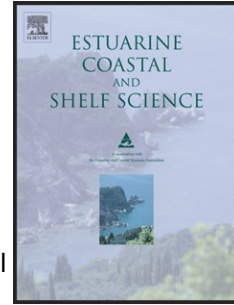


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1 **Long-term changes in the production by estuarine macrobenthos affected by multiple**
2 **stressors**

3
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11
12 **Abstract** The macrobenthic production of an estuarine system was evaluated over a 14-year
13 study period in a seagrass bed and in a sandflat. Over this period, the estuary suffered severe
14 eutrophication and extreme weather events with important impacts on the community,
15 impairing system functioning and ultimately the goods and services provided by the estuary
16 (decline in the seagrass bed, decreased community production and/or a boost in the
17 production by opportunist species, such as *Hydrobia ulvae*). Following the anthropogenic
18 impacts, management measures were introduced which allowed a gradual recovery of the
19 seagrass bed and a new macrobenthic community structure manifested by production
20 increases of slow-growing species, such as *Scrobicularia plana* and *Hediste diversicolor*.
21 There was a gradual re-orientation of energy into population biomass instead of population
22 density but this was not translated into higher community production, mainly due to the
23 decreased production of opportunist species (*H. ulvae* and several polychaetes). Several
24 weather extreme events occurred during this post-mitigation phase - floods, heatwaves and
25 droughts, all of which had negative impacts on macrobenthic dynamics and production. The

26 heatwaves led to the greatest decreases in macrobenthic production, mainly due to *S. plana*
27 perhaps associated with its physiological intolerance of higher temperatures. The prolonged
28 drought that followed the heatwaves maintained low levels of production by *S. plana* and *H.*
29 *ulvae*. With climate change, the frequency and intensity of extreme weather events are likely
30 to increase worldwide so that the recovery of impacted/disturbed systems from impacts such
31 as eutrophication may be seriously affected by these additional stressors, compromising
32 attempts to improve the ecological quality of estuarine ecosystems.

33

34 **Keywords:** Macrobenthos production, estuary, eutrophication, climate extremes, recovery

35

36 1. Introduction

37 Estuaries provide many goods and services which are essential to society and a balance
38 needs to be struck between human usage and the sustainable use and conservation of these
39 systems. This is recognised and acknowledged in much of the legislation produced to protect
40 and promote the recovery of transitional and coastal areas worldwide (Airoldi and Beck,
41 2007; Borja and Dauer, 2008). Assessing ecological processes and resources in terms of the
42 goods and services that they provide is attractive to, and resonates with, policy makers and
43 non-scientists (Beaumont et al., 2007; Pinto et al., 2010) and one dimension of this is
44 secondary production which is often a direct measure of food provision delivered by an
45 ecosystem, and which has clear social-economic meaning, especially when a monetary value
46 is attached (Costanza et al., 1997; Pinto et al., 2010). Production is also a measure of
47 ecosystem function and may reveal greater insights into ecosystem change than static
48 parameters such as diversity, density or biomass. Combining production with long-term
49 datasets will increase our level of understating of system functioning (see for instance,
50 Dolbeth et al., 2007; Pranovi et al., 2008). Environmental impacts on the biota, and hence of

51 the goods and services they underpin, may only be revealed with long-term data series (Boero
52 et al., 2009) and in this period of widespread and rapid global change, it is important to
53 document ecosystems before further changes occur. Thus, the present study documents
54 changes in a well-documented estuarine system, the Mondego estuary, Portugal, over a 14-
55 year period, with a particular focus on macrobenthic community production and seagrass bed
56 dynamics, building on previous studies by Dolbeth et al. (2007) which described some of the
57 changes in the macrobenthic assemblages in relation to various stressors that led to an overall
58 decline in environmental quality. Following this, management measures were implemented to
59 promote recovery of the system although these have been hampered by subsequent extreme
60 climate events. The present study extends that work, adding more data to the long-term series
61 to evaluate other important events: 1) the success of the seagrass beds recovery, following the
62 implementation of management measures in the estuary, and its implications for overall
63 estuarine integrity, and 2) the impact of climatic extremes, such as floods, heatwaves and
64 droughts.

65

66 **2. Materials and Methods**

67 **2.1 Study area**

68 The Mondego estuary, in a warm temperate region on the Atlantic coast of Portugal
69 (40°08'N, 8°50'S), is a small estuary of 8.6 km², comprising two arms, north and south,
70 separated by an island. The north arm is deeper (4-8 m during high tide, tidal range 1-3 m),
71 highly hydrodynamic, is a main navigation channel and hosts the Figueira da Foz harbour.
72 The south arm is shallower (2-4 m during high tide, tidal range 1-3 m) and is characterized by
73 large areas of exposed intertidal flats during low tide. Several human activities led to an
74 ongoing process of eutrophication since the end of the 1980's, mainly in the south arm. The
75 downstream areas of the south arm support *Spartina maritima* marshes and a *Zostera noltii*

76 (seagrass) bed. In the upstream area, the seagrass community has completely disappeared and
77 blooms of the opportunistic macroalga *Ulva* spp. were common. Until the end of 1998, this
78 part of the estuary was almost silted up, with water circulation mainly dependent on tides and
79 on the freshwater input from the Pranto river (Fig. 1), artificially controlled by a sluice
80 according to rice field irrigation needs in the lower Mondego valley (Dolbeth et al., 2007;
81 Cardoso et al., 2008a).

82 The south arm is recently and gradually recovering from the effects of eutrophication after
83 the implementation of mitigation measures in 1998. These improved water transparency and
84 decreased nutrient loading (Lillebø et al., 2005; Cardoso et al., 2010). The measures included:
85 1) the re-establishment of the south arm riverhead connection, improving freshwater
86 circulation; 2) nutrient loading reduction, essentially ammonium (Lillebø et al., 2005;
87 Cardoso et al., 2010); 3) seagrass bed protection from human disturbance; 4) public education
88 of the ecological importance of intertidal vegetation for the health and related socio-economic
89 activities of the estuary.

90

91 **2.2 Sampling and biological material processing**

92 Samples were taken from 1993 to 2006 during low tide in two areas (Fig. 1): 1) the *Zostera*
93 area, characterized by muddy sediments covered with *Zostera noltii*, higher organic matter
94 content (mean $6.2\% \pm 1.76$) and higher water velocity ($1.2 - 1.4 \text{ m s}^{-1}$); 2) a sandflat area,
95 characterized by sandy sediments, which has not supported rooted macrophytes for more than
96 20 years, has a lower organic matter content (mean $3.0\% \pm 1.14$), lower water flows ($0.8 - 1.2$
97 m s^{-1}) and was seasonally covered by green opportunist macroalgae.

98 On each sampling occasion and at each site, ten (during the first 18 months) to six
99 sediment cores (141 cm^2 core sectional area) were taken randomly to a depth of 20 cm by
100 using a manual corer. Samples were collected in the morning, during low tide, fortnightly for

101 the first 18 months and monthly thereafter. Each sample was sieved through a 500 μm mesh
 102 using estuarine water, the organisms retained identified to the species level, counted and
 103 measured. Plant material was sorted and separated into green macroalgae and *Zostera noltii*.
 104 For both faunal and plant material the ash-free dry weight (AFDW) was estimated after
 105 combustion for 8 h at 450°C (shells of molluscs included). Additionally, temperature, oxygen,
 106 pH and salinity were measured in situ in intertidal pools, and water samples were collected to
 107 determine nutrient content (for further details see Cardoso et al., 2010).

