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1 Increasing species richness of the macrozoobenthic fauna on tidal flats of the
2 Wadden Sea by local range expansion and invasion of exotic species

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5 Netherlands)

6 Keywords: long-term changes; species per unit area; macrozoobenthos; intertidal; soft
7 sediment; introduced species; temperature change

8 ABSTRACT

9 A 40-y series of consistently collected samples (15 fixed sampling sites, constant sampled area
10 of 15 x 0.95 m², annual sampling only in late-winter/early spring seasons, and consistent sieving
11 and sorting procedures; restriction to 50 easily-recognizable species) of macrozoobenthos on
12 Balgzand, a tidal-flat area in the westernmost part of the Wadden Sea (The Netherlands),
13 revealed significantly increasing trends of species richness. Total numbers of species annually
14 encountered increased from ~28 to ~38. Mean species density (number of species found per
15 sampling site) increased from ~13 to ~18 per 0.95 m². During the 40 y of the 1970-2009 period
16 of observation, 4 exotic species invaded the area: (in order of first appearance) *Ensis directus*,
17 *Marenzelleria viridis*, *Crassostrea gigas*, and *Hemigrapsus takanoi*. Another 5 species recently
18 moved to Balgzand from nearby (subtidal) locations. Together, these 9 new species on the tidal
19 flats explained by far most of the increase in total species numbers, but accounted for only one
20 third of the observed increase in species density (as a consequence of the restricted
21 distribution of most of them). Species density increased particularly by a substantial number of
22 species that showed increasing trends in the numbers of tidal-flat sites they occupied. Most of
23 these wider-spreading species were found to suffer from cold winters. During the 40-y period of
24 observation, winter temperatures rose by about 2 °C and cold winters became less frequent.
25 The mean number of cold-sensitive species found per site significantly increased by almost 2
26 per 0.95 m². Among the other species (not sensitive to low winter temperatures), 6 showed a
27 rising and 2 a declining trend in number of occupied sites, resulting in a net long-term increase

28 of species density amounting to another gain of 1.6 per 0.95 m². Half of the 50 studied species
29 did not show such long-term trend, nor were invaders. Thus, each of 3 groups (local or alien
30 invaders/ winter-sensitive species/ other increasing species) contributed to a roughly similar
31 extent to the overall increase in species density.

32

33 INTRODUCTION

34 Though there is widespread and right concern on global-wide declining biodiversity, reports of
35 increasing species richness in specific areas have been reported as well. Such increases of
36 species numbers in local areas can arise from introductions of invaders from distant locations
37 (exceeding numbers of extinctions) or from changes in environmental conditions (when these
38 changes promote more species than they do harm). Both types of causes can be directly
39 influenced by man: invasions by increased shipping (Reise et al. 1999) and changes in habitat
40 diversity and suitability by management (protection/ restoration) and disturbance. A special
41 class of changing environmental conditions affecting species richness is the ongoing climate
42 change by which some species are locally promoted and others put at a disadvantage.

43 For invertebrates in the marine environment, few homogeneous data series of sufficient
44 length appear to be available to reliably judge long-term trends in species richness and relate
45 possible trends to underlying causes. There are several reports on successful introductions of
46 exotic species leading to increases in species numbers, as displacement of autochthonous
47 species appear to be a rare phenomenon (Reise et al. 1999; Wolff 2000). A warming climate
48 generally results in pole-ward shifts of distribution areas, southern species increasing in
49 abundance and northern species declining in the northern hemisphere (Sagarin et al. 1999). As
50 species richness generally declines with increasing latitude, species gains tend to exceed
51 species losses in areas at higher latitudes (Hawkins et al. 2009).

52 The present study is based on a 40-y series of consistently collected quantitative data on
53 macrozoobenthos in a vast area in the Dutch Wadden Sea. The Wadden Sea is an estuarine area
54 of geologically-young age and was seriously human-altered for the last centuries (Lotze et al.

2005). Such areas appear to be particularly vulnerable for exotic invaders (Wolff 1999). The Wadden Sea is characterized by vast tidal mud and sand flats which are inhabited by a fauna with high biomass and low species diversity (Beukema 1976; Beukema and Cadée 1997). Part of the species suffer from severe winters (Beukema 1979; 1990) and may profit from the warming climate (Beukema 1992). Data series reviewed by Van der Graaf et al. (2009) point to increasing species numbers in various parts of the Wadden Sea for recent decades. However, for methodological reasons, these trends should be considered with caution. Avoiding these methodological problems by a restriction to a delimited group of conspicuous species, we analyze changes in total species numbers as well as in species density (number of species per unit area) and relate these changes to some possible underlying processes, such as invader introductions, climate change and human disturbance.

METHODS

Since around 1970, data on macrozoobenthos have been collected twice annually at 15 permanent (marked) sampling stations (“sites”) located on Balgzand, a 50-km² tidal flat area in the westernmost part of the Wadden Sea. For the present study we used only data collected in late-winter/early spring, mostly in March, when numbers are at an annual minimum. Most (12) sites were 1-km long transects where 50 bottom samples of nearly 2 dm² each were taken at distance intervals of 20 m, together 0.95 m² per site. The 3 other sites were squares of 900 m² where 9 samples of nearly 0.1 m² each were taken at randomly chosen places. The sites covered the entire intertidal range and nearly the full range of sediment types on Balgzand (Beukema and Cadée 1997). There was little change in these abiotic conditions during the 40-y period of observation. Hard substrates such as dikes were not sampled, but animals attached to shells of mussels or oysters were included. The samples were sieved (1-mm square meshes) in the field and sorted alive in the laboratory. All living animals were picked out, sorted to species level as much as possible, and counted. Further details on the sampling area, the sampling stations, and the methods can be found in Beukema and Cadée (1997).

Temperature data were taken from Van Aken (2008). We used monthly means of surface water temperatures in the nearby Marsdiep tidal channel and averaged for each winter the means of December, January and February to obtain a mean winter water temperature.

84 *Sources of error*

85 Thin worms will be underestimated or completely missed, as a high proportion of them will pass
86 the 1-mm sieve. Such species were completely excluded (e.g. nematodes, oligochaetes, tiny
87 spionid polychaetes such as *Pygospio* sp.). Inevitably, sorting sieved samples with lots of debris
88 (peat, empty shells) is imperfect: some small and inconspicuous specimens will at least partly be
89 overlooked, even by experienced researchers. We standardized sorting and counting procedures
90 as much as possible. Another problem arises in identification: some closely related species are so
91 similar in external appearance that they cannot routinely be counted separately in macroscopic
92 procedures. To reduce these errors, we decided to limit the present study to a list of 50 species
93 that are sufficiently conspicuous and easily identifiable. To this end, we treated resembling
94 species as one species, e.g. *Corophium volutator* and *C. arenarium* were recorded as *C.sp.*, all
95 barnacles as balanoids, and all sea anemones as Anthozoa. The full list of taxa can be found at
96 the bottom of Table 1.

