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

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Abstract The macrobenthic production of an estuarine system was evaluated over a 14-year study period in a seagrass bed and in a sandflat. Over