108

109 **2.3 Secondary production**

110 Secondary production was estimated by the increment summation method after definition
 111 of cohorts through size–frequency distribution analysis of successive sampling dates (after
 112 Ferreira et al., 2007; Cardoso et al., 2008b and Grilo et al., 2009) for the dominant species in
 113 the estuary: *Hydrobia ulvae* (Gastropoda), *Cyathura carinata* (Isopoda), *Ampithoe valida*, and
 114 *Melita palmata* (Amphipoda), according to:

$$115 \quad P_{cn} = \sum_{t=0}^{T-1} \left(\frac{N_t + N_{t+1}}{2} \right) \times (\bar{w}_{t+1} - \bar{w}_t) \quad \text{equation 1}$$

116 where P_{cn} is the growth production of cohort n; N is the density (ind m^{-2}); \bar{w} is the mean
 117 individual weight (g WW m^{-2}); and t and $t+1$, consecutive sampling dates. Population
 118 production estimates correspond to the sum of P_{cn} (each cohort production).

119 Brey's (2001) method, version 4-04 (worksheet for model computation provided in Brey
 120 2001, <http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.htm>.)
 121 was used as an alternative empirical method for secondary production estimation (after
 122 Dolbeth et al., 2005) for other abundant species - *Carcinus maenas* (Decapoda), *Alkmaria*
 123 *romijni*, *Capitella capitata*, *Chaetomatus setosa*, *Hediste diversicolor*, *Heteromastus*
 124 *filiformis*, *Streblospio shrubsolii* (Polychaeta), *Tubificoides* sp., Oligochete sp. (Oligochaeta),
 125 *Cerastoderma edule*, *Scrobicularia plana* (Bivalvia), *Haminoea hydatis*, *Littorina littorea*

126 (Gastropoda), Dipteran larvae (Insecta). The weight-to-energy ratios needed for the
127 application of the empirical method are also provided in Brey (2001). For those species with
128 lower densities and biomasses, production was estimated by summing the increases in
129 biomasses from one sampling date to the other, using the cohort increment summation
130 equation, but without following the cohorts.

131 Mean biomass and P/\bar{B} ratios (annual production divided by the annual mean biomass)
132 were also computed for the main species.

133

134 **2.4 Data analysis**

135 The production distribution within the macrobenthic community at both areas and in
136 different years was explored using ANOSIM (from PRIMER routines), with regard to spatial
137 (*Zostera* and sandflat areas) and temporal (14 years) differences. Similarities in the
138 production data were calculated as the Bray-Curtis coefficient after square-root-
139 transformation of the raw data to scale down the scores of the very productive species (Clarke
140 and Warwick, 2001). Non-metric Multidimensional Scaling (nm-MDS) was performed
141 subsequently. For each group identified by the ANOSIM, the Similarity Percentages-species
142 contributions (SIMPER) was used to determine which species' production contributed most to
143 the differences found among groups.

144 For each area, the relationship between the species production identified with SIMPER and
145 environmental variables were explored using CANOCO v 4.5 software. Initially, a detrended
146 correspondence analysis (DCA) was performed with the biotic data (species production) to
147 evaluate the type of model response. Since a linear response was detected, a redundancy
148 analysis (RDA) was applied to examine the relationships between biotic and abiotic
149 parameters. Prior to the analyses, the species production data were square root transformed, in
150 order to scale down the scores of the very productive species. Several environmental variables

151 were analysed and their significance evaluated with the forward selection procedure (Monte
152 Carlo permutation tests) after checking for and removing the collinearity.

153 Precipitation and freshwater inflow values were acquired from the Portuguese Water
154 Institute, INAG (www.snirh.inag.pt) and the Portuguese Weather Institute, IM
155 (www.meteo.pt).

156

157 **3. Results**

158 **3.1 Anthropogenic impacts on macrophyte and macroalgal dynamics**

159 At the beginning of the study period the major impacts in the estuary were anthropogenic,
160 mainly eutrophication, which indirectly decreased the biomass and spatial extension of
161 *Zostera noltii* (Fig. 1, 2A) as well as macroalgal (*Ulva* spp) blooms (Fig. 2B) (Cardoso et al.
162 2008a, 2010; Dolbeth et al., 2007). Changes in nutrient dynamics are discussed with more
163 detail in Cardoso et al. (2010). Seagrass biomass showed a significant decline over the pre-
164 mitigation period, from 1993 to 1997 (Fig. 2A, $R^2 = 0.89$). In the post-mitigation period, the
165 seagrass biomass started to increase gradually until extreme weather events occurred,
166 described in more detail below. An increase occurred from 1999 until July 2002 (Fig. 2A, R^2
167 $= 0.56$), with significant differences between the post-mitigation and the pre-mitigation period
168 (Wilcoxon two sample test, $W = 4041$, $p < 0.05$), declining again late 2002/early 2003,
169 followed by a subsequent gradual increase to July 2006 (Fig. 2A, $R^2 = 0.33$).

170 In the eutrophic area, there was a spring macroalgal bloom in 1993 (maximum biomass of
171 $415 \text{ g AFDW m}^{-2} / 508 \text{ g DW m}^{-2}$ in April 1993), followed by a crash in early summer (Fig.
172 2B), reported by Leston et al. (2008). In 1995, macroalgal biomass again reached high values,
173 but not sufficient to be considered a spring bloom (maximum biomass of $111 \text{ g AFDW m}^{-2} /$
174 $142 \text{ g AFDW m}^{-2}$ in April 1995). Macroalgal blooms in the eutrophic area were present
175 throughout the pre-mitigation period, particularly during dry years, but blooms were never

176 recorded after the post-mitigation measures were implemented (Fig. 2B) (Wilcoxon two
177 sample test, $W = 3138$, $p < 0.05$).

178

179 **3.2 Climate**

180 Over the study period, several unusual weather phenomena related to atmospheric
181 temperature and precipitation occurred, compared to the climatic normal of 1971-2000 (Fig.
182 2C, D). A climatic normal is the mean value of a climate element over a prescribed 30-year
183 interval. This interval, defined by the World Meteorological Organization (WMO), is
184 sufficiently long to filter out short-term inter-annual fluctuations and anomalies, but short
185 enough to reflect long-term climatic trends (IM - Portuguese Weather Institute). From 1999
186 onwards, after the introduction of management measures, several climate extremes occurred
187 which became the major impacts acting on the estuary.