97 In fact, many more than these 50 macrozoobenthic species are present on Wadden Sea
98 tidal flats and some tens of them were regularly or occasionally found in our samples. Some
99 hundreds of benthic invertebrate species have been reported from the tidal plus subtidal parts of
100 the international Wadden Sea, most of them small-sized (Wolff and Dankers 1981; Petersen et al.
101 1996). By reducing a full list to 50 selected items, we are convinced that we anticipated a
102 possible positive bias in the species-richness trend due to a growing skill in recognizing species.

103 RESULTS

104 *Long-term trends in species numbers and temperature*

105 During the 1970-2009 period, the annual benthos samples taken showed significantly
106 increasing numbers of macrozoobenthic species. Total numbers observed at $15 \times 0.95 = 14.25$
107 m^2 increased from ~ 28 in the early-1970s to ~ 38 in the late-2000s (solid points in Fig. 1b). The
108 mean rate of increase amounted to 0.21 ± 0.04 (mean and 1 s.e.) species y^{-1} . Likewise, the 15-
109 site means of species number per sampling site of 0.95 m^2 increased from ~ 12 to ~ 18 (open
110 points in Fig. 1b), at a mean rate of $0.13 \pm 0.02 \text{ y}^{-1}$. Long-term means of species numbers
111 amounted to 32.4 ± 0.6 and 15.2 ± 0.3 for sampled areas of 14.25 and 0.95 m^2 , respectively.

112 Note that these numbers are underestimates of the true numbers of macrozoobenthic species
113 present, because they are out of a maximal number of 50 listed species (considered as easily-
114 recognizable and not to be overlooked).

115 In accordance with the recent trend of rising temperatures which is particularly strong in
116 Dutch coastal waters and occurs in all seasons (Van Aken 2008, 2010), annual mean water
117 temperatures rose by a mean rate of $\sim 0.05\text{ }^{\circ}\text{C y}^{-1}$ during the 1970-2009 period of observation
118 (Fig. 1a). Annual means increased from about 10 to almost 12 $^{\circ}\text{C}$ (correlation with year number
119 $r = 0.63$, $n = 39$, $p < 0.0001$); fluctuations in winter (Dec-Jan-Feb periods) temperatures were
120 stronger and more irregular (open points in Fig. 1a), but nevertheless winter water
121 temperatures showed a significantly positive correlation with year number ($r = 0.36$, $n = 39$,
122 $p < 0.05$), again at a mean rate of increase of $\sim 0.05\text{ }^{\circ}\text{C y}^{-1}$. Among the 40 winters of the period of
123 observation, 8 were particularly cold (mean winter water temperature $< 3\text{ }^{\circ}\text{C}$): 1970, 1979,
124 1982, 1985, 1986, 1987, 1996, and 1997 (see open points of Figs 1a and 1c). Such severe
125 winters appear to occur less frequently during the last than the first half of the 1970-2009
126 period.

127 Species numbers observed after severe winters were usually lower than after
128 neighbouring mild winters, compare open and solid points in Fig. 1c. The influence of winter
129 temperature on species richness can be removed by addition or subtraction a number of 1.7
130 (totals per 14.25 m^2) or 1.0 (means per 0.95 m^2) species (values taken from Fig. 3a) for each $^{\circ}\text{C}$
131 the water temperature of the preceding winter was lower or higher, respectively, than the
132 long-term mean of $4.2\text{ }^{\circ}\text{C}$. The thus temperature-corrected values for species numbers still
133 showed a statistically significant increasing trend in the course of the period of observation (Fig.
134 1d).

135 In early 1991, the species numbers were particularly low (crosses in Fig. 1c). In that year,
136 not any mussel bed was present on Balgzand as a consequence of heavy fishing in the summer
137 of 1990 (Beukema 1993; Beukema and Cadée 1996). In 1991, the number of species was not
138 only reduced by the absence of the one species *Mytilus edulis*, but also by the absence of
139 species that use mussel shells as a hard substrate such as barnacles and periwinkles.

140 *Effects of winter temperatures*

141 Several zoobenthic species living on Wadden Sea tidal flats are sensitive to low winter
142 temperatures, i.e. they show significantly reduced survival rates in severe winters (Beukema
143 1979). Some of these species completely or almost completely disappear from the intertidal
144 after the coldest winters, either at all intertidal zones (Beukema 1990) or only at the sampling
145 sites at high intertidal levels (Beukema 1985). Beukema (1990) listed 11 of such winter-sensitive
146 species of benthic animals on Balgzand. They are all included in the present 50-species list, and
147 10 of them showed a significantly positive relationship between winter temperature and
148 number of sites subsequently occupied: the bivalves *Cerastoderma edule* (Fig. 2d), *Abra tenuis*
149 (Fig. 2b), *Tellina tenuis* (Fig. 2b) and *Mysella bidentata* (Fig. 2c), the polychaete worms *Lanice*
150 *conchilega* (Fig. 2a) and its commensal *Malmgreniella lunulata* (Fig. 2a) and *Nephtys hombergii*
151 (Fig. 2c), the group of Nemertean (Fig. 2d), and the crustaceans *Crangon crangon* (Fig. 2e) and
152 *Carcinus maenas* (Fig. 2f). The 11th species (*Bylgides sarsi*) that was reported to show reduced
153 survival in cold winters did not show a significant relationship as shown in Fig. 2, nor did it show
154 a long-term trend in numbers of site occupied.

155 As to be expected from the substantial share of winter-sensitive species among the
156 macrozoobenthic fauna on Balgzand, the total numbers of species found were higher after mild
157 than after cold winters, both for 14.25 and 0.95 m² sampling areas (solid and open points of Fig.
158 3a). To allow for the interaction between year number and winter temperatures, the species
159 numbers were de-trended, i.e. they were augmented by 0.21 (number per 14.25 m²) or 0.13
160 (number per 0.95 m²) for each year before 1990 and reduced by the same amount for each
161 year after 1990 (correction values taken from Fig. 1b). The thus year-influence-corrected
162 species numbers were still significantly positively correlated with preceding-winter water
163 temperatures (Fig. 3b), increasing by ~1.1 (14.25 m²) and ~0.6 (0.95 m²) species per 1 °C
164 temperature rise.

165 At least 6 frequently observed species were completely absent after the coldest winters
166 (zero points in Fig. 2 at the lowest temperatures) and some of them needed a few years after a
167 severe winter to recover and thus remained absent for another 1 or 2 y (most of the zero points

168 in Fig. 2 at winter temperatures of $>4^{\circ}\text{C}$). Some other species (e.g. *N. hombergii* and *C. edule*,
169 Figs 2c and 2d) occurred at reduced numbers of sites after the coldest winters, but were never
170 completely absent. Complete absence affects the total species number per 14.25 m^2 as well as
171 the mean number per 0.95 m^2 , whereas absence at part of the sampling sites only reduces the
172 mean species number per 0.95 m^2 .

