed factor.

215 The categorisation was done to simplify interpretation of the results since two more factors

216 was included in the design, and to standardise the trawling intensity gradient into informative
217 statistical groups representing low to high intensities. Year of sampling was fixed and
218 sampling station a random factor nested in trawling intensity. Community composition were
219 weighted both by abundance and biomass of species. Resemblance matrices were constructed
220 using Bray-Curtis similarity and abundance and biomass data was fourth root transformed to
221 reduce the influence of dominant species. Posthoc comparisons were done using pairwise
222 PERMANOVA, and results were visualized with Canonical Analysis of Principal Coordinates
223 (CAP). All data was evaluated for distance based test for homogeneity of multivariate
224 dispersions using the function PERMDISP.

225

226 To further explore the effect of the gradient in trawling intensity and to account for the
227 potential covariance of trawling intensity and depth related environmental factors known to be
228 important in the Kattegat (Petersen 1913, Rosenberg & Möller 1979, Rosenberg et al. 2000,
229 Agrenius and Göransson 2009, Pommer et al. 2016, Leonardsson et al. 2016), we evaluated
230 depth together with trawling intensity as predictors for community composition weighted by
231 species abundance and biomass using Distance based Linear modelling (DistLM) and
232 Distance based redundancy analysis (dbRDA). The predictors were checked by draftsman
233 plots and trawling intensity was transformed by $\log(X+1)$ and depth by square root to reduce
234 skewness. Depth and trawling intensity were checked for collinearity and a correlation of 0.64
235 was estimated for these variables. This is below the critical correlation level of 0.7 as
236 suggested by Dormann et al. (2013). The “Best” selection procedure was chosen together with
237 the selection criteria modified Akaike Information Criterion (AICc) for model selection, and
238 only predictor variables that were significant in marginal tests were selected. Individual
239 species contributing to the multivariate dbRDA model was evaluated using correlations
240 (Pearson’s R) between species abundance and the axis that explained most of the variation

241 correlating with trawling intensity. In addition, correlations were done between species
242 abundance and trawling intensity.

243

244 **Univariate analysis of macrofauna metrics along the trawling intensity gradient**

245 The effects of bottom trawling on macrofauna may be expected to depart from a linear
246 relationship. For this reason we analysed univariate response variables using generalized
247 additive models (GAMs). GAMs use non-parametric functions which allow to model non-
248 linear relationships without prior knowledge on their actual shape. The effect of trawling was
249 tested by applying GAM on the following univariate response variables: number of species
250 *Nspp*, total abundance *Nind*, total biomass *Biom*, abundance of the two dominant species
251 *Amphiura filiformis* and *Amphiura chiajei*, Richness index *d* (Margalef 1958), Shannon
252 diversity $H'(\log_2)$ (Shannon & Weaver 1949) and Benthic Quality Index (BQI). BQI was
253 calculated according to Leonardsson et al. (2016) without the correction for depth as depth is
254 included in the GAM model (see below). The BQI is used by Sweden for benthic quality
255 assessments under the EU Water framework directive (2000/60/EC) and combines abundance
256 weighted species sensitivities with species diversity into one index. All the variables were
257 calculated at the level of individual sampling stations (i.e., for each year y and geographical
258 location ρ, φ identified by longitude and latitude degrees) and the analysis performed
259 accordingly. The models were formulated as follows:

260

$$261 \quad \text{Response}_{(y,\rho,\varphi)} \sim \alpha_y + s(D_{(\rho,\varphi)}) + s(TI_{(y,\rho,\varphi)}) + s(Nind_{(y,\rho,\varphi)}) + \gamma_{(\rho,\varphi)} + e_{(y,\rho,\varphi)}$$

262

263 where α is the year specific intercept, s is a one-dimensional (Wood 2004) smoothing function
264 on depth (D) and trawling intensity (TI). To account for dependency among sampling stations
265 which are closer in space, the error part of the model was separated into a Gaussian spatially

266 autocorrelated component (γ) (Venables and Ripley 2002, Dormann et al. 2007), which was
267 treated as a random effect (Pinheiro and Bates 2000), and a normally distributed error term
268 (e). The total abundance (N_{ind}) was included as a predictor only for the model using N_{spp} as
269 a response variable to account for changes in the detection probability of new species as
270 abundance increases. Model overfitting was controlled by constraining to 3 the maximum
271 degrees of freedom on the depth variable. Inspection of models' residuals revealed no major
272 departure from the model assumptions of normality and homogeneity of variance. The GAM
273 models were fitted using R and the library *mgcv* (Wood 2011).

274

275 **Effects of reduction in trawling intensity by the establishment of the marine protected** 276 **area**

277

278 In the evaluation of the closure for trawling within the MPA, we expected potential temporal
279 changes in the macrofauna assemblage within the MPA to deviate from changes outside the
280 MPA where trawling continues. No benthic sampling was carried out prior to the
281 establishment of the MPA in 2009. However, we assume that the macrofauna community
282 status of 2009 sampled five months after the enforcement of the MPA can be considered as a
283 reasonable baseline since the impact of previous years bottom trawling was likely to remain
284 longer (i.e. > 1.9 years) for macrofauna (Hiddink et al. 2017).

285

286 Samples were collected at the same stations in 2009, 2010, 2011 and 2014. Stations sampled
287 within the MPA prior to the establishment in 2009 and outside over all the years, were
288 defined as trawled if trawling intensities were above the median trawling intensity (≥ 2.5)
289 estimated from all sampling stations and the whole study period. As expected a reduction in
290 trawling intensity by the establishment of the MPA in 2009 was seen over time. However,

291 trawling intensity was not reduced to zero at all stations inside the MPA indicating some
292 noncompliance or misclassification of vessels on transit at slow speed (Fig. S2).

293

294 The experimental effect of the MPA on the temporal development of the species assemblage
295 was evaluated using PERMANOVA with year of sampling and treatment i.e. closure versus
296 continuously trawled as fixed factors, and station as random factor nested in treatment. The
297 effect of the closure on the macrofauna community will thus be the interaction between Year
298 of sampling and Treatment (i.e. the “closed” area versus the area outside the MPA that was
299 continuously “trawled”). Dependent variables examined were species composition weighted
300 by abundance, biomass, or abundance of the two most dominant species (*Amphiura filiformis*
301 and *Amphiura chiajei*), and univariate total abundance, total biomass and number of species.
302 As significant effects were detected for the dominant species these were as well examined by
303 a factorial ANOVA with the same design. Dependent variables i.e. abundances of the species
304 were transformed by $\log X + 1$ and tested for unequal variances by Welsch’s test. Univariate
305 statistics were analysed using the statistical package JMP pro 12.0.1.

306

307 **RESULTS**

308 **Multivariate analysis of macrofauna structure along the trawling intensity gradient**

309

310 Trawling intensity estimated as swept area ratio ranged from 0 – 15 yr⁻¹ and was heavily
311 skewed towards the lower range (median 2.1 yr⁻¹). The ranges and distributions of trawling
312 intensity verified the stratification of the design and were stable over the four years sampled
313 with the exception of the anticipated decrease at the 7 stations protected due to the
314 establishment of the MPA from 2009 (Fig. S1 and S2, supplement).

315

316 The PERMANOVA based on species abundance indicated significant effects of both year (p
317 = 0.0001) and trawling intensity (p = 0.0001) on the community composition of the
318 macrofauna, but no interaction between these two factors (p = 0.0749; Fig. 2). Pairwise
319 comparisons of trawling intensity effect showed that the effect of trawling intensity categories
320 differed between the overlapping two lower quartiles and the two highest overlapping
321 quartiles. Similar statistical results as for abundance were achieved using species biomass
322 without large bodied species (year: p = 0.0001; trawling intensity categorised into quartiles: p
323 = 0.0001, and no interaction between these two factors: p = 0.1045). Pairwise comparisons of
324 trawling intensity categories again showed that the effect of trawling intensities differed
325 between the overlapping two lower quartiles and the two highest overlapping quartiles (for
326 details on statistics, see Supplement tables S1 on macrofauna abundance and table S2 on
327 biomass). The multivariate PERMANOVA analysis thus indicated that the macrofauna
328 assemblage was structured differently over the years and along the trawling intensity gradient
329 of the sampling stations, but that the effect of variation in trawling intensity did not change
330 over time.