188 Air temperature variation was typical of temperate systems, with increasing values in the
189 spring (March-June), reaching highest values in the summer (July-September) and lowest
190 values in the winter (December-February) (Fig. 2C). Mean monthly values were within those
191 of the 1971-2000 mean (range between maximum and minimum means). In the spring and
192 summer of 2003 and 2005, higher mean monthly temperatures were recorded (Fig. 2C) when
193 the maximum temperature was above 40°C on several occasions. In fact, in most of the
194 Portuguese territory, one heatwave was recorded in July-August (lasting for 16-17 days) in
195 2003, two in June 2005 (lasting for 8 to 12 days), and three in June, July and August 2006
196 (lasting for 6 to 7 days). A heatwave occurs when the maximum air temperature increases by
197 5°C relative to the mean daily value of the reference period (in this case the climatic normal
198 1971-2000), for at least 6 consecutive days (IM - Portuguese Weather Institute). The
199 heatwaves did not extend to the Mondego estuary, but translated into much higher
200 temperatures in that period (IM - Portuguese Weather Institute).

1993/94 and 1995/96 were considered atypical with respect to rainfall (IM), with high precipitation mainly in autumn 1993 and winter 1996. This translated into higher runoff to the estuary in those periods (Fig. 2D). In 2000/01, there was an unprecedented flood caused by heavy winter precipitation that resulted in high runoff (Fig. 2D) and which was considered the major flood of the last century (IM). During the floods, salinity decreased considerably to around 5 or less. In contrast, in 2004 and 2005 extremely lower rainfall was recorded compared to the 1971-2000 mean, and these years were considered dry and extremely dry, respectively (Fig. 2D). The lowest annual precipitation was observed in 2005 (486.1 mm against 905.1 mm for 1971-2000 mean), with below-mean precipitation periods quite evident practically during all the year from January until September 2005 (Fig. 2D). 2005 was considered the driest in the last 60 years (IM). Consequently, freshwater runoff from the Mondego river basin was severely reduced in both 2004 and 2005, with values considerably lower (on average 1/3 lower) than those observed over the rest of the study period (Fig. 2D).

3.3 Macrobenthic production

Macrobenthic production in the sandy flat and the seagrass bed was divided into 3 periods based on the anthropogenic and climate events described above: a) the period before the mitigation measures were implemented (1993 to 1996), together with the decline of the *Z. noltii* – henceforth termed PRE; b) the period after the mitigation measures were put in place until the occurrence of the large flood in 2002, the first recovery phase (1999-2002) – henceforth termed POST 1; and c) the period after the large flood, with the occurrence of several drought and heatwaves events, considered a second recovery phase (2003 – 2006) – henceforth called POST 2 (Fig. 3).

3.3.1 Seagrass vs sand flat macrobenthic production

226 Secondary production was in general higher in the *Zostera* bed than in the sandflat area
227 (Fig. 4A, B), and these differences were significant (ANOSIM, $R = 0.886$, $p = 0.001$), with
228 the species responsible for that production clearly separated in the MDS plot (Fig. 5).
229 Relatively few species were responsible for more than 97% of the whole community
230 production in both areas, although the dominant species differed in the two areas (Table 1).
231 Of the 75 species recorded over the whole study period, only 13 were associated with the
232 production of the *Zostera* bed macrobenthos (Table 1), and 8 for the sandflat area (Table 1).
233 Even so, the major contributor to the annual production of the *Zostera* bed (and to the
234 differences found between areas) was the gastropod *Hydrobia ulvae*, accounting for more
235 than 57% of the total production (Table 1). Other relevant taxa with higher production in the
236 *Zostera* bed were *Melita palmata*, *Cerastoderma edule*, *Carcinus maenas*, *Littorina littorea*,
237 *Tubificoides* sp., *Hediste diversicolor* and *Heteromastus filiformis* (Table 1). In the sandflat
238 area, *H. ulvae* was also an important species, but a higher percentage of the production was
239 accounted for by the isopod *Cyathura carinata* and the bivalve *Scrobicularia plana* (Table 1).
240 The small polychaetes *Alkmaria romijni* and *Streblospio shrubsolii* attained higher production
241 levels in the sandflat area (Table 1). The mean P/\bar{B} ratios over the study period were
242 generally higher for species inhabiting the sandflat area (Table 1). More than half of the
243 community production was due to detritivores (Table 1). In the seagrass bed, grazers also
244 contributed a high proportion of the production, mostly due to the *H. ulvae*, while in the
245 sandflat area omnivores made up a higher proportion (Table 1).

246 Since *H. ulvae* was a highly dominating species, especially in the *Zostera* bed, production
247 was also estimated without this species, resulting in higher annual production of the
248 remaining species in the sandflat area over the study period (Fig. 4C, D).

249

250 3.3.2 Temporal differences in macrobentic production

251 There was a decline in production in the *Zostera* bed through time, while production was
252 more consistent in the sandflat area (Fig. 4A, B) although no significant differences were
253 found between the recovery phases in the *Zostera* bed (ANOSIM pairwise tests grouped
254 POST 1 and POST 2, $p > 0.05$) although these were separated from the pre-mitigation (PRE)
255 production values ($p = 0.029$) (Fig. 5). This discrimination is largely due to *H. ulvae* in the
256 pre-mitigation period, whereas after the mitigation measures were put in place this species
257 declined considerably and *S. plana* and *H. diversicolor* increased (Table 1). Also, *C. edule*
258 and *L. littorea* had considerably higher production in the pre-mitigation period than in the
259 whole post-mitigation period (Table 1).

260 With respect to the sandflat area, the production in PRE and POST 2 was similar
261 (ANOSIM pairwise tests, $p > 0.05$) but different from that in POST 1 ($p = 0.029$), related to
262 the large increase in *S. plana* (Table 1). However, MDS did not clearly group these temporal
263 differences suggesting that other groupings might exist than those defined *a priori* (Table 1).
264 The production during 1993 was clearly different from all the following years (Fig. 5).
265 Differences between the samples include the marked decline in *H. ulvae* and *A. rominji*
266 production within the study period, and the gradual increase of *H. diversicolor* production
267 (Table 1).

268 There was much higher variability in production from year to year within the *Zostera* bed,
269 and in the POST 2 period more consistent production values occurred (Fig. 4A). In the
270 sandflat, similar production values were obtained over the whole post-mitigation period,
271 while these were also more variable in the pre-mitigation period (Fig. 4B).

272 When *H. ulvae* is excluded from the analysis, there are similar production values over the
273 entire period in the *Zostera* bed (Fig. 4C); clearly, *H. ulvae* is responsible for the high
274 variability observed (see also Table 1). In the sandflat area production of the remaining

275 community tended to increase after the mitigation measures were put in place, though there
276 was a slight decrease in the 2nd recovery phase from 2003 onwards (Fig. 4B).

277

278 **3.4 Macrobenthic production and environmental variables**

279 Initially, 14 or 15 environmental variables were explored within the RDA: mean dissolved
280 oxygen, water temperature, salinity, pH, organic matter, total nitrogen, N/P ratio, atmospheric
281 temperature (mean, maximum absolute value registered in the whole year and year range
282 between minimum and maximum values), total precipitation, runoff, mean *Z. noltii* (only in
283 the *Zostera* bed) and *Ulva* spp. biomass. These variables were first checked for co-linearity
284 (using draftsman plot and variation inflation factors) and if appropriate removed from the
285 forward selection procedure describe in the Methods section. A second analysis was
286 performed only with the significant variables (Fig. 6).