173 After most of the mild winters, all of the above 10 winter-sensitive species were present
174 at one or more sites. In these years, the group contributed a number of 10 to the total (per
175 14.25 m^2) species number (solid squares in Fig. 1c). After cold winters, only about half of these
176 species were present at one or more sites, resulting in a contribution of ~ 5 winter-sensitive
177 species to total species numbers (open squares for 1970, 1979, 198, 1985, 1986, 1987, 1996,
178 and 1997 in Fig. 1c). Whenever a severe winter had occurred at least 3 years ago (as in the
179 1974-1978, 1991-1995, and 2000-2009 periods), the contributions of winter-sensitive species
180 were 10 or close to 10 species (solid squares of Fig. 1c). Likewise, but less pronounced, mean
181 contributions of winter-sensitive species per 0.95 m^2 were higher after mild than after cold
182 winters (solid and open circles in Fig. 1c) and were particularly high in years long after a severe
183 winter.

184 *Introduced species*

185 In the course of the 1970-2009 period of observation, at least 4 non-native species turned up in
186 the samples. The first to appear was the American jack-knife clam *Ensis directus* in 1982, about
187 5 y after its first find in the Wadden Sea and Europe (Beukema and Dekker 1995; Von Cosel
188 2009). The species was observed in the Balgzand samples in nearly all years after 1982 (solid
189 squares in Fig. 5). The next invader was the American spionid worm *Marenzelleria viridis* in
190 1989, 7 and 6 y after its first records in the North Sea and Wadden Sea, respectively (Essink
191 1999, Essink and Dekker 2002: as *M. cf. wireni*, but see Sikorsky and Bick (2004)). It rapidly
192 spread over the entire Balgzand area, occurring at 13 to 15 out of the 15 sampling sites ever
193 since 1996 (open circles in Fig. 5). The third exotic invader was *Crassostrea gigas*, appearing in
194 the samples in 2001, about 40 and 30 y after its first deliberate introduction from East Asia into
195 Europe and the Wadden Sea (Wolff 2005). Since 2003, it was regularly found at 2 or 3 sites

196 (crosses in Fig. 5). Finally, the Asian decapod *Hemigrapsus takanoi* (see Asakura and Watanabe
197 2005) turned up in the samples in 2006, more than 20 y after its first find in Europe (Gollasch
198 1999). It was subsequently found every year at 1 to 3 sites (triangles in Fig. 5).

199 Apart from the above 4 invasive species that recently arrived in Europe, 5 more species
200 (that were already present in the North Sea area for at least decades) were only recently
201 observed on the Balgzand tidal flats: *Crepidula fornicata*, *Glycera alba*, *Lepidochitona cinerea*,
202 *Echinocardium cordatum*, and *Ophiura ophiura*. This small group of newcomers on the Balgzand
203 tidal flats was observed in small numbers (mostly only 1 specimen) at few sites (mostly only 1
204 site), thus contributing little to species numbers per 0.95 m² (open points in Fig. 4b).

205 *Other species*

206 Among the remaining 31 species (50 - 10 - 4 - 5), 6 showed a statistically significant upward and
207 2 a significant downward trend in the numbers of sites where they were encountered in the
208 successive years of the 1970-2009 period of observation. Together, the 6 species with a positive
209 trend (*Littorina littorea*, *Nereis* spp. (mostly *Alitta succinea*, but also including some *A. virens*
210 and *Eunereis longissima*), *Eteone* spp., *Urothoe poseidonis*, *Gammarus locusta*, and the group of
211 Balanoids) showed an increase of mean numbers of species per site from ~0.7 to ~2.7 species
212 per 0.95 m² (Fig. 4c). The 2 species with a negative trend (*Magelona johnstoni*, *Scolelepis*
213 *foliosa*) showed a decline from ~0.7 to ~0.3 species per 0.95 m² (Fig. 4c). Thus, the net
214 contribution to species density of the 8 species with a significant trend amounted to a positive
215 value of 2.0 - 0.4 = 1.6 species per 0.95 m². The remaining 24 species did not contribute
216 (neither positively nor negatively) to species density (Fig. 4d).

217 DISCUSSION

218 A long period of consistent sampling of the macrozoobenthic fauna on the Balgzand tidal flats
219 revealed a gradual increase of species richness. Expressed as total number of species
220 encountered, the increase amounted to about 35% (~28 to ~38) over the entire 40-y period of
221 observation. Expressed as a mean number per sampling site, the increase was of a similar
222 magnitude (~13 to ~18 per 0.95 m²). As a measure of species richness, we consider the latter

223 estimate of species density superior to total species number, because the total number found
224 in any year strongly depends on finds of just one individual of a rare species. Each of such finds
225 would add about 3% to total species number, but only about 0.5% to the number per site ($1 /$
226 $15 = 0.07$, being 0.5% of 14.2, the long-term mean number of species per 0.95 m^2).

227 The above numbers refer to a limited group of 50 species, all easily identifiable and
228 relatively conspicuous. This limitation was thought imperative to exclude a possibly serious
229 influence of growing experience of the observers in sorting samples and/or recognizing rare or
230 similar-looking species, which would lead to undeservedly increasing estimates of numbers of
231 species found during the long period of observation.

232 We identified various groups of species to contribute to the increasing trend in species
233 richness. The 10 winter-sensitive species (mentioned in Fig. 2) contributed together ~ 1.8
234 species per 0.95 m^2 to the increase in species density (Fig. 4a), in accordance with the
235 increasing trend of winter temperatures and the declining frequency of occurrence of cold
236 winters (Fig. 1a). The species belonging to this group hardly affected the total species numbers,
237 because they were all present at one or more sites both at the start and at the end of the 40-y
238 period. The appearance of 8 invaders, either of exotic or local origin, explained almost
239 completely the long-term increase in total species number (amounting to 10 species). The
240 contribution to the long-term increase in species density of exotic and local newcomers
241 amounted to 1.5 and 0.2 species per 0.95 m^2 , respectively (Fig. 4b). A substantial share of the
242 observed increase in species density was contributed by species that showed a long-term
243 positive or negative trend in the numbers of sites occupied, but without an apparent coupling
244 to a known change in environmental conditions. This contribution amounted to +2.0 and -0.4
245 (net +1.6) species per 0.95 m^2 (Fig. 4c). Taken together, the above groups contributed $1.8 + 1.7$
246 $+ 1.6 = 5.1$ species per 0.95 m^2 and this is close to the observed overall increase in species
247 density of 5.2 species per 0.95 m^2 (Table 1). Note that not just a few species accounted for the
248 long-term changes in species density, but that more than half (26 / 50) of the studied species
249 were in some way involved in the explanation of this increase. On the other hand, the one 8-

250 species group of newcomers (including 4 truly exotic species and 4 showing only local range
251 extension) could almost completely explain the observed increase in total species number.