331

332 To further explore the effect of the gradient in trawling intensity, depth together with trawling
333 intensity were evaluated as continuous predictors of community composition by Distance
334 based Linear modelling (DistLM) and Distance based redundancy analysis (dbRDA). Since
335 the year factor did not show interaction with trawling intensity in the foregoing
336 PERMANOVA analysis, data from all years were pooled to increase the generality of the
337 tests. The marginal test showed both trawling intensity and depth to be significant predictors
338 contributing to the model (log X+1 trawling intensity F = 10.1, p = 0.0001, and square root
339 depth F = 15.3, p = 0.0001). Using the best model selection procedure, i.e. all variable
340 combinations, and Akaike's Information Criterion with second order correction (AICc) both

341 predictors were identified and explained together 7.4 % of the variation in the community
342 composition. The Distance based redundancy analysis (dbRDA) visualise how the stations
343 with differing trawling intensity and depth relates to the multivariate dbRDA axes 1 and 2
344 (Fig. 3). Trawling intensity correlated with dbRDA 1 (multiple partial correlation 0.52) that
345 explained 6.4 % of the total variation and to dbRDA 2 (0.85) that explained 0.9 % of the total
346 variation. Depth also correlated with both dbRDA 1 (multiple partial correlation 0.85) and
347 dbRDA 2 (0.52). The testing procedure above was also done using biomass of species as
348 dependent variable which showed the similar effects (log X+1 trawling intensity $F=9.5$, $p =$
349 0001 and square root depth $F = 14.5$, $p = 0.0001$) and correlations to the dbRDA axis 1 and 2
350 (multiple partial correlation 0.52 and 0.86 respectively) and overall contribution to the total
351 variation 6.1 and 1 %. Depth also correlated with both dbRDA 1 (multiple partial correlation
352 0.86) and dbRDA 2 (0.52).

353

354 Correlations between the multivariate ordination axis that explained most of the total
355 variation and abundance of individual species indicated that 40 macrofauna species had a
356 decreasing trend in abundance along the axis while 13 increased. Correlations between
357 individual species abundance and trawling intensity showed agreement with the species that
358 decreased along the axis for 58 % of the species that had the negative trends e.g. *Ampelisca*
359 *tenuicornis* and *Phoronis muelleri*. For the species increasing 31 % showed conformity with
360 the positive trend along e.g. *Amphiura chiajei* and *Labidoplax buskii* (Table 1).

361

362 **Univariate analysis of macrofauna metrics along the trawling intensity gradient**

363

364 Trawling intensity had a similar significant effect on the number of species, richness,
365 diversity and the benthic habitat quality (BQI), while its effect was non-significant on the

366 total biomass and abundance of benthos (Fig. 4). The effect of trawling intensity was negative
367 for values below approx. 5 yr^{-1} , which include 64% of the sampling stations, and the
368 relationship became slightly positive for larger values. Depth had no significant effect in all
369 the models with the exception of the benthos abundance which significantly decreased ($p <$
370 0.01) in response to increasing depth until approximately 40 m (Fig. 4). The GAM model of
371 the number of species has a R^2 value of 0.34. In the other models the R^2 ranged between 0.10
372 and 0.19 with the exception of the model on biomass which had a value of 0.015 (Table 2).

373

374 The soft mud macrofauna community in the area investigated was dominated by the
375 burrowing brittle stars *Amphiura filiformis* and *Amphiura chiajei*. Together these two species
376 represented 50 % in the overall number of individuals, and 58 % of the biomass. *A. filiformis*
377 was present in 98 % and *A. chiajei* in 83 % of the samples. The two species presented an
378 opposite response to depth below 40 m, with *A. chiajei* increasing in deeper waters while *A.*
379 *filiformis* decreasing in abundance in the same depth range (Fig. 5). The response to trawling
380 intensity was non-significant for *A. filiformis* but positive for *A. chiajei* at low to medium
381 trawling intensities and decreased only for trawling intensity levels above 5 yr^{-1} .

382

383 **Effects of reduction in trawling intensity by the establishment of the marine protected** 384 **area**

385 To evaluate the potential recovery of the macrofauna within the MPA we hypothesized that
386 the temporal development of the macrofauna within the MPA deviate from the area outside
387 where trawling continued. Multivariate PERMANOVA tests of abundance and biomass and
388 univariate tests with PERMANOVA number of species (Fig. 6a), total abundance (Fig. 6b)
389 and total biomass (Fig. 6c) showed no interactions between the year and treatment (Table S3).
390 However, abundance of the dominating species (*A. chiajei* and *A. filiformis*) showed a

391 significant interaction between the factors treatment and year (Table S4 and 5). Post-hoc
392 comparison with pairwise PERMANOVA indicated that the last year 2014 differed from the
393 earlier years 2009 - 2011 within the closed area, while no difference between years occurred
394 in the area where trawling continued. Examining the pattern with factorial ANOVA indicated
395 the same interaction with a decrease for both species within the closed area in 2014 compared
396 to earlier years and no temporal trend within the trawled area (Fig. 7), however, only at a
397 significance level of $\alpha = 0.10$.

398

399 **DISCUSSION**

400

401 In this study, we found shifts in the structure of the macrofauna community in soft mud
402 substrate along a wide gradient in trawling intensity. We investigated this using a stratified
403 sampling design covering a wide and precisely estimated gradient in bottom trawling
404 intensity, taking the establishment of a marine protected area (MPA) into account to ensure as
405 far as possible that untrawled as well as intensively trawled sites were included in the
406 gradient. Our results show small but significant shifts in community composition and a
407 decrease in number of species and indices of diversity as trawling intensity increases from
408 low to medium levels i.e. below 5 yr^{-1} . Several taxa had a negative trend along the gradient of
409 increasing trawling intensity while a few taxa increased. The dominant brittle star species
410 showed different responses as *Amphiura chiajei* increased at low to medium trawling
411 intensities and decreased only at trawling intensity above 5 yr^{-1} , while *Amphiura filiformis*
412 showed no conclusive response. Effects along the trawling intensity gradient were non-linear
413 and in general more evident at the lower range. Responses for number of species and diversity
414 indices appear inverted at high levels of trawling intensity, but the large confidence intervals
415 related to the low number of observations suggest high uncertainty of the model to explain the

416 effect of fishing intensity at the high end of the range. There was temporal change to the
417 benthic community over the duration of the study, but the effect of trawling intensity on the
418 benthos was consistent over time. As expected, the macrofauna community was also
419 structured according to depth which was included in the statistical models to avoid
420 confounding effects.

421
422 In a study similar to ours, Pommer et al. (2016) concluded that nearly 100 % of the habitats
423 below 22 m in the Kattegat were impacted by bottom trawling, and their analysis could not
424 discriminate between effects on the macrofauna in lightly trawled versus heavily trawled
425 areas. Differences between the studies can be explained by higher spatial resolution of
426 trawling intensity in our study in combination with the use of the MPA to ensure that
427 sampling was done across a wide range of trawling intensity to detect effects by bottom
428 trawling on the benthic macrofauna. In another similar study of otter trawl disturbance at *N.*
429 *norvegicus* soft sediment fishing grounds in the Irish Sea, Hinz et al. (2009) found negative
430 effects of trawling intensity on macrofauna abundance, number of species and total biomass.
431 Similar ranges of trawling intensities were observed by Hinz et al. (2009) and in our study
432 (maximum 18.2 in the Irish Sea and 15.8 yr⁻¹ in our study), however, in the Irish Sea
433 comparable stations with trawling intensity below 1.3 yr⁻¹ could not be identified while our
434 study included low ranges and untrawled comparable conditions in the MPA. The species
435 decreasing with trawling intensity show some commonalities between the two studies for the
436 following taxa: the Phoronida *Phoronis* sp., crustacean amphipods of the genus *Ampelisca*
437 and the polychaete *Magelona alleni*, however, also contradicting results in that the
438 dominating brittle star *A. filiformis* appears tolerant to bottom trawling in our study while
439 decreased in response to trawling in the Irish Sea. In explaining the differences, we emphasize
440 the need to consider non-linear effects, detailed spatial estimates of trawling intensity, and

441 again the necessity of including untrawled and lightly trawled conditions in gradient studies
442 as effects are most prominent at low levels of the gradient. The most sensitive species are
443 likely affected and depleted already at low trawling intensities, and the benthic fauna left are
444 the more resilient species (National Research Council 2002). Our results support this pattern
445 of response as the macrofauna composition and the decrease in number of species and indices
446 of diversity is evident mainly at the lower range of trawling intensity.