287 In the *Zostera* bed, only the *Z. noltii* annual mean biomass and silica concentration were
288 statistically significant ($p < 0.05$), with the resulting constraint ordination explaining 60% of
289 the variability in the data. Samples from the pre-mitigation period (1993-1995) and those
290 from 2005 had higher similarities, being associated with higher *Z. noltii* biomass and with *C.*
291 *edule*, *L. littorea*, *M. palmata*, *H. filiformis* and *C. maenas* (Fig. 6A). The main species
292 responsible for the high annual production values in 1994 and 2002 were *H. ulvae* and the
293 small polychaetes *A. romijni* and *S. shrubsoli*. The long-lived species *S. plana*, and *H.*
294 *diversicolor*, as well as Diptera larvae and *C. carinata* were associated with the post-
295 mitigation samples and with higher silica content in the intertidal pools (Fig. 6A).

296 In the sandflat area, only *Ulva* spp. annual mean biomass and pH were statistically
297 significant, with the resulting constraint ordination explaining 64% of the variability. 1993
298 was clearly differentiated from the remaining samples (Fig. 6B), confirming MDS results
299 (Fig. 5). 1993 had the highest macroalgal biomass, with which *H. ulvae*, *C. edule* and the

300 small polychaetes *H. filiformis* and *A. romijni* were associated (Fig. 6B); the last two species
301 had the highest P/\bar{B} ratios (Table 1). After the bloom in 1993 and associated with higher pH
302 values (within the range 8.4-9.0), *C. carinata* attained the highest production values (1994-
303 1996). This production was also associated with the post-mitigation period, but only with
304 2005 and 2006. For the remaining post-mitigation period, *S. plana*, *H. diversicolor* and *S.*
305 *shrubsolii* co-occur having higher production values from 1999 to 2004 (Fig. 6B).

306

307 **Discussion**

308 **Spatial comparisons**

309 In the past, the seagrass bed and the sand flat areas have responded quite differently with
310 regard to eutrophication impacts and these changes have been described in detail elsewhere
311 (Cardoso et al., 2008a, b; Dolbeth et al., 2007; Leston et al., 2008, see also Introduction).
312 Today, these areas are distinct habitats: one being seagrass-dominated and the other being a
313 bare sandy flat, although it previously supported seagrass, and now small patches are starting
314 to re-appear. It seems, therefore, that the management measures imposed new dynamics on
315 the system and have been at least partially effective: 1) nutrient loading was reduced (Cardoso
316 et al., 2010) although nitrogen loads are still considered high (Baeta et al., 2009); 2)
317 macroalgal blooms were controlled; 3) seagrass is gradually increasing, at least in spatial
318 extent, but biomass remains much lower than in 1993 especially compared to the most recent
319 years.

320 The benefits of seagrass beds for both invertebrates and fish are well known, with habitat
321 heterogeneity, shelter and higher food resources all important in this respect (Duarte, 2002;
322 Blanchet et al., 2004; Baeta et al., 2009). In the present study, higher production levels were
323 observed in the seagrass bed, as also reported in other transitional ecosystems (Sprung, 1994;
324 Heck et al., 1995), and there were generally higher levels of diversity (Dolbeth et al., 2007;

325 Cardoso et al., 2010). Closer inspection of the production dynamics of this habitat showed
326 that the greater part was due to *Hydrobia ulvae*, similar to other studies where this species
327 dominates seagrass areas (Asmus and Asmus, 1985; Blanchet et al., 2004). The production of
328 the community with *H. ulvae* production excluded was higher in the sandflat area, especially
329 in the post-management period. In the Mondego estuary, *H. ulvae* production has been
330 considerably boosted after disturbance events, turning the production dynamics more erratic
331 in the *Zostera* bed. Thus, production increased in the years that followed the bloom and the
332 flood (1994 and 2002 respectively, more detail in Dolbeth et al., 2007), but decreased after
333 the heatwaves and drought, showing that benthic responses can vary significantly depending
334 on the frequency and intensity of disturbance (Whomersley et al., 2010). Although benthic
335 community production was higher in the seagrass area, the dominance of *H. ulvae* could
336 compromise its resilience to disturbance, following the idea that higher functional diversity
337 would increase resilience (Peterson et al., 1998; Wardwell et al., 2008).

338 When *H. ulvae* is excluded, the mean annual production for the 14-year period was much
339 less variable, although different species were responsible at different times. *Z. noltii* biomass
340 was one of the major components influencing the overall macrobenthic production, and
341 several amphipods and the molluscs *C. edule* and *L. littorea* had higher production in the pre-
342 mitigation period. Although *Z. noltii* seems to be recovering in recent years, the species
343 contributing to production have changed, with an increase of *S. plana* and *H. diversicolor*
344 production in the post-mitigation period and a gradual decrease of *H. ulvae* production
345 dominance. In this period, silica has increased, probably related to changes in
346 microphytobenthos communities (diatoms) (Laruelle et al., 2009), an important component of
347 the diet of these species (Baeta et al., 2009, personal communication). A new community
348 structure is becoming evident in the *Zostera* area, with a gradual increase of slow-growing
349 species and omnivore species contributing to production. Nevertheless, these community

350 changes did not lead to an overall increase in community production, mostly because of the
351 decline in *H. ulvae*.

352 In the sandflat area, the presence of macroalgae was an important determinant for the
353 production; the highest annual production occurred in 1993, when there was a bloom. Small
354 body size species, with high turnover ratios, such as *H. ulvae*, *A. rominji* and *H. filiformis*,
355 were associated with the algae, reflecting their opportunistic behaviour. Historically, the
356 sandflat area is eutrophic, implying that diversity and production have yet to recover to pre-
357 eutrophic levels, when the sandflat area is presumed to have had seagrass. Despite this, when
358 the production contribution of *H. ulvae* is excluded, production is still higher, mostly due to
359 *Cyathura carinata* and *S. plana*. Higher production levels of *C. carinata* seemed to be
360 associated with years that have higher mean annual pH, but this was not significant. After the
361 mitigation measures were put in place, production of slow growing species like *S. plana*
362 increased considerably, together with a gradual increase in *H. diversicolor*, whilst *H. ulvae*
363 declined. This trend was continued throughout the recovery period, perhaps suggesting that
364 the sandflat area might have reached a new stable state.

365 Estuaries are characterized by relatively few species with abundant populations that can
366 attain high production levels in natural conditions, making it difficult to dissociate
367 anthropogenic from natural stress, the estuarine quality paradox of Elliott and Quintino
368 (2007). Overall, production was distributed more evenly in the sandflat area across three or
369 four species, while in the seagrass bed more than 60% of the production was due to a single
370 species. From 2003 onwards, production was more evenly distributed among three species.
371 For both areas, there was a higher investment in individual body mass, instead of growth,
372 consistent with a shift from r-strategists to K-strategists following management, as also
373 observed by Marquiegui and Aguirrezabalaga (2009). From an economic perspective, the
374 recovery measures have increased an economic resource, for example *S. plana* and *H.*

375 *diversicolor*, which has also increased, are heavily predated by several important commercial
376 fish in the estuary (Dolbeth et al., 2008a).