252 The observed increases in macrozoobenthic species richness may not be limited to the
253 westernmost part of the Wadden Sea. A recent survey of the macrozoobenthos of the Wadden
254 Sea (Van der Graaf et al. 2009) indicates increasing trends of species numbers at all 3 sites
255 (Balgzand, Groninger Wad, Norderney) that were continuously sampled ever since the 1970s.
256 However, as the authors rightly remark, part of these increases in species numbers will have
257 been caused by methodological reasons (viz. the above discussed improved species
258 identification). In the north Frisian Wadden Sea near the island of Sylt, Reise et al. (1989) report
259 increases in numbers of infauna species, particularly in polychaetes, between the 1930s and
260 1980s, resulting in enhanced numbers of species per 0.2 m² (compare figure 8b of Lotze 2005).
261 Van der Graaf et al. (2009) could not confirm a suggested “polychaete take-over”. In the central
262 western North Sea, a 33-y data series by Frid et al. (2009) revealed a significant increase in
263 numbers of genera found per 0.5 m² from ~100 in the 1970s to ~120 in the 1990s and early-
264 2000s.

265 Though the trends in species richness may usually be upward, species losses have been
266 reported from the Wadden Sea. The main causes of (local or total) species extinction in the
267 Wadden Sea appear to be habitat change or destruction and exploitation (compare figure 3 of
268 Lotze et al. 2005). Several cases of habitat destruction were caused by fishery (Reise et al. 1989;
269 Piersma et al. 2001), including disturbance of the upper bottom layer and complete removal of
270 oyster and mussel banks. Mussel (and oyster) beds are usually richer in species than their
271 surroundings, as these structures offer locally hard substrates to species that cannot live on the
272 surrounding soft sediments (Buschbaum et al. 2009). The few sampling sites on Balgzand that
273 usually included mussel beds showed higher species densities than other sites. The removal of
274 all mussel beds in 1990 (Beukema and Cadée 1996) resulted in exceptionally low estimates of
275 species richness at the next sampling occasion in early-1991 (see + and x points in Figs 1c, 1d,
276 and 3b), but species richness and mussel numbers had largely recovered already by 1992, due
277 to highly successful reproduction in many species (including mussels) in the summer of 1991.

278 As in other areas, part of the increasing species richness on Balgzand was due to
279 invaders. In Wadden Sea invertebrates, the numbers of newly introduced species exceeded
280 those of species that became extinct (compare figure 2 of Lotze et al. 2005). No cases appear to
281 be known of extinction caused by an invasive species in the Wadden Sea (Wolff 2000; Lotze et
282 al. 2005) and examples of invaders reducing abundance of other species appear to be few. An
283 example of such negative interaction may be the local declines of biomass of *Nereis* spec. and
284 other species simultaneously with the rapid increase of biomass of *Marenzelleria viridis* after
285 their introduction (Essink et al. 1998; Essink and Dekker 2002). Markert et al. (2010) and Troost
286 (2010) found no indication of a suppression of indigenous species by the recent establishment
287 of reefs of Pacific oysters *Crassostrea gigas* in the German and Dutch Wadden Sea, respectively.

288 A substantial part of the observed increase in species density could be attributed to the
289 warming climate: the 10 winter-sensitive species (Fig. 2) became more abundant and were
290 found at an increasing number of sampling sites (Table 1; Fig. 4a). Declines in numbers of
291 occupied sites were observed in a few species, but these declines appeared to be unrelated to
292 temperature change. A few species, notably the bivalve *Macoma balthica* do suffer from the
293 warming climate and showed declining trends in abundance for recent decades (Beukema et al.
294 2009). So far, however, this did not result in declining numbers of sites where they were found.
295 Thus, the long-term warming trends resulted in increasing species richness on the Balgzand
296 tidal flats. This conclusion is in accordance with that of Hawkins et al. (2009) for British rocky-
297 shore fauna, that more southern (warm-water) species have been recorded advancing than
298 northern (cold-water) species retreating. A similar conclusion was reached by Sagarin et al.
299 (1999) for the Californian rocky intertidal.

300 The two processes (invasions and advancement of species, mostly by climate change)
301 that caused the increase in species richness on Balgzand tidal flats are still in progress and may
302 be expected to continue. Immigration of alien species by a.o. transport in ballast water,
303 attachment to ship hulls or to imported organisms (such as oysters) cannot completely be
304 prevented. Brackish estuaries and other coastal areas appear to offer plenty of open niches for
305 newcomers (Wolff 1999; Reise et al. 1999). Further spread of lower-latitude species into a pole-

306 ward direction (in fact largely a re-colonization process ever since the Ice Ages) will rapidly
307 continue as long as global warming continues. So far, there are no signs of extirpation of
308 species in the study area as a consequence of warming. Warming promoted the distribution of
309 winter-sensitive species that were already present in the area. Occasional cold winters caused
310 an immediate but temporary reduction in species number and species density, but recovery
311 went rapidly. In conclusion: we expect further increases of species numbers and species-density
312 values from all processes underlying the observed increase in species richness.

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317

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405 LEGENDS

406 Fig. 1. Long-time (1970-2009) series of data on:

407 (a) Annual means of water temperatures in the main tidal inlet of the western Wadden
408 Sea, for (solid points) the entire year and (open points) the 3-months winter periods
409 Dec/Jan/Feb.

410 (b) Numbers N of species (among a list of 50 easily recognizable macrozoobenthic species)
411 found in late-winter/early spring in: (solid points) all samples together (15 sites x 0.95
412 m²) and (open points, with 1 standard error, n = 15) mean number per sampling site.

413 (c) Numbers as in (b), but separately for samplings following a very cold winter (open
414 points) or (solid points) a normal or mild winter. The + and x points refer to 1991, when
415 the area was devoid of mussel beds.

416 (d) Numbers as in (c), but corrected for the influence of temperature of the preceding
417 winter (see text).

418 Best linear fits are:

419 (b, solid points: 14.25 m²) $N = -385 + 0.21 \text{ year}$ ($r = 0.62$, $n = 40$, $p < 0.0001$),

420 (b, open points: 0.95 m²) $N = -251 + 0.13 \text{ year}$ ($r = 0.73$, $n = 40$, $p < 0.0001$),

421 (d, solid points, full line: 14.25 m²) $N = -215 + 0.124 \text{ year}$ ($r = 0.50$, $n = 38$, $p = 0.001$),

422 (d, open points, dashed line: 0.95 m²) $N = -162 + 0.089 \text{ year}$ ($r = 0.72$, $n = 38$, $p < 0.0001$).