447

448 However, our results differ from other studies (e.g. Hiddink et al. 2006, Hintz et al. 2009,
449 Reiss et al. 2009, Hiddink et al. 2011, Johnson et al. 2015) in that we could not detect any
450 shifts in total biomass. A possible explanation to this difference might be that in our study,
451 one of the two dominant species *A. chiajei* increased along the trawling intensity gradient
452 which may then mask the decrease in other less common species negatively affected. Reiss et
453 al. (2009) in their study of beam trawling impact on macrofauna communities found that even
454 in areas of high trawling disturbance, further increase still caused additional damage to the
455 faunal communities in terms of biomass and number of species. The ground-gear used in
456 beam trawling penetrate the seafloor deeper than otter trawling (Eigaard et al. 2016), which
457 might explain the different responses between our study and others where beam trawling is
458 common (e.g. Hiddink et al. 2006, Reiss et al. 2009). However, all these other studies
459 analysed the effect of trawling intensity using much coarser spatial resolutions (approximately
460 1 X 1 nm or larger) compared to our analysis making the studies difficult to compare.

461

462 It is crucial to assess the spatial distribution of bottom trawling intensity at a fine resolution if
463 the aim of impact studies is to cover long term impact and effects of direct disturbance on the
464 seafloor. This is because relationships between trawling and responses might otherwise be
465 confounded by misclassification of the pressure at the site where the impact is monitored.

466 Our study had access to reliable raw VMS data and logbooks from all the nations fishing in
467 the area i.e. Sweden and Denmark, and was thus able to reconstruct with high precision the
468 daily bottom trawling intensity at each station sampled for benthic macrofauna from 2006 to
469 2014. The VMS derived effort is considered to be an underestimate since vessels smaller than
470 15 m was not included in the gradient. However, we consider the gradient established to be
471 reliable since the main fishing grounds for trawlers in the Kattegat are expected to be similar
472 for large and small vessels without VMS due to the large coverage of the soft mud habitat,
473 and that the smaller trawlers target the same species composition as the larger fleet.
474 Differences in compliance between small and large vessels, however, may have introduced
475 bias in the estimates of trawling intensity within the MPA due to the lack of VMS monitoring
476 of smaller vessels. The examination of the trend over time within the closed area indicate only
477 a decrease over time for the dominating brittle star species. Non-compliance during the two
478 first year after enforcement of the MPA is evident as the VMS indicate rather high activity.
479 This might explain the lacking of a response over time for the macrofauna community over
480 the relatively short period studied following the closure.

481

482 The choice of grid cell and resolution will always be a trade-off with the risk of mismatch
483 between the direct impact at each sampling location and the patchiness of the trawling
484 pressure. In this study, we used a fine scale search radius to the stations studied as we
485 prioritized to capture and be able to ascertain the low-end part of the trawling intensity
486 gradient, i.e. lightly or untrawled areas within the Kattegat *Nephrops* fishing ground.
487 However, it is unclear whether the indirect ecological disturbance by bottom trawling acting
488 on macrofaunal assemblages, e.g. due to shifts in predator–prey relationships (van Denderen
489 et al. 2013, Hiddink et al. 2016) will be larger than the direct localized physical disturbance
490 by a single trawl path. Response curves to trawling intensity from indirect effects may further

491 differ both in shape and trigger levels as these impacts might act on larger temporal and
492 spatial scales. Impacts might reflect how the communities connect to each other and how fast
493 animals can recolonize an impacted site either by migration or recruitment of new animals, as
494 discussed by Lambert et al. (2012) who found the most significant relationships between
495 spatial resolution of 2 km by 2 km to 4 km by 4 km which represents a 20 - 80 times coarser
496 cell resolutions than this study.

497

498 It should to be considered that even though our study included stations within the MPA that
499 had not been trawled for 5 years, stations with pristine conditions were not represented. We
500 could not find any trend in the macrofauna community indicating recovery within the closed
501 area, possibly due to the short period of time since the MPA was established and the lack of
502 compliance by the fleet during the first two years following enforcement of the MPA. Taking
503 a longer historical perspective, the trawl fishery in the Kattegat was likely more widespread
504 when the fishery targeted cod *Gadus morhua* before quotas were severely enforced around
505 year 2000. However, no reliable VMS data coupled to logbooks is available before 2005 to
506 support this statement. Also, the Kattegat is a eutrophicated coastal sea area that had recurrent
507 problems of oxygen deficiency mainly in the 1980's which resulted in large areas with
508 mortality of benthic invertebrates (Rosenberg & Loo, 1988, Baden et al. 1990). The large
509 number of stations sampled, however, allows historical comparison of the macrofauna
510 community sampled in the early 1900's. Around this time, when industrial trawling started,
511 Petersen (1913) made extensive quantitative benthic macrofauna mapping of the Kattegat that
512 showed differences but also large similarities with the assemblages observed today, e.g. large
513 areas dominated by the brittle stars *Amphiura* spp. Pearson et al. (1985) re-assessed Petersen's
514 stations in the Kattegat and found generally higher abundances and biomass, and that *A.*
515 *filiformis* had increased in dominance at over 70 % of the stations compared. Also, in the

516 beginning of the 1900's, a large area in the south-eastern Kattegat was dominated by
517 amphipods i.e. the *Haploops* community which has not been found again in the area
518 following revisits (Göransson 1999). Only 15 specimens of *Haploops* spp. were noted in four
519 of our samples within the historical main distribution area of these species. Petersen (1913),
520 in contrast reported thousands of individuals per m² at the beginning of the century. Several
521 other species were described to be associated to Petersens *Haploops* community, including
522 the brittle star *Ophiura robusta*, the clams *Pseudamussium peslutrae* and *Limea loscombi*, the
523 ostracod *Philomedes brenda*, the bivalves *Nuculana pernula* and *Nuculana minuta* and the
524 brittle stars *Ophiura albida* and *Ophiocten affinis* (Petersen 1913, Göransson 2002,
525 Göransson et al. 2010). Several of these species were noted at a few stations in our study
526 between but in comparably low numbers, and the species *O. robusta*, *P. peslutrae* and *L.*
527 *loscombi* were not found at all in the investigated area. Oxygen deficiency and bottom
528 trawling has been put forward as possible explanations to the disappearance of *Haploops* and
529 shift in species assemblages (Göransson 1999). Interestingly, in a study from the southern
530 hemisphere in New Zealand, a similar shift in macrofaunal assemblages have been described
531 (Handley et al. 2014). In that study amphipods, ostracods and bivalves numerically dominated
532 soft mud communities within a relatively pristine untrawled protected area, while nearby
533 trawled comparable mud habitats were dominated by burrowing brittle stars (*Amphiura* sp.)
534 and polychaetes. In summary, our results confirm the disappearance of dense *Haploops*
535 dominated communities in the Kattegat and supports that bottom trawling contribute to the
536 shift towards brittle star dominated communities since the two *Amphiura* species were
537 tolerant to bottom trawling, and that *A. chiajei* increased in abundance at low to medium
538 trawling intensities.
539

540 The *Amphiura* species dominate abundance and biomass over large areas in the Kattegat,
541 Skagerrak and the North Sea with localized maxima of >1000 ind. m^{-2} (Duineveld et al. 1986,
542 Gogina et al. 2016). Given that this distribution coincides with areas fished extensively by
543 bottom trawls (Eigaard et al. 2016b, and this study), it is evident that these two species are
544 resilient to trawling. Characteristic traits for these brittle stars are that they have planktonic
545 larvae with great dispersal capability, are burrowed with their disc ca 5 cm in the sediments
546 with their arms protruding above the sediment surface, and frequently autotomize their arms
547 or even discs in *A. filiformis*, as a response to attacks from predators (Sköld et al. 1994). Their
548 arm regeneration potential is great but differ considerably between the two species in that *A.*
549 *filiformis* regenerate an arm about 5 times faster than *A. chiajei* (Sköld & Gunnarsson 1996).
550 Both species are deposit feeders and *A. filiformis* is also a facultative suspension feeder (Loo
551 et al. 1996, Solan & Kennedy 2002). Populations are often stable, comprised of adults and
552 longevity has been estimated to more than 20 years (O'Connor et al. 1983). The frequency of
553 sub-lethal predation can be assessed by counting scars on arms of brittle stars (Aronson
554 1989), and differences have been documented between species and among trawled versus
555 untrawled areas, with lower incidence of scars of *A. filiformis* in trawled areas in the
556 Skagerrak – Kattegat (Sköld & Rosenberg 1996). Mechanical damage of ophiuroid arms by
557 trawling have not been investigated, however, storms do not appear to cause arm damage in
558 brittlestar populations on tropical reefs, and predation is considered to be the prime source of
559 arm injuries (Aronson, 1991). Important predators of *Amphiura* spp. are demersal fish species
560 and crustaceans, e.g., haddock *Melanogrammus aeglefinus*, dab *Limanda limanda*, American
561 plaice *Hippoglossoides platessoides*, plaice *Pleuronectes platessa* and Norway lobster
562 *Nephrops norvegicus* (Duineveld & Van Noort, 1986, Baden et al, 1990, Mattson, 1992, Pihl,
563 1994, Kaiser & Ramsey 1997, Hiddink et al. 2016). Fishing effort is intense and stable in the
564 fishing grounds examined and targeted as well as by-catches of the above listed predators are

565 significant (Hornborg et al. 2016). In addition, some of these predators are stationary, in
566 particular *N. norvegicus* in its adult stages. We thus conclude that reduced predation pressure
567 due to local depletion of these predators at fished stations may be one important mechanism
568 behind the increase of *A. chiajei* along the trawling intensity gradient. The examination of the
569 trend over time within the closed area supports this conclusion as the dominating species i.e.
570 both *Amphiura* species., indicate a decrease over time which could be due to increased
571 abundance of fish and *Nephrops* following cessation of the fishery and accordingly increased
572 local predation pressure.