377

378 **Post-mitigation period and climate events impact**

379 After the implementation of the mitigation measures, two recovery periods can be
380 recognised in the seagrass bed (Fig. 3), with climate events being the main driver. Thus,
381 although there was a major flood in 2000/01, *Z. noltii* biomass continued to increase until
382 2003, when it then declined following heatwaves. *Zostera noltii* can cope with a wide range
383 of salinities (Charpentier et al., 2005) so that the marked decrease in salinity (and increase in
384 flow) following the flood events did not seem to have a large impact on *Z. noltii* biomass.
385 However, high temperatures might have induced great metabolic stress for the seagrass. These
386 two recovery periods are also reflected in macrobenthic community dynamics, with important
387 consequences for biodiversity (Cardoso et al., 2010) and, as seen by the present study, for
388 production.

389 The ongoing human impacts (eutrophication) cannot be separated from climate impacts
390 (Cardoso et al. 2008a, Dolbeth et al. 2007, Lloret et al. 2008, Whomersley et al. 2010), but
391 macrobenthic production in the recovery period (post-mitigation) was clearly compromised
392 by extreme weather events. Relationships between climate variables and selected species were
393 not clearly revealed in the multivariate analyses, probably because of indirect effects (e.g.
394 climate affected seagrass bed dynamics, which in turn affected the associated fauna) or
395 because for certain variables only mean annual values (salinity, water temperature) were used,
396 not the extremes. However, in addition to the seagrass dynamics, the flood, heatwaves and
397 drought might have impacted the macrobenthic community more directly due to the
398 physiological tolerances of species to higher temperatures, osmotic stress and physical
399 resistance to changes in water flow (e.g. Wilson, 1981; Kimmerer, 2002; MarLin database -

400 <http://www.marlin.ac.uk/>), which may also affect species interactions (e.g. Freitas et al.,
401 2007), and indirectly through changes in allochthonous material from terrestrial sources and
402 changes in turbidity, both of which are driven by precipitation, runoff and water management
403 plans. Macrobenthic food resources are a mix of terrestrial organic matter, microalgae and
404 macroalgae (Baeta et al., 2009), and the terrestrial component is likely to be lower during
405 drought events (see also Attrill and Power (2000) and Salen-Picard et al. (2002, 2003)).

406 Similarly to the changes in *Z. noltii* biomass, the greatest decrease in macrobenthic
407 production followed the high temperatures of 2003 and this lower production continued in the
408 following drought period of 2005. Macrofauna mass mortalities following the 2003 heatwave
409 were also observed in the NW Mediterranean (Garrabou et al., 2009) with *H. ulvae* in the
410 seagrass area and *S. plana* in both areas suffering the highest decline during these events.
411 Since the production of *H. ulvae* increased at the sandflat area, its decline may be related to
412 the *Z. noltii* decline. High temperatures, which in the intertidal pools could reach 40°C, were
413 probably responsible for decline in *S. plana*, which has a lethal temperature of 27.5°C in
414 summer conditions (Wilson, 1981). The response to the heatwaves varied between species:
415 some, such as *H. diversicolor* and some amphipods (for more detail see Grilo et al., 2009),
416 seemed not to be strongly affected. The following prolonged drought contributed to the lower
417 levels of production, possibly due to decreased food sources since freshwater runoff was
418 severely reduced (see above). The effects of floods are also expected to vary between species,
419 depending on feeding habits and the habitat itself (Norkko et al., 2002, Salen-Picard et al.,
420 2003). Production decreased after the flood, but it recovered relatively quickly in the
421 following year, mostly due to *H. ulvae*, consistent with Salen-Picard et al. (2003), who found
422 that communities dominated by opportunistic or tolerant species could be favoured by floods.
423 The tendency for production levels to be lower after weather extremes was also seen in the
424 fish production of the estuary which decreased considerably following the drought (Dolbeth et

425 al., 2008b). Extreme weather events have implications for the food provision services of
426 estuary, since the production of commercially important species (e.g. the shellfish *S. plana*
427 and *C. edule*, in the present study; and fish, *Dicentrarchus labrax*, *Solea solea*, *Platichthys*
428 *flesus*, in Dolbeth et al. (2008b)) declined after these events. In addition to food provisioning
429 services, changes in community composition and structure may also have repercussions for
430 other ecosystem services and functions, such as nutrient cycling or carbon fluxes (Beaumont
431 et al., 2007).

432 The measures introduced for the management of eutrophication in the Mondego estuary
433 seemed partially effective, since a recovery in both the seagrass and macrobenthic community
434 has begun. A new community structure is evident, with increased production of slow growing
435 species. However, weather extremes have halted and even reversed system recovery with
436 considerable negative impacts on community production, which in turn may affect their
437 functioning and the goods provided by the system.

438

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443

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Table 1 Species discriminating each study area (from SIMPER analyses, 90% cut-off applied), with indication of mean production (g AFDW m⁻² y⁻¹) per time period, P/ \bar{B} values for all the study period (1993-2006 mean, minimum and maximum values between brackets), sum of the species production with the % relative to whole community production, and the % of each trophic group production. *Trophic groups definition according to Baeta et al. (2009).

Taxa	Species	Trophic group*	ZOSTERA BED AREA				SANDFLAT AREA			
			PRE 1993-1995 mean	POST 1 1999-2002 mean	POST 2 2003-2006 mean	P/ \bar{B} 1993-2006 mean & range	PRE 1993-1995 mean	POST 1 1999-2002 mean	POST 2 2003-2006 mean	P/ \bar{B} 1993-2006 mean & range
Amphipoda	<i>Melita palmata</i>	Grazer	1.3	0.1	0.2	4.4 (0.4-11.2)				
Bivalvia	<i>Cerastoderma edule</i>	Grazer/ Detritivore	6.0	0.7	0.4	0.9 (0.7-1.2)	0.3	0.2	0.3	3.8 (1.7-5.9)
	<i>Scrobicularia plana</i>	Detritivore	3.6	11.8	10.2	0.9 (0.6-1.8)	10.1	29.8	10.9	1.2 (0.6-1.6)
Decapoda	<i>Carcinus maenas</i>	Omnivore	1.3	1.0	1.5	2.1 (1.8-2.8)				
Gastropoda	<i>Hydrobia ulvae</i>	Grazer/ Detritivore	145.8	87.8	36.1	2.1 (1.3-3.0)	17.0	4.3	5.2	3.4 (2.4-4.8)
	<i>Littorina littorea</i>	Grazer/ Detritivore	1.2	0.4	0.2	1.4 (0.7-3.4)				
Insecta	Diptera (larvae)	Unknown	0.01	0.4	0.2	5.8 (1.3-12.5)				
Isopoda	<i>Cyathura carinata</i>	Detritivore/ Omnivore	2.0	2.4	0.4	2.7 (2.1-3.5)	19.9	17.4	16.0	2.1 (1.5-3.4)
Polychaeta	<i>Alkmaria romijni</i>	Detritivore	0.3	0.1	0.03	8.1 (5.7-11.3)	1.0	0.4	0.3	9.6 (4.6-13.2)
	<i>Hediste diversicolor</i>	Omnivore	0.5	6.9	9.4	1.6 (1.4-2.0)	1.2	3.6	4.4	1.9 (1.1-3.0)
	<i>Heteromastus filiformis</i>	Detritivore	1.5	0.9	0.6	3.4 (3.0-4.0)	0.4	0.2	0.5	3.3 (1.5-6.3)
	<i>Streblospio shrubsolii</i>	Detritivore	0.1	0.1	0.1	8.7 (3.7-11.9)	0.1	0.6	0.3	10.4 (3.0-13.9)
Oligochaeta	<i>Tubificoides</i> sp.	Detritivore	1.2	0.4	1.2	6.0 (4.9-7.8)	1.0	0.4	0.3	9.6 (4.6-13.2)
		Detritivore	51%	53%	51%		60%	74%	60%	
		Grazer	47%	39%	31%		18%	4%	7%	
		Omnivore	2%	8%	18%		23%	22%	32%	
		Simper species production	164.8 (97%)	112.6 (98%)	60.5 (97%)		50 (97%)	56.5 (97%)	38.2 (98%)	
Whole community production			170.6	114.3	62.6		51.4	58.5	39.0	