423 Fig. 2. Relationships between mean water temperature (T in °C) in the preceding winter

424 (temperatures as open points in Fig. 1a) and number N of sampling sites (among a total of 15)

425 where at least 1 specimen was found in the subsequent late-winter/early-spring sampling of 10

426 winter-sensitive species:

427 (a) (open circles) *Lanice conchilega*, (solid squares) *Malmgreniella lunulata*;

428 (b) (open circles) *Tellina tenuis*, (solid squares) *Abra tenuis*;

429 (c) (open circles) *Mysella bidentata*, (solid squares) *Nephtys hombergii*;

430 (d) (open circles) Nemertean worms, (solid squares) *Cerastoderma edule*;

431 (e) *Crangon crangon*;

432 (f) *Carcinus maenas*.

433 Best linear fits:

434 (a, *L. conchilega*) $N = -2.68 + 1.83 T$ ($r = 0.71$, $n = 39$, $p < 0.0001$), (a, *M. lunulata*) $N = -0.66 + 0.45 T$ (r
435 $= 0.40$, $n = 39$, $p < 0.05$), (b, *T. tenuis*) $N = 0.55 + 0.34 T$ ($r = 0.36$, $n = 39$, $p < 0.05$), (b, *A. tenuis*) $N =$
436 $-0.41 + 0.53 T$ ($r = 0.55$, $n = 39$, $p < 0.001$), (c, *M. bidentata*) $N = -0.57 + 0.55 T$ ($r = 0.48$, $n = 39$, p
437 $= 0.002$), (c, *N. hombergii*) $N = 5.4 + 1.41 T$ ($r = 0.72$, $n = 39$, $p < 0.0001$), (d, Nemertean worms) N
438 $= -0.2 + 0.58 T$ ($r = 0.54$, $n = 39$, $p = 0.0004$), (d, *C. edule*) $N = 7.1 + 1.00 T$ ($r = 0.68$, $n = 39$, $p <$
439 0.0001), (e, *C. crangon*) $N = 2.45 + 1.15 T$ ($r = 0.58$, $n = 39$, $p = 0.0001$), and (f, *C. maenas*) $N =$
440 $4.94 + 0.73 T$, $r = 0.42$, $n = 39$, $p < 0.01$).

441 Fig. 3. Relationships between mean water temperature (T in $^{\circ}\text{C}$) in the preceding winter (as
442 open points in Fig. 1a) and (a) actual numbers N of species (among a list of 50 easily
443 recognizable macrozoobenthic species) found in late-winter/early spring in (solid points) all
444 samples together (15 sites \times 0.95 m^2) and (open points) mean number per sampling site (0.95
445 m^2). In (b) these numbers of species have been de-trended for the influence of year number
446 (see text). The numbers found in 1991 are indicated separately by crosses (+ for 14.25 and x for
447 0.95 m^2 , respectively). Best linear fits:

448 (a, full line, solid squares) $N = 25.1 + 1.70 T$ ($r = 0.67$, $n = 39$, $p < 0.0001$),

449 (a, dashed line, open circles) $N = 11.0 + 1.00 T$ ($r = 0.72$, $n = 39$, $p < 0.0001$),

450 (b, full line, solid squares) $N = 27.9 + 1.11 T$ ($r = 0.57$, $n = 38$, $p < 0.002$),

451 (b, dashed line, open circles) $N = 12.7 + 0.63 T$ ($r = 0.71$, $n = 38$, $p < 0.0001$).

452 Fig. 4. Long-term (1970-2009) changes in the contributions to total species richness ($n =$ mean
453 number of species per 0.95 m^2) of 4 groups of species:

454 (a) the 10 species of Fig. 2 that showed a statistically significant relationship between
455 winter temperature and number of sites where they were found,

456 (b) two groups of invaders: (solid points) the 4 exotic species that were newly found in the
457 Wadden Sea, and (open points) 5 non-exotic species observed on Balgzand only in
458 recent years,

459 (c) (solid points) the 6 other species that showed an increasing trend and (open points) the
460 2 species that showed a decreasing trend in number of sites occupied,
461 (d) all other 24 species belonging to the list of 50 easily-recognizable species.

462 Best linear fits (shown as straight lines in Figure only if statistically significant):

- 463 (a) $n = -65.6 + 0.035 Y$ ($r = 0.39$, $n = 40$, $p = 0.01$);
464 (b) (solid points) $n = -93 + 0.047 Y$ ($r = 0.92$, $n = 40$, $p < 0.0001$),
465 (open points) $n = -6.6 + 0.003 y$ ($r = 0.52$, $n = 40$, $p < 0.001$);
466 (c) (solid points) $n = -89.7 + 0.046 y$ ($r = 0.89$, $n = 40$, $p < 0.0001$)
467 (open points) $n = 19.3 - 0.0095 Y$ ($r = 0.68$, $n = 40$, $p < 0.0001$)
468 (d) $n = 12.7 - 0.001 y$ ($r = -0.02$, $n = 40$, $p = 0.9$).

469

470 Fig. 5. Numbers of sampling sites (among a total of 15) where at least 1 specimen was found in
471 the samples taken in late-winter/early spring in the indicated year of 4 newly- introduced
472 species. (a) (solid squares) *Ensis directus* and (open circles) *Hemigrapsus takanoi*; (b) (solid
473 squares) *Marenzelleria viridis* and (open circles) *Crassostrea gigas*.

474

475 Table 1. Summary of contributions by various groups of species to long-term (1970-2009)
 476 changes in macrozoobenthic species richness on Balgzand, expressed in (changes of) mean
 477 number of species per site (n, per 0.95 m²). N is number of species allotted to each group.

N	Group	n	species	
4	non-indigenous invaders	+ ~1.5 (Fig. 4b)	see Fig. 5	
5	local invaders	+ ~0.2 (Fig. 4b)	<i>Crep, Gly, Lep, Ech, Oph*</i>	
10	winter-sensitive	+ ~ 1.8 (Fig. 4a)	see Fig. 2	
6	up-ward trend	+ ~2.0 (Fig. 4c)	<i>Lit, Ner spp., Ete, Uro, Gam, Bal**</i>	
2	down-ward trend	- ~0.4 (Fig. 4c)	<i>Mag, Scolel***</i>	
15	no trend, common	~0 (Fig. 4d)	note-1	
9	no trend, rare	~0	(Fig. 4d)	note-2
50	all	+ ~5.1		
Total (see Fig. 1b)	+ 5.2			

478

479 **Crepidula fornicata, Glycera alba, Lepidochiton cinerea, Echinocardium cordatum, Ophiura*
 480 *ophiura.*

481 ***Littorina littorea, Nereis spp. (mostly Alitta succinea), Eteone spp., Urothoe poseidonis,*
 482 *Gammarus locusta, Balanoids (Balanus crenatus, Semibalanus balanoides, Austrominius*
 483 *modestus).*

484 ****Magelona johnstoni, Scolelepis foliosa.*

485 Note-1: *Macoma balthica*, *Mya arenaria*, *Mytilus edulis*, *Scrobicularia plana*, *Hydrobia ulvae*,
486 *Retusa obtusa*, *Phyllodoce* sp. (mostly *Ph. mucosa*), *Arenicola marina*, *Bylgides sarsi*,
487 *Heteromastus filiformis*, *Hediste diversicolor*, *Scoloplos armiger*, *Bathyporeia* sp., *Corophium* sp.,
488 Anthozoa (mostly *Metridium senile* and *Sagartia troglodytes*).