573

574 Several indirect effects of bottom fishing on fish and vice versa have been documented
575 (Collie et al. 2016), and studies from the Irish sea (Hiddink et al. 2011, Johnson et al. 2015),
576 and the Kattegat (Hiddink et al. 2016) at soft seafloor otter trawl fishing grounds link the
577 chronic trawling effects to the condition of predators, and explain the results as responses to
578 the ratio of prey to predator biomass and dietary shifts. Our study emphasizes the complex
579 interplay between predators, their benthic prey and the interaction with bottom trawling.
580 *Amphiura* spp. have their arms protruding above the sediment surface when feeding and arms
581 are frequently preyed on by fish and *Nephrops*. As these heavily fished predators are locally
582 removed by trawling, *Amphiura* spp. being released from predation causes its population to
583 grow. That is, if predators are more strongly affected than their prey by bottom trawling, prey
584 may increase with bottom trawling until trawling becomes so intense that the prey is also
585 affected.

586

587 Conclusion

588 Our results show shifts in the macrofauna assemblage and a decrease in number of species
589 and indices of diversity at low to medium trawling intensities. The dominant brittle stars *A.*

590 *filiformis* and *A. chiajei* are evidently resistant to trawling at low to intermediate intensities
591 and *A. chiajei* showed positive response to increasing trawling intensity possibly caused by
592 reduction in predation by demersal fish and the target species *N. norvegicus*. Furthermore, the
593 study contributes to the understanding of how chronic bottom trawling contribute to the
594 documented historical shifts in benthic macrofauna assemblages of soft seafloors by reducing
595 diversity and benefitting resistant species like brittle stars. The Kattegat is representative for
596 similar soft seafloor coastal and shelf areas exploited by bottom otter trawl fisheries for fish
597 and crustaceans. The large MPA provides a unique potential for further studies of recovery of
598 the benthic fauna following cessation of bottom trawling.

599

600 **Acknowledgements**

601

602 We thank 4 anonymous reviewers for critical and fruitful comments on the manuscript. The
603 EUFP7 project “BENTHIS” (grant 693 agreement number 312088) and the Swedish agency
604 for marine and water management, SwAM (Dnr 74915 and 482113) funded the research. VB
605 and PJ were partially funded by the Swedish Research Council Formas, grant no. 2012942.
606 The benthic sampling was financed by SWaM and the County Administration of Halland,
607 Sweden.

608

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876 **Figures and tables**

877

878 Table 1. Linear trends of individual species abundance in relation to ordination along axis
 879 dbRDA 1 that best contributed to the total variation (6.4 %) and correlate with Trawling
 880 intensity (0.52). Correlations between species abundance and trawling intensity are given
 881 within brackets. Only significant correlations with the dbRDA axis 1 are shown i.e., Pearson
 882 correlation coefficient $R \geq 0.14$, $df = 252$, $p < 0.05$.

883

Species decreasing with trawling intensity and axis dbRDA 1		Species increasing with trawling intensity and axis dbRDA 1	
	R		R
<i>Ampelisca tenuicornis</i>	-0.41 (-0.24)	<i>Amphiura chiajei</i>	0.50 (0.30)
<i>Phoronis muelleri</i>	-0.38 (-0.20)	<i>Ophiocten affinis</i>	0.26 (0.05)
<i>Rhodine gracilior</i>	-0.37 (-0.22)	<i>Labidoplax buskii</i>	0.25 (0.18)
<i>Mysella bidentata</i>	-0.34 (-0.21)	<i>Lipobranchius jeffreysii</i>	0.22 (0.13)
<i>Nephtys hombergii</i>	-0.33 (-0.19)	<i>Philomedes brenda</i>	0.22 (0.02)
<i>Turritella communis</i>	-0.29 (-0.17)	<i>Abyssoninoe hibernica</i>	0.22 (0.25)
<i>Prionospio fallax</i>	-0.29 (-0.25)	<i>Nuculana pernula</i>	0.21 (0.05)
<i>Mysia undata</i>	-0.28 (-0.16)	<i>Brada villosa</i>	0.21 (0.09)
<i>Scoloplos armiger</i>	-0.28 (-0.23)	<i>Ophiodromus flexuosus</i>	0.21 (0.23)
<i>Praxillella praetermissa</i>	-0.27 (-0.05)	<i>Panthalis oerstedii</i>	0.19 (0.10)
<i>Pholoe baltica</i>	-0.26 (-0.19)	<i>Leucon nasica</i>	0.18 (0.00)
<i>Eudorella truncatula</i>	-0.25 (-0.21)	<i>Photis longicaudata</i>	0.16 (0.00)

Aoridae	-0.25 (-0.17)	<i>Hyala vitrea</i>	0.15 (0.07)
<i>Amphiura filiformis</i>	-0.25 (-0.11)		
<i>Chamelea striatula</i>	-0.24 (-0.17)		
<i>Trichobranchus roseus</i>	-0.24 (-0.05)		
<i>Pectinaria auricoma</i>	-0.23 (-0.10)		
<i>Nucula nitidosa</i>	-0.21 (-0.14)		
<i>Scalibregma inflatum</i>	-0.21 (-0.11)		
<i>Edwardsia</i> spp.	-0.20 (-0.21)		
<i>Terebellides stroemi</i>	-0.20 (0.09)		
<i>Sphaerodorum flavum</i>	-0.19 (-0.11)		
<i>Ampelisca brevicornis</i>	-0.19 (-0.16)		
<i>Dosinia lupines</i>	-0.19 (-0.17)		
<i>Abra nitida</i>	-0.19 (0.09)		
<i>Corbula gibba</i>	-0.19 (0.00)		
<i>Harpinia antennaria</i>	-0.19 (-0.16)		
<i>Notomastus latericeus</i>	-0.17 (-0.11)		
<i>Levinsenia gracilis</i>	-0.17 (-0.01)		
<i>Bela brachystoma</i>	-0.17 (-0.14)		
<i>Anobothrus gracilis</i>	-0.17 (-0.09)		
<i>Cylichna cylindracea</i>	-0.17 (0.02)		
<i>Spiophanes bombyx</i>	-0.16 (-0.15)		

<i>Gari fervensis</i>	-0.16 (-0.11)
<i>Magelona alleni</i>	-0.16 (-0.15)
<i>Chone fauveli</i>	-0.15 (-0.12)
<i>Spio filicornis</i>	-0.14 (-0.16)
<i>Arctica islandica</i>	-0.14 (-0.20)
<i>Virgularia mirabilis</i>	-0.14 (-0.13)
<i>Westwoodilla caecula</i>	-0.14 (-0.05)