Figure captions

Fig. 1 Location of the Mondego estuary showing sampling stations. Expanded area maps show evolution of the *Zostera noltii* bed's area and cover, since 1986 until 2006.

Fig. 2 Long-term monthly variation in A) *Zostera noltii* biomass in the *Zostera* bed area; and B) *Ulva* spp. biomass in both *Zostera* bed and sandflat areas; C) atmospheric temperature (monthly means, absolute maximum value registered and mean for the period 1971-2000); D) rainfall (total cumulative per month and mean for the period 1971-2000) and runoff for *Zostera* bed and sandflat areas. In x-axis: J, January; M, May; S, September.

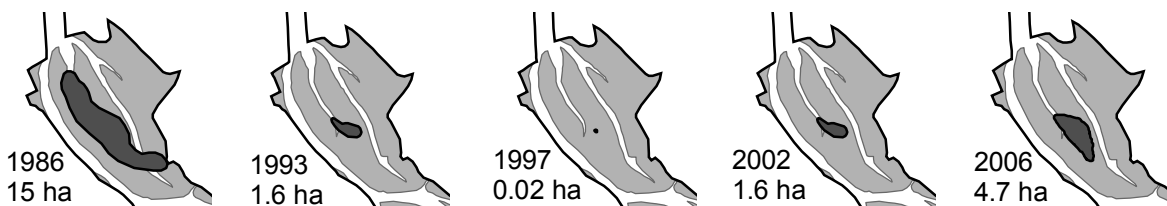
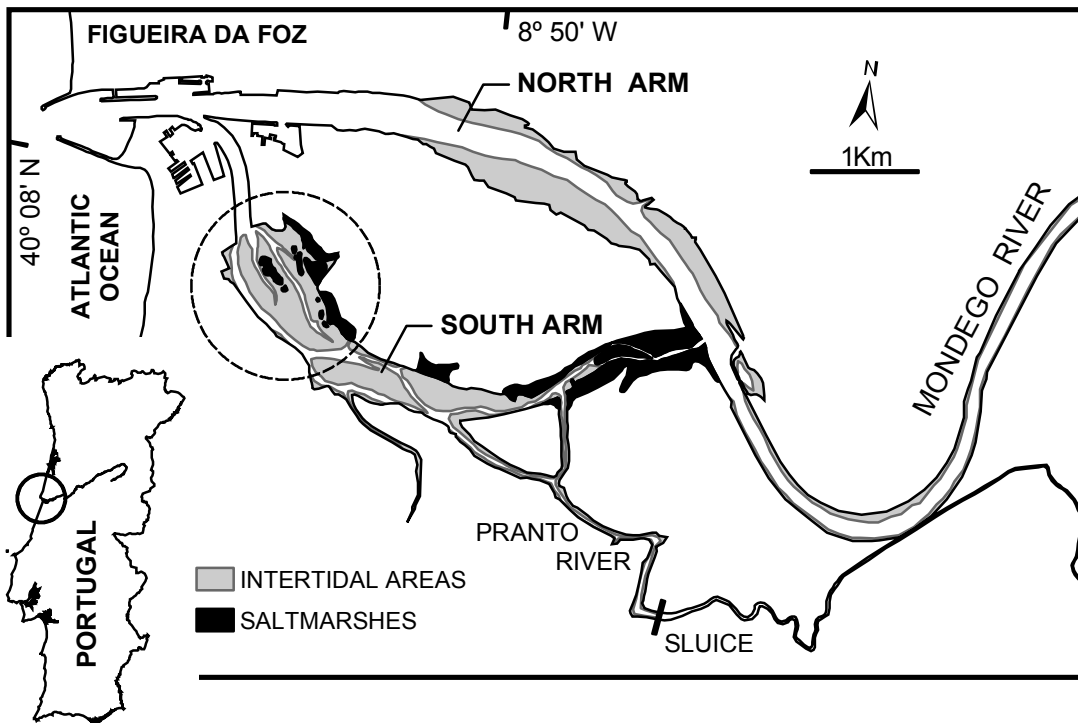
Fig. 3 Synthesis of the main anthropogenic and climate impacts occurring in the Mondego estuary during the study-period, with delimitation of 4-year time periods regarding those impacts.

Fig 4. Annual production for both areas during the study period, regarding A, B) the whole macrobenthic community and C, D) the community with the production of *Hydrobia ulvae* excluded, with indication of the mean annual production for each 3-year and 4-year scenarios: PRE – decline, black symbols; POST 1 – 1st recovery phase, light grey symbols; POST 2 – 2nd recovery phase, dark grey symbols.