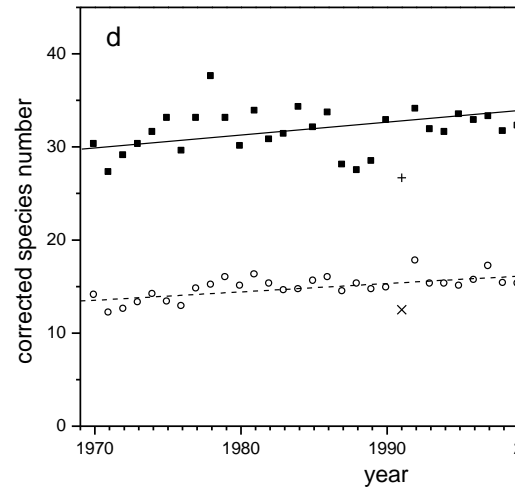
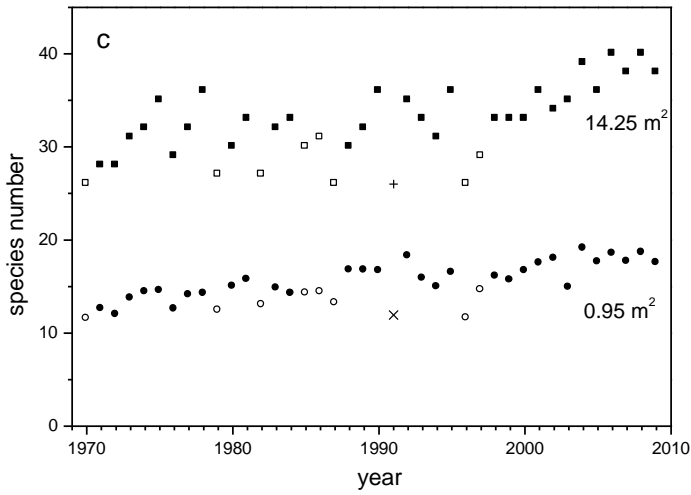
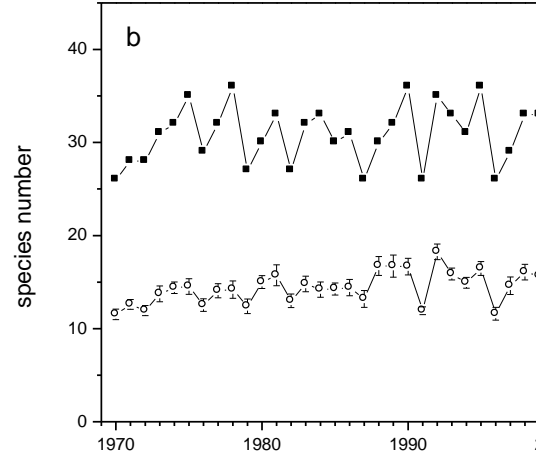
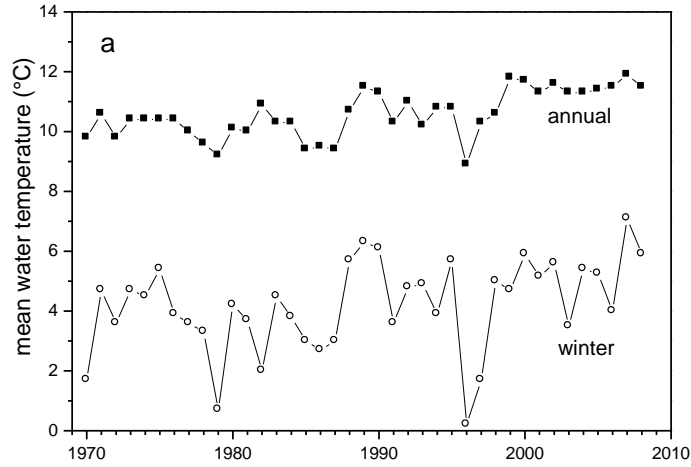
489 Note-2: *Abra alba*, *Petricola pholadiformis*, *Spisula subtruncata*, *Tellina (Angulus) fabula*,
490 *Littorina obtusata*, *Crepidula fornicata*, *Pectinaria koreni*, *Neomysis / Praunus* sp., *Asterias*
491 *rubens*.