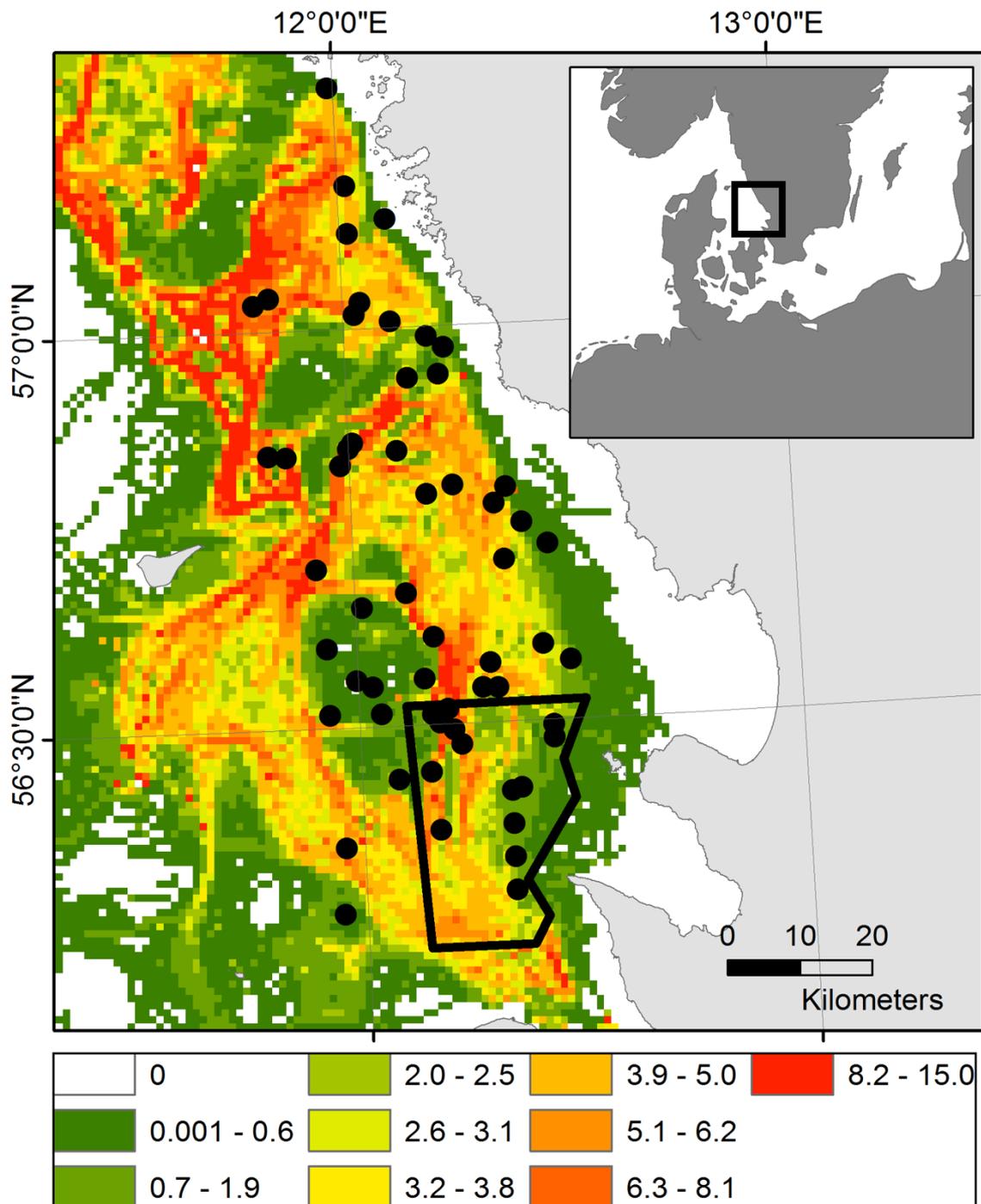
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886 Table 2. Summary statistics of GAM of number of species (*Nspp*), total abundance (*Nind*),
887 biomass (*Biom*), Richness according to Margalef (*d*), diversity according to Shannon (*H'*),
888 Benthic Quality Index (BQI), and for the dominating *Amphiura* species by abundance.
889 Equivalent degrees of freedom, is reported for the non-parametric predictors depth (D),
890 trawling intensity (TI) and total abundance (Nind) and statistical significance (* $P < 0.05$, **
891 $P < 0.01$) for all terms. The family distribution adopted for each model and the R^2 are
892 included.
893

Response	Predictor variable				R^2	Family
	a Year	s(D)	s(TI)	s(Nind)		
<i>Nspp</i>	**	1.00	2.29**	1.00**	0.344	Poisson
<i>Nind</i>		1.93**	1.00		0.130	Poisson
$\ln(\text{biomass})$	*	1.00	1.00		0.015	Gaussian
\sqrt{d}		1.57	2.64**		0.177	Gaussian
<i>H'</i>	**	1.00	2.36**		0.103	Gaussian
<i>BQI</i>	**	1.76	2.54**		0.187	Gaussian
<i>Amphiura chiajei</i>		1.95**	2.64**		0.283	Poisson
<i>Amphiura filiformis</i>		1.91**	1.00		0.132	Poisson

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896 Fig. 1. Map of the study area in Kattegat. Colours indicate yearly averaged trawling intensity

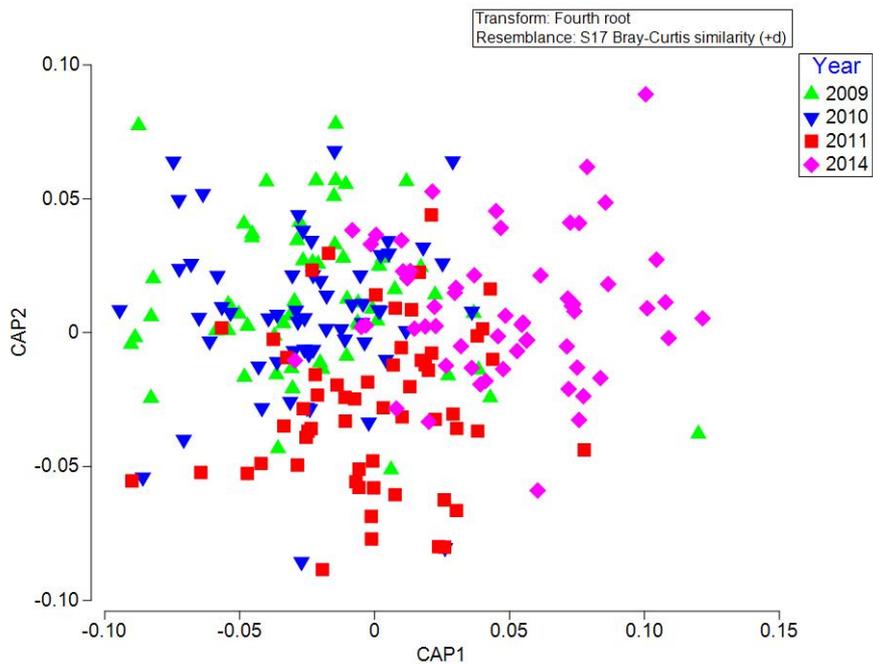
897 averaged per year for 2006-2008, i.e. the period before the MPA was established in 2009.

898 Trawling intensity is estimated from Danish and Swedish VMS and logbook data of bottom

899 trawl fleets as the total area swept yearly in grid cells of 1×1 km divided by grid cell size.

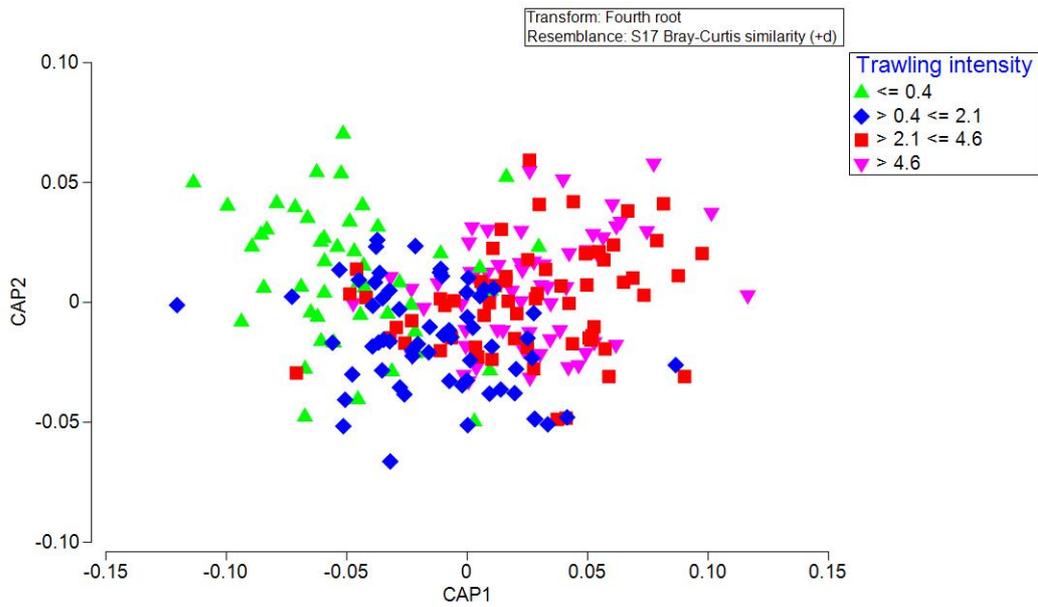
900 Sampling stations for benthic macrofauna are indicated with black dots and the MPA is

901 delineated.