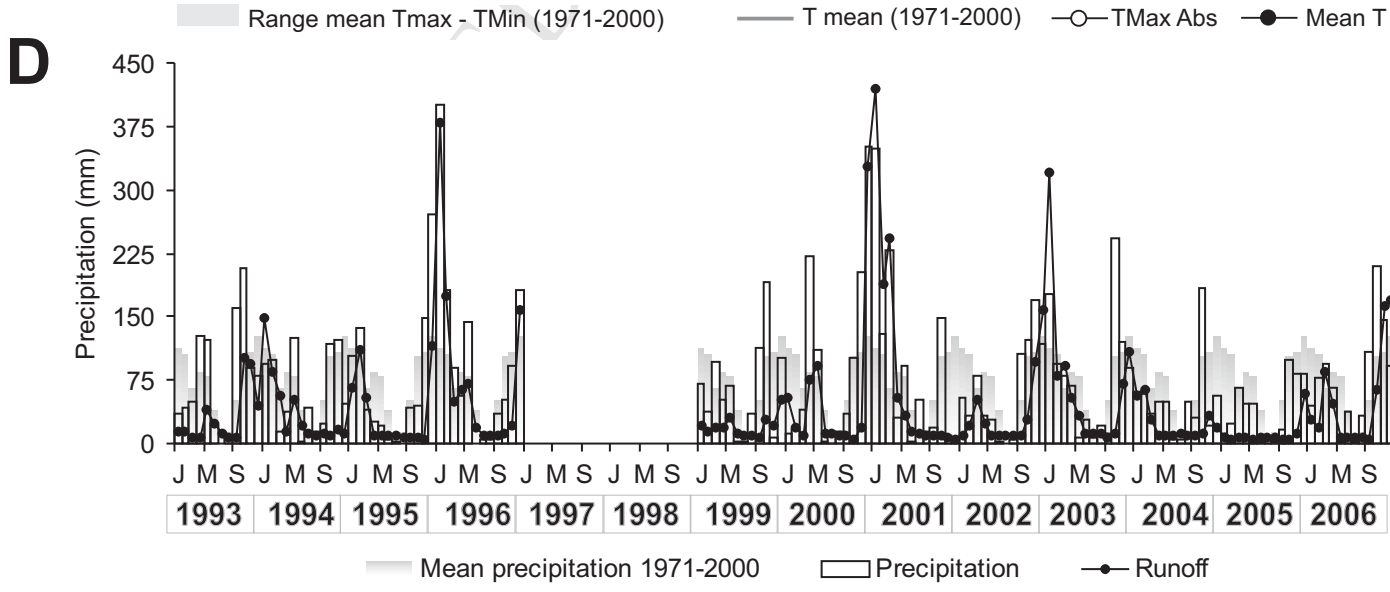
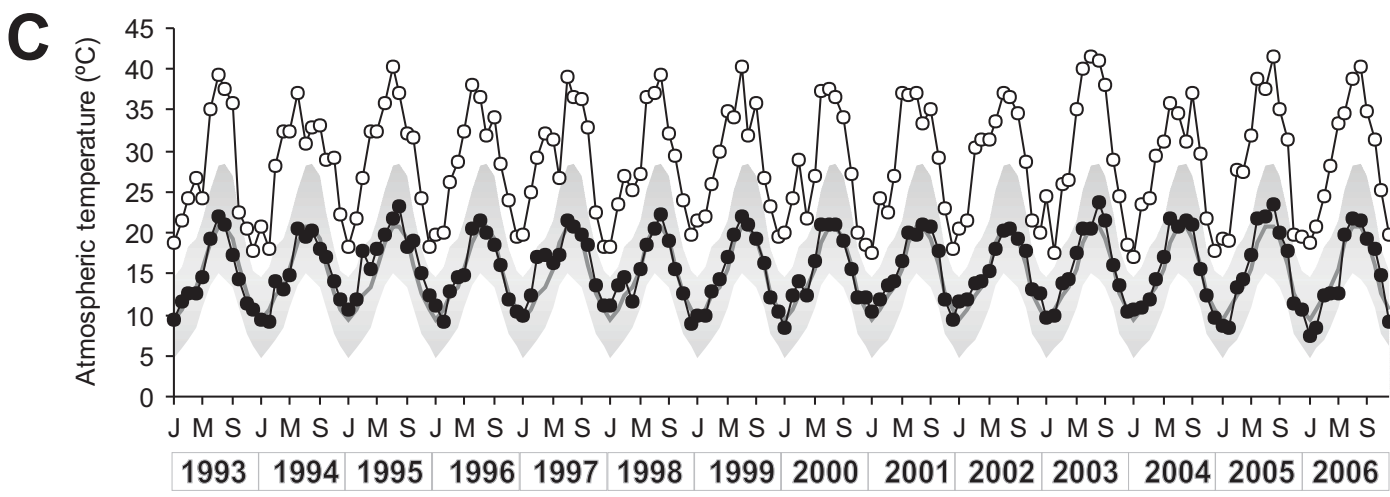
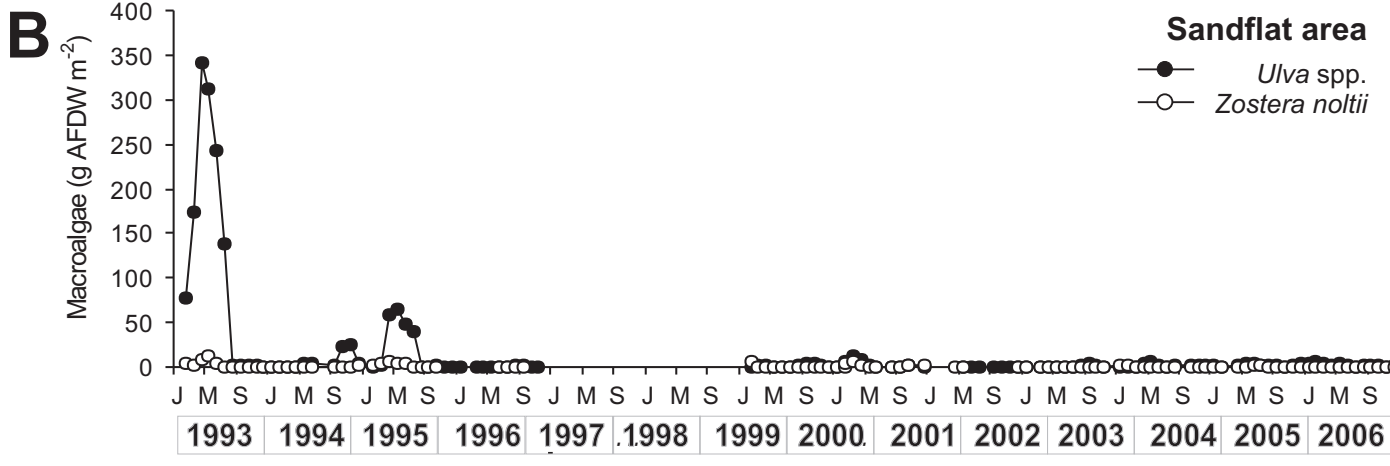
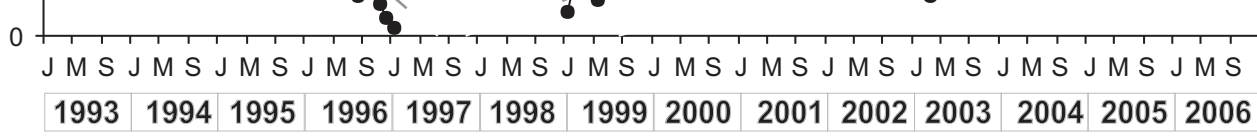
Fig. 5 Two-dimensional nm-MDS ordination plot of macrobenthic community production for *Zostera* bed area (circles) and sandflat area (squares), with indication of study periods: PRE – decline, black symbols; POST 1 – 1st recovery phase, light grey symbols; POST 2 – 2nd recovery phase, dark grey symbols