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Figure 1



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Figure 2

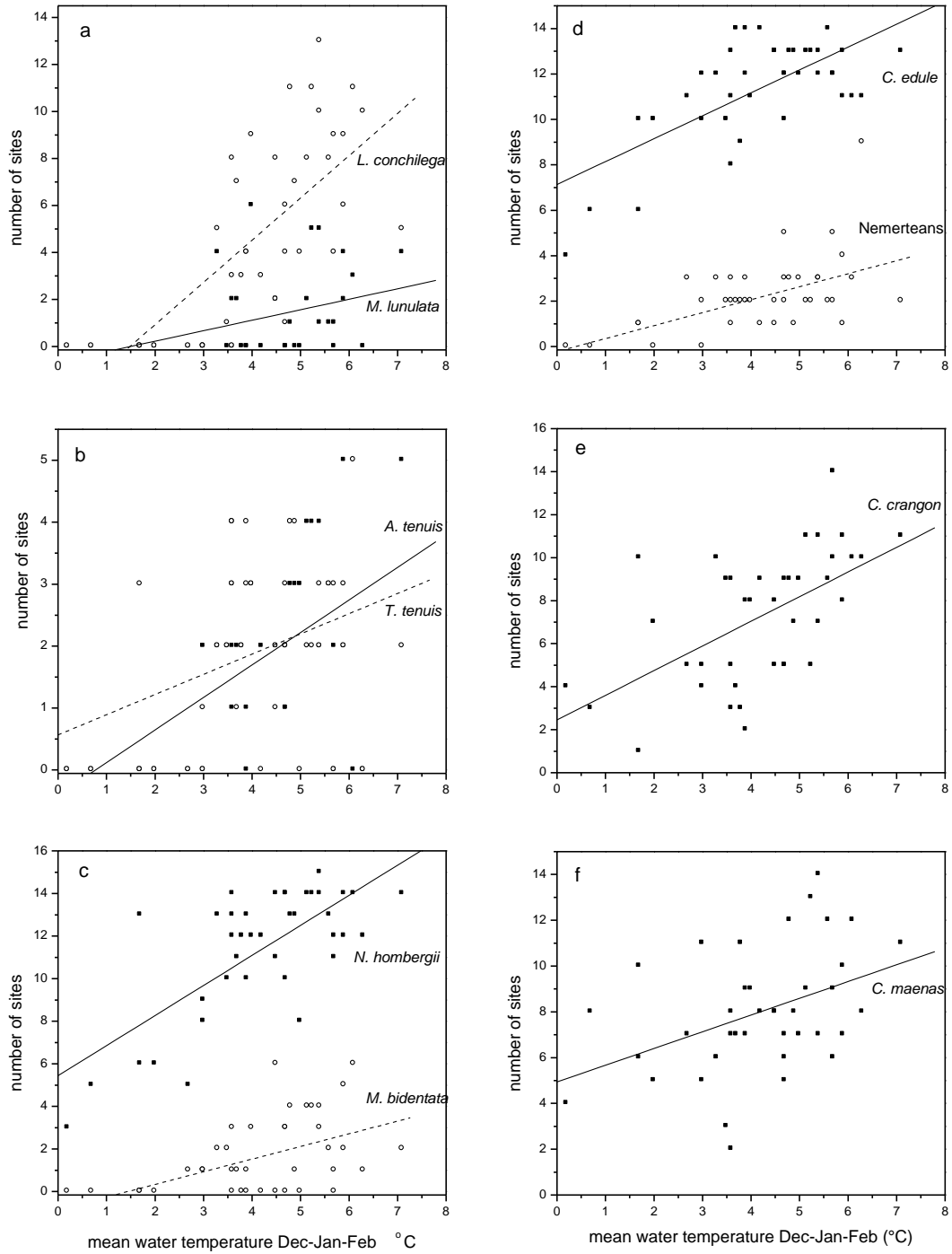
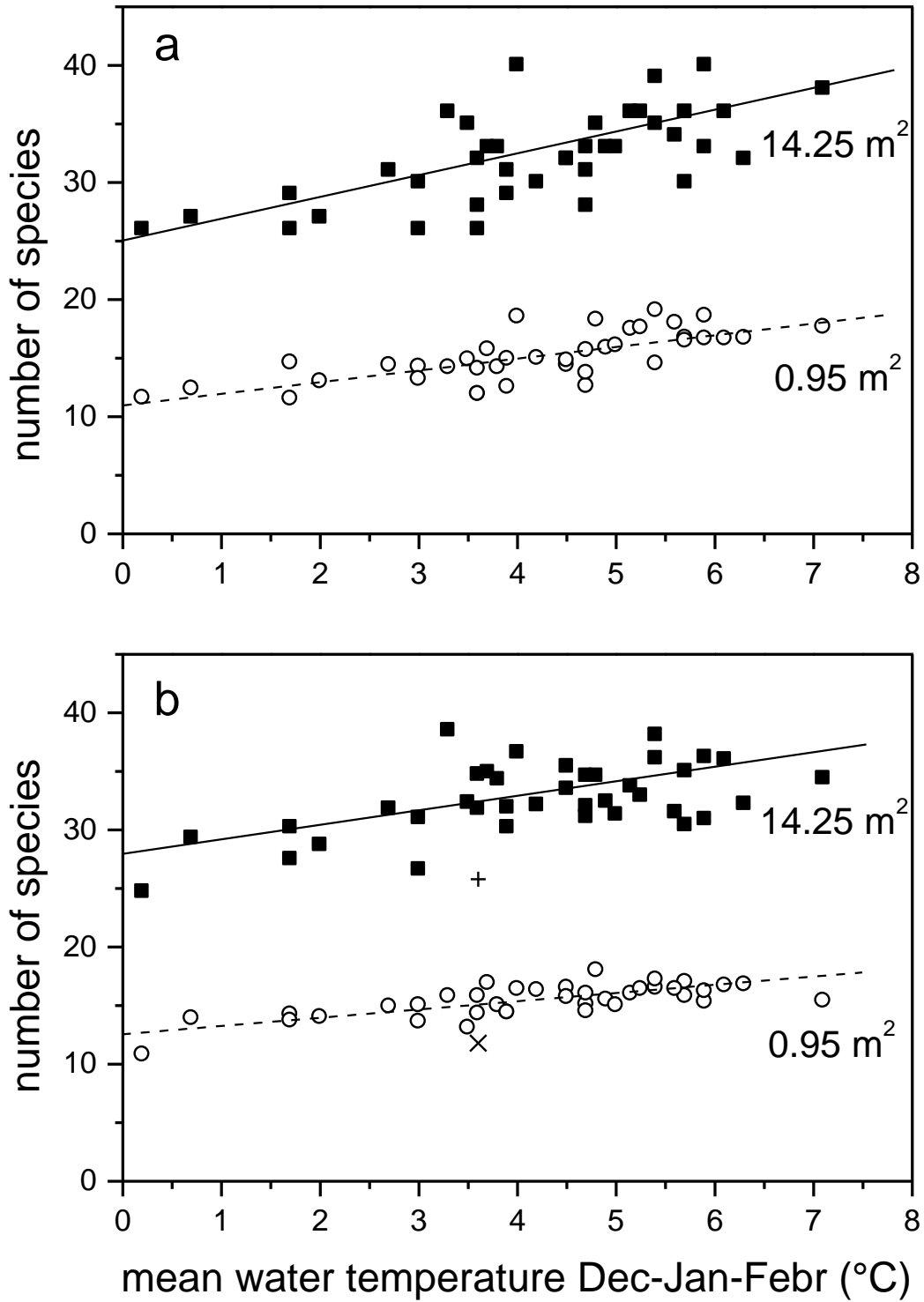