902 a.

903



904 b.

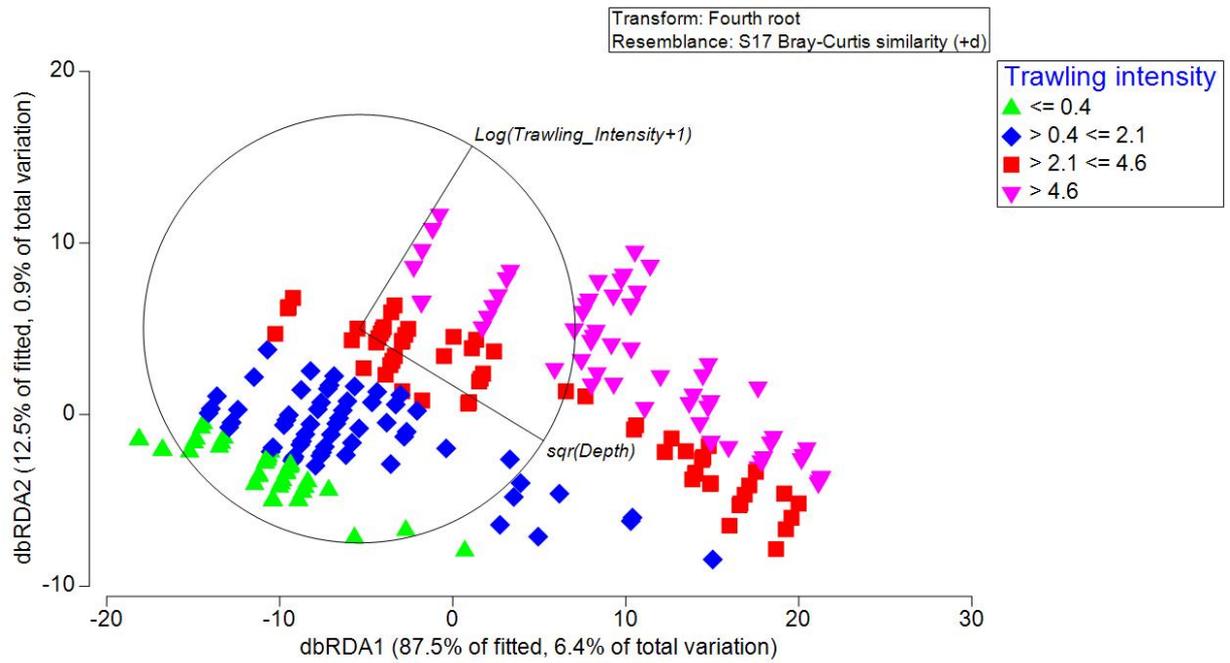
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906 Fig. 2. Canonical analysis of principal coordinates (CAP) for visual presentation of

907 macrofauna community composition (abundance of species) as shaped by (a) Year and (b)

908 Trawling intensity (yr^{-1}) grouped into statistical quartiles as indicated in the legend.

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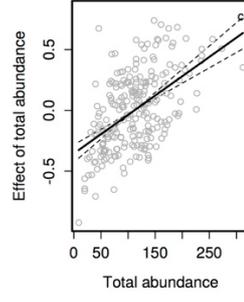
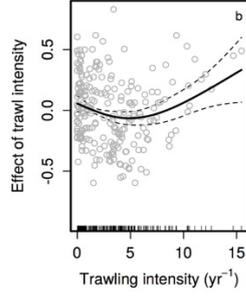
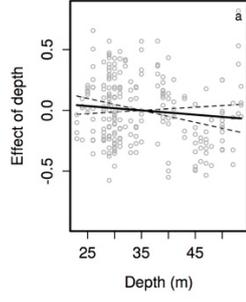
911 Fig. 3. Distance based redundancy analysis (dbRDA) ordination of the fitted model of the
 912 macrofaunal community composition. The gradient in trawling intensity grouped into
 913 quartiles is illustrated by the sampling stations colour according to the legend and vectors of
 914 the predictors trawling intensity and depth are indicated in the plot.

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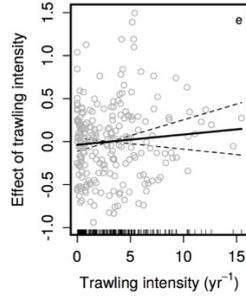
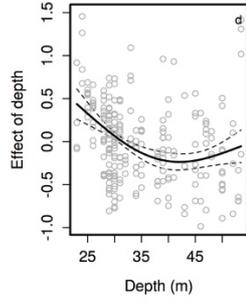
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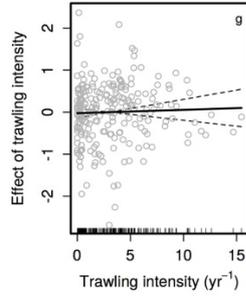
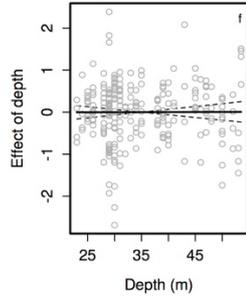
Number of Species



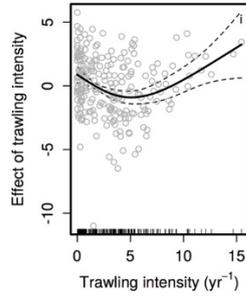
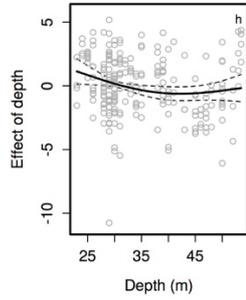
Total Abundance



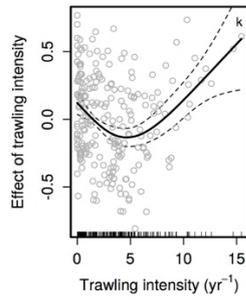
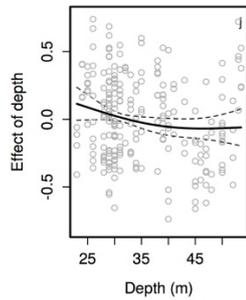
Biomass



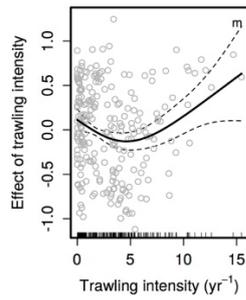
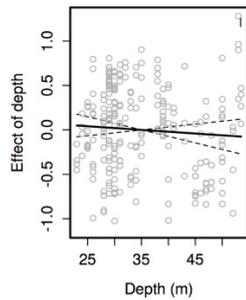
Benthic Quality Index