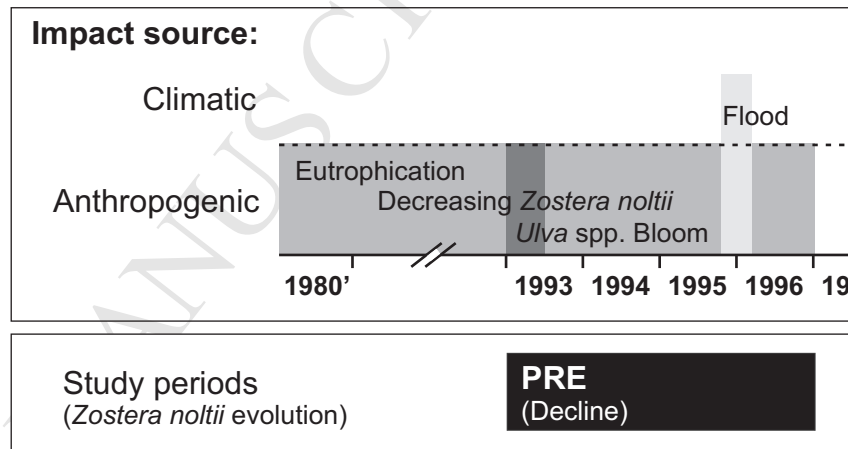
Fig. 6 RDA ordination triplot relating simpler species production (grey vector lines) and significant environmental variables (after Monte Carlo permutation tests, black vector lines) along the study period for A) *Zostera* area and B) sandflat area, with indication of the study periods: PRE – decline, black symbols; POST 1 – 1st recovery phase, light grey symbols; POST 2 – 2nd recovery phase, dark grey symbols.

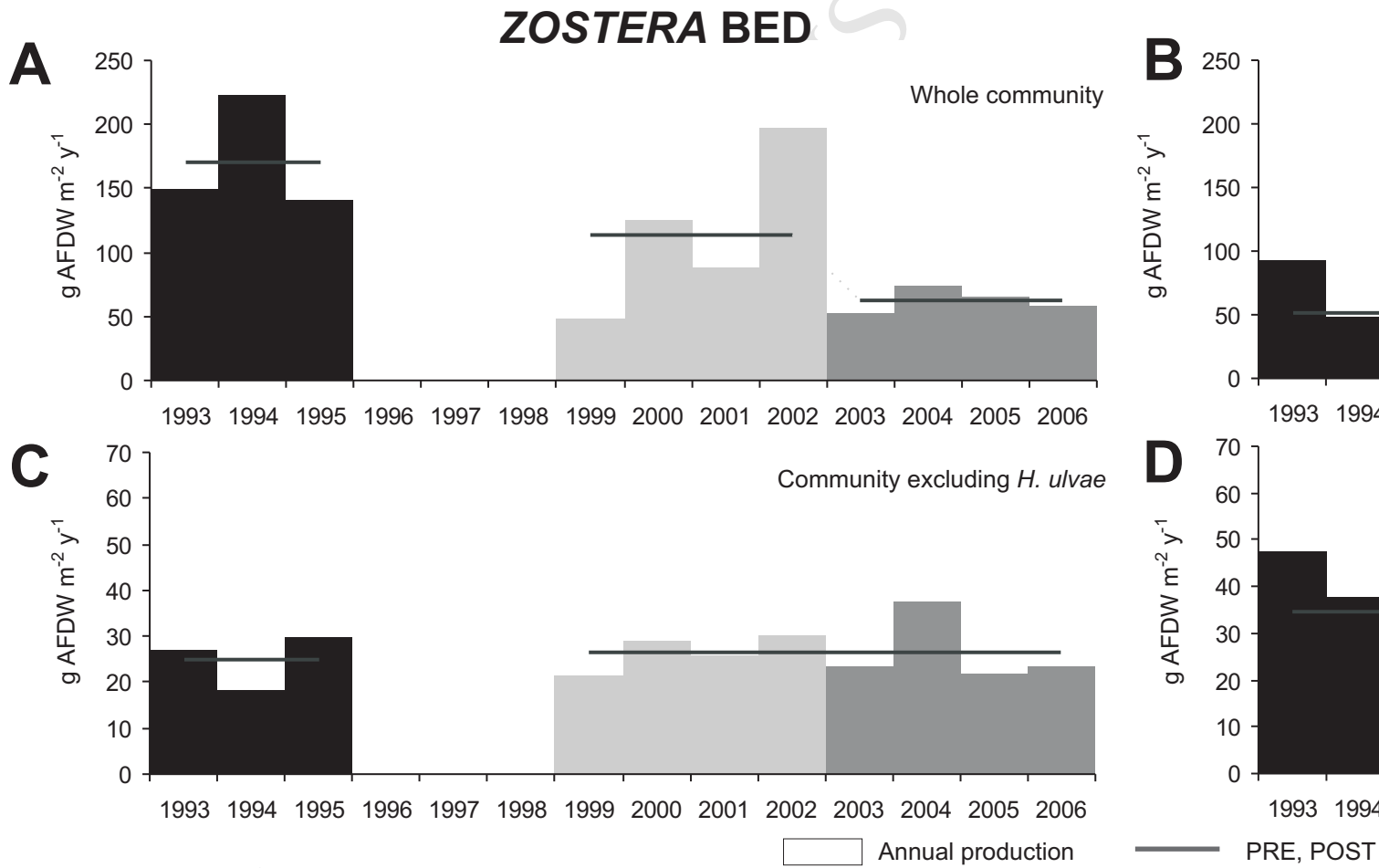
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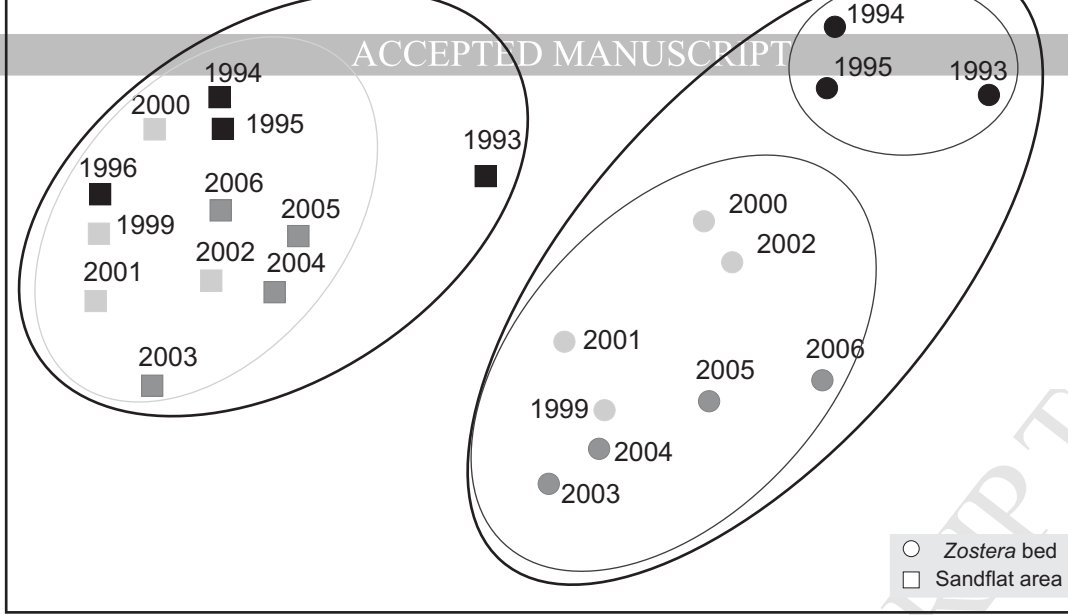


■ *Zostera noltii*









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