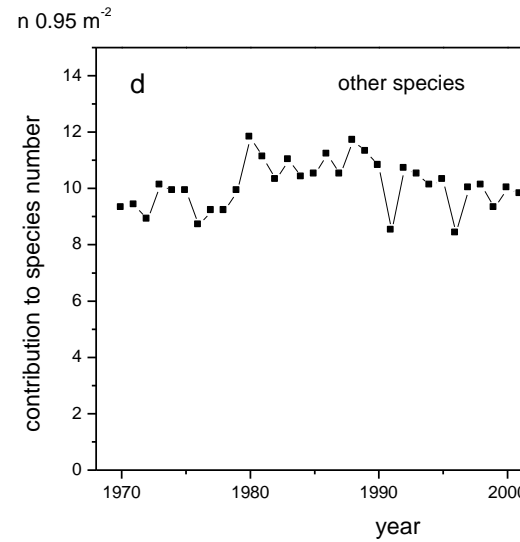
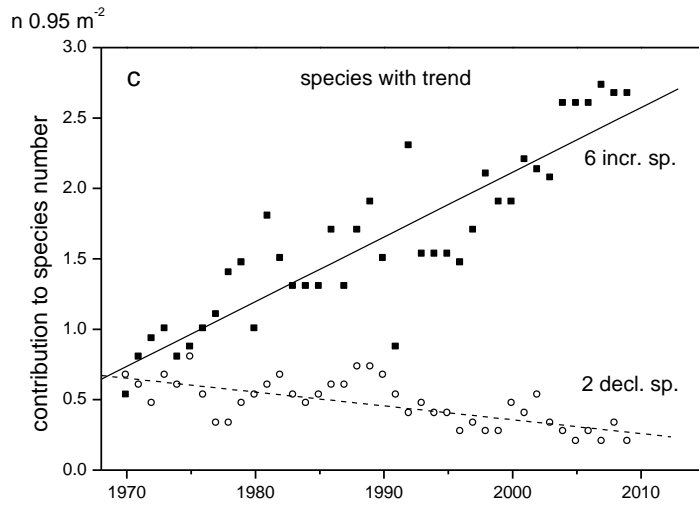
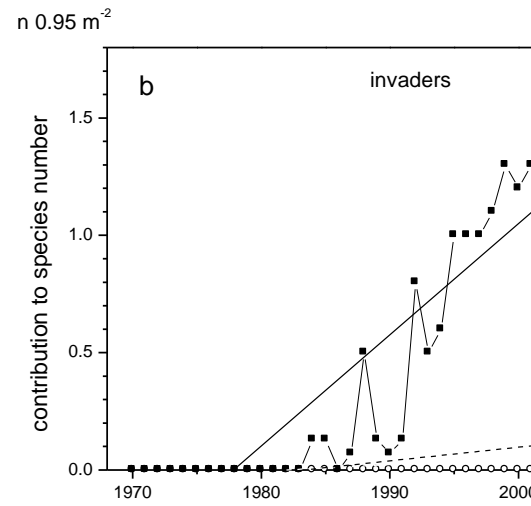
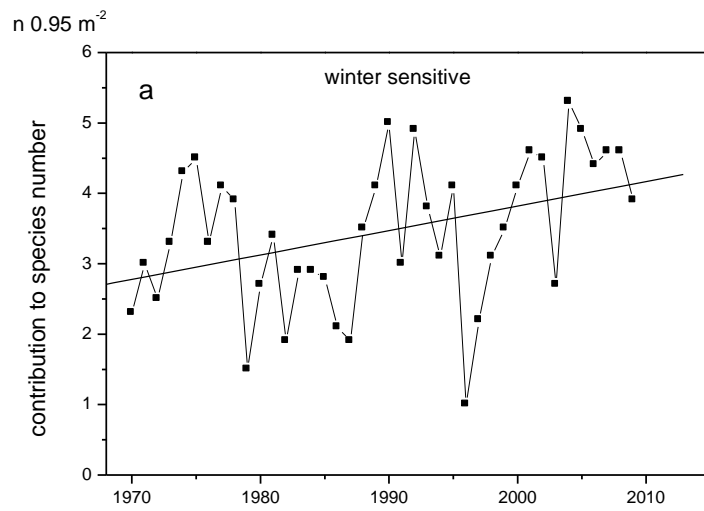
Figure 3



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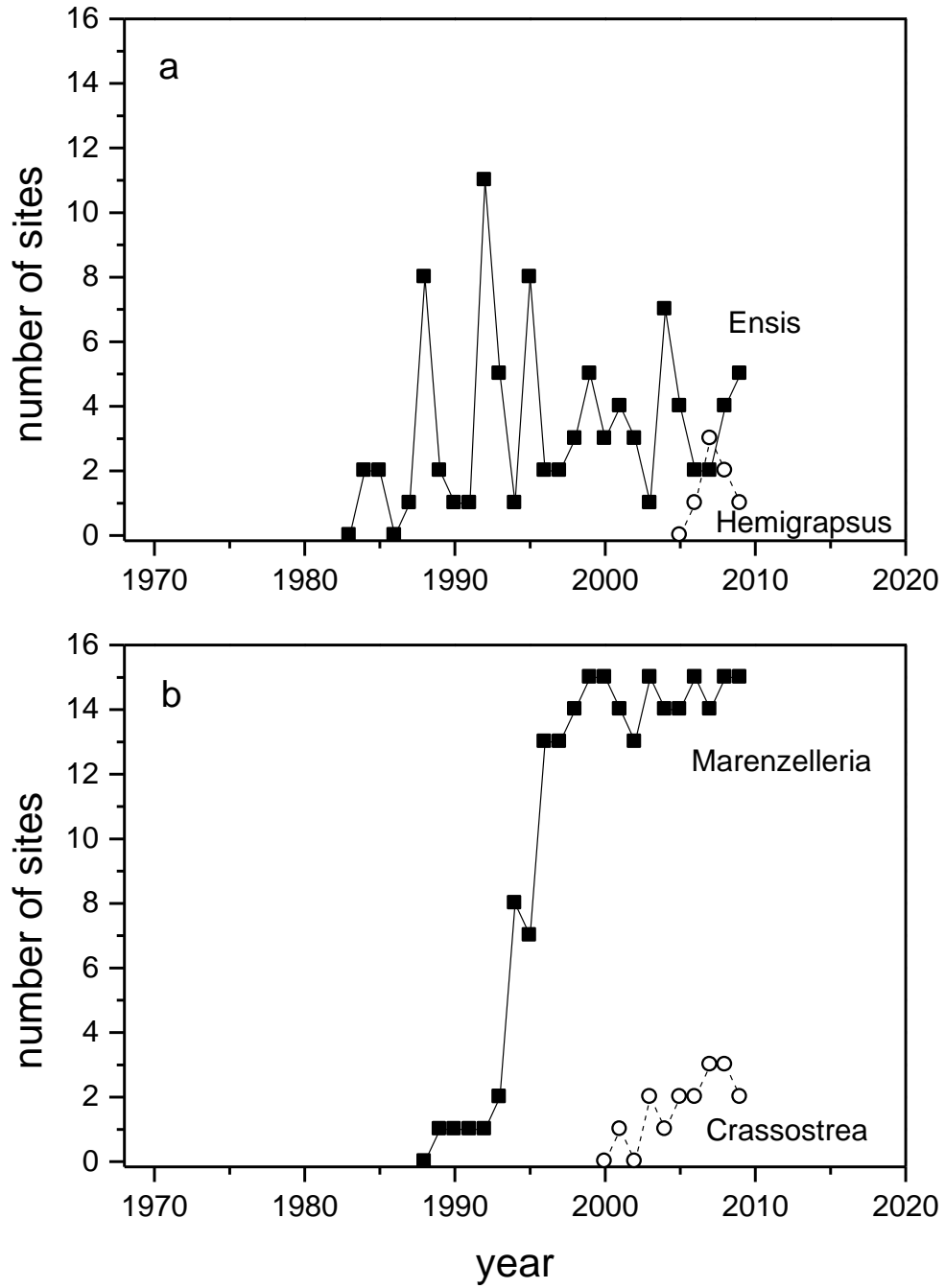
Figure 4



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Figure 5



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