Species Richness



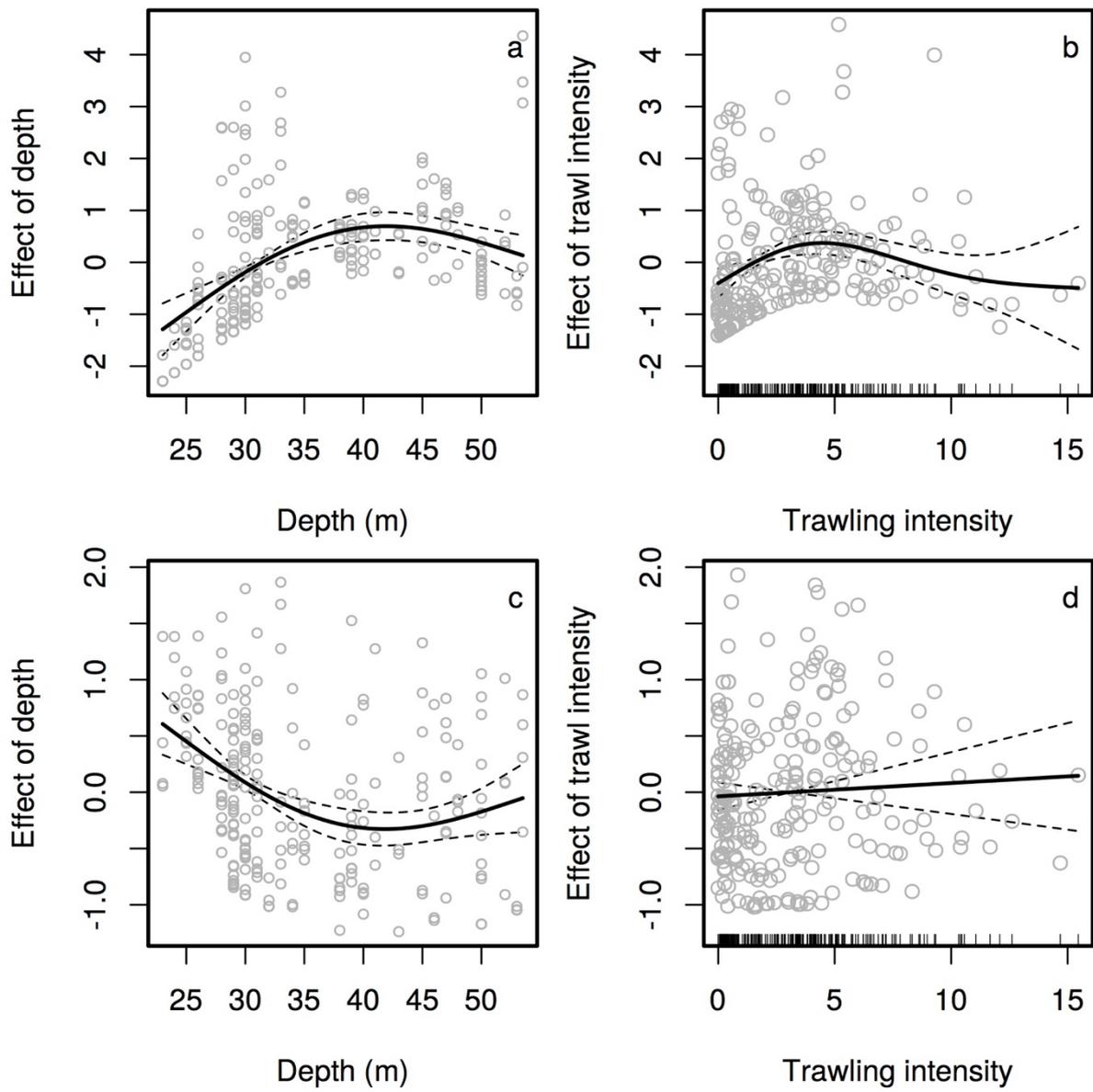
Species Diversity



919 Fig. 4. Effect of different predictors on the number of species $Nspp$ (a-c), total abundance
920 $Nind$ (d-e), biomass (f-g), Benthic Quality Index (BQI , h-i) Richness according to Margalef
921 (d , j-k), diversity according to Shannon (H' , l-m) as estimated from GAMs with 95%
922 confidence interval (dotted lines) and partial residuals (grey dots).
923

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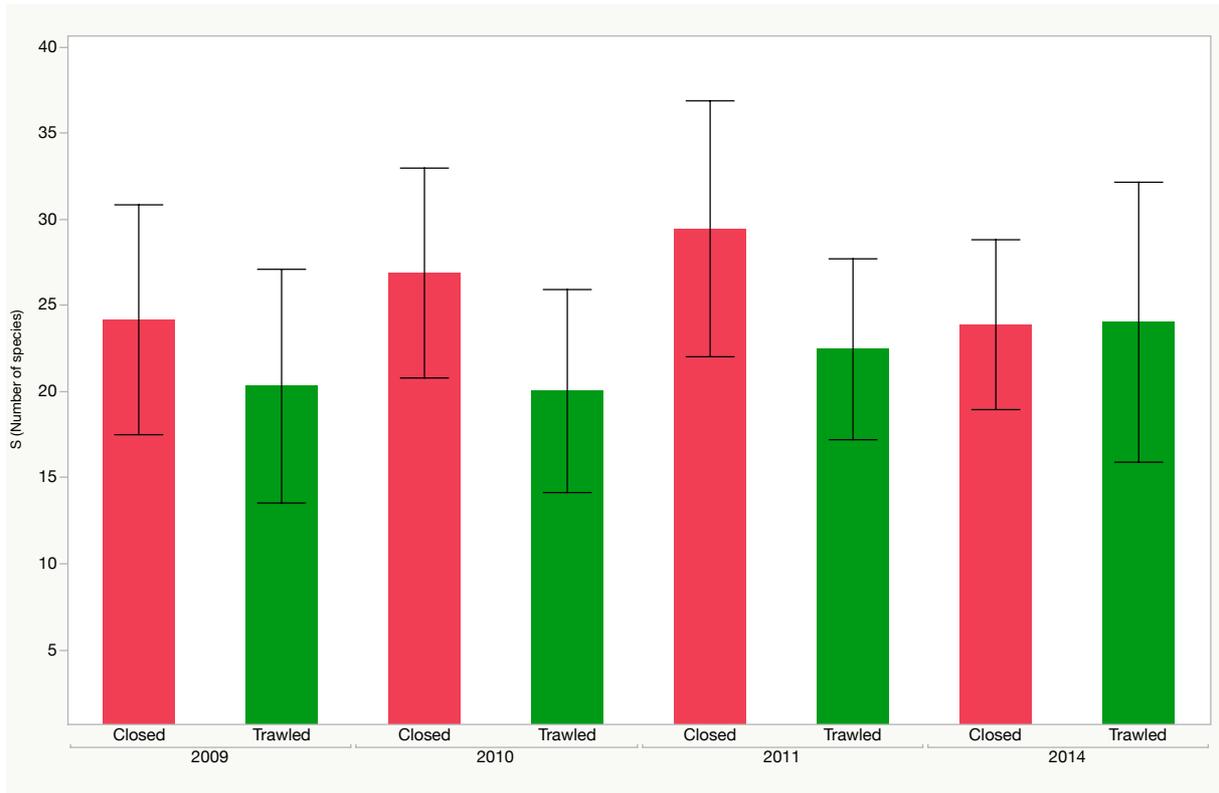
927 Fig. 5. Effect of different predictors on abundance of *Amphiura chiajei* (a-b) and *Amphiura*

928 *filiformis* (c-d) as estimated from GAMs with 95% confidence interval (dotted lines) and

929 partial residuals (grey dots).

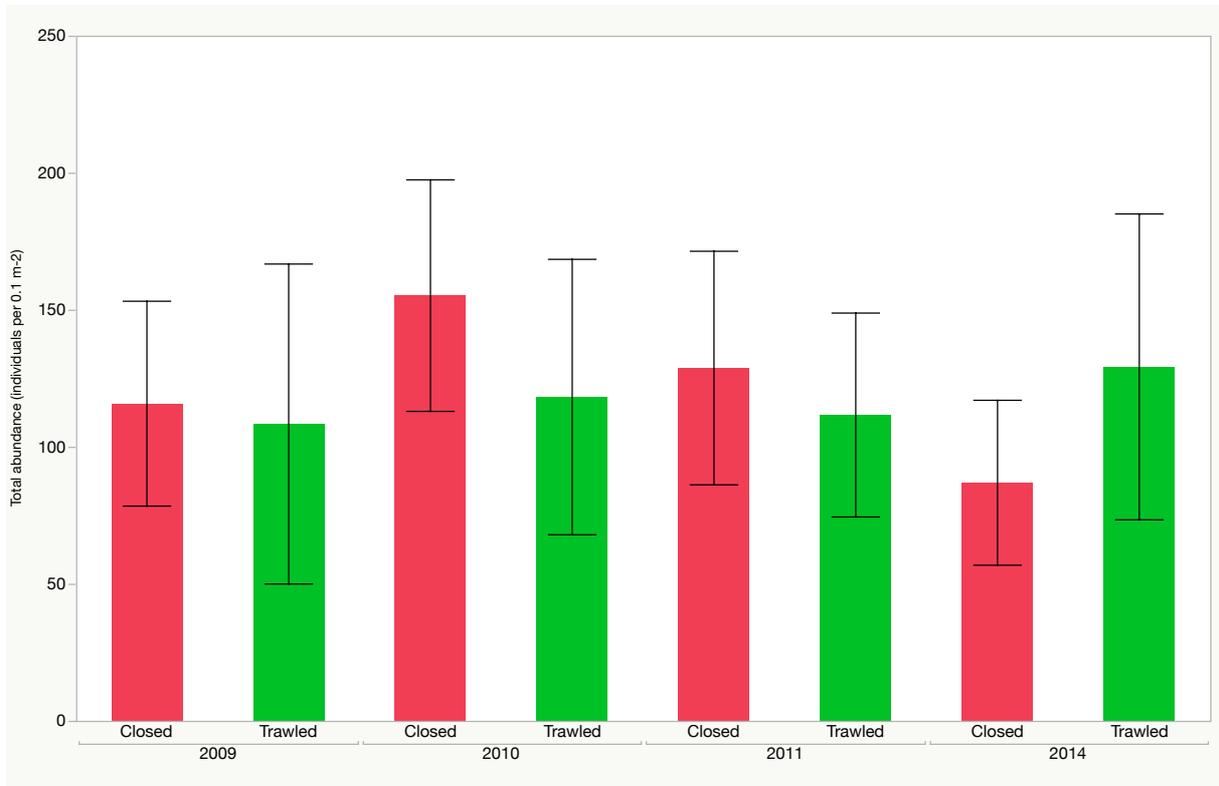
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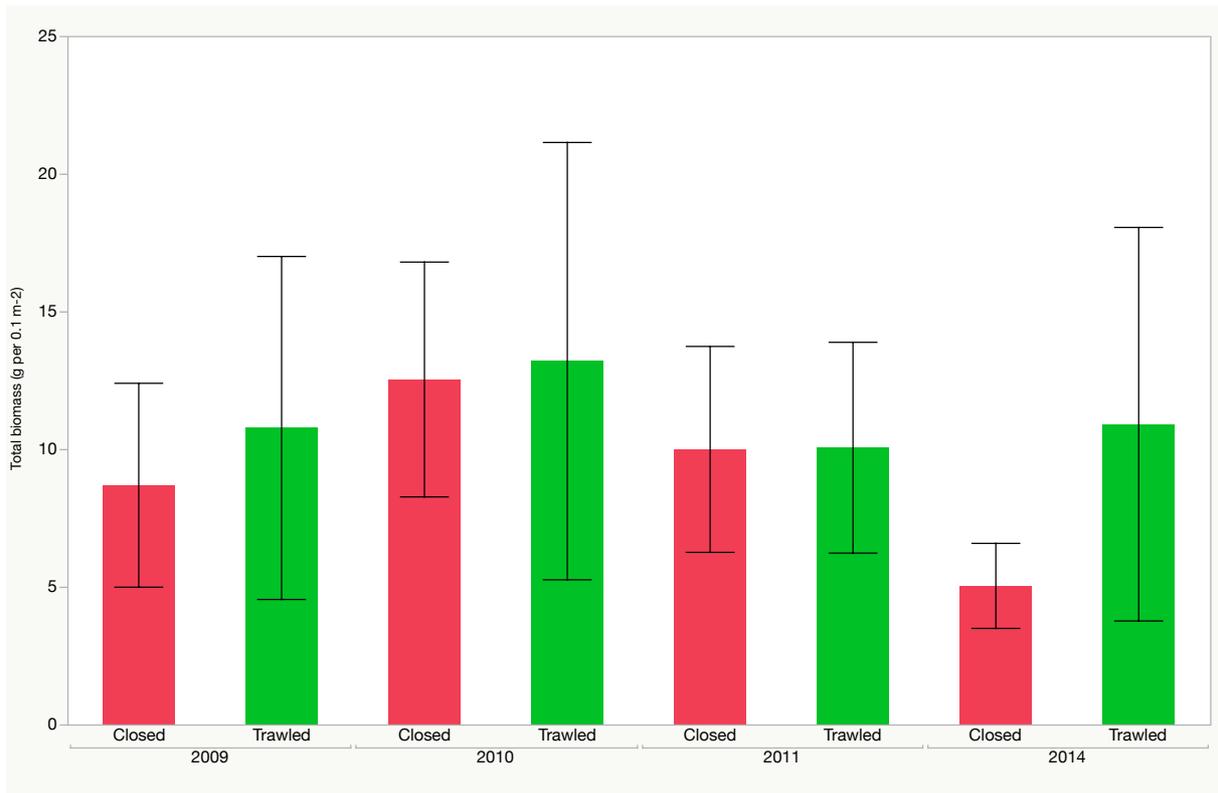
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933 a)



934

935 b)



936

937 c)

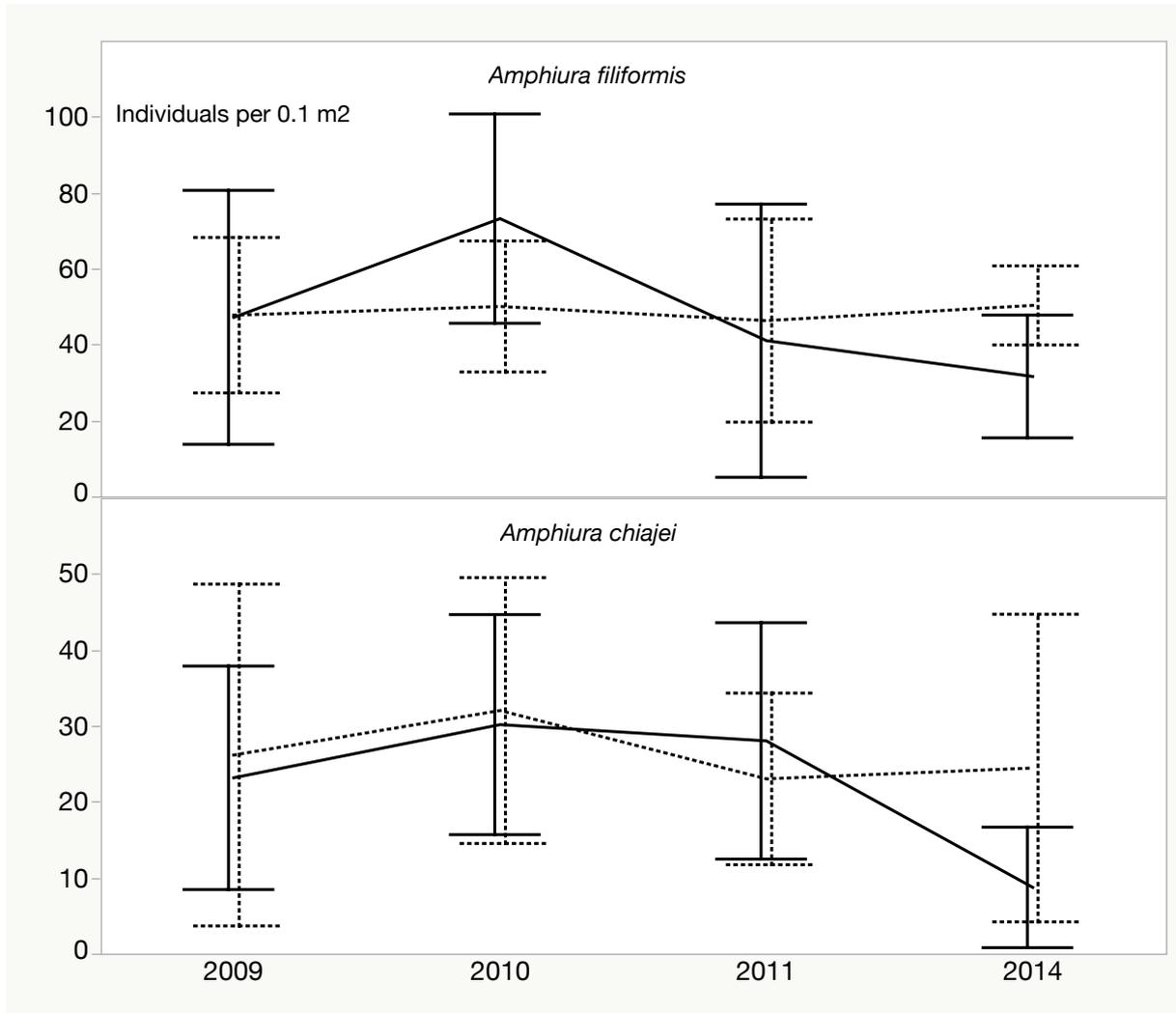
938 Fig. 6. Macrofauna number of species (a), total abundance (b) and total biomass excluding

939 large bodied species (c) across years in the MPA (red, n=7) and continuously trawled area

940 (green, n=7). Error bars are 95 % confidence intervals.

941

942



943

944 Fig. 7. Abundance of *Amphiura filiformis* (upper panel) and *Amphiura chiajei* (lower panel)

945 across years in the closed MPA (solid line, n=7) and continuously trawled area (dotted line,

946 n=7). Error bars are standard deviation of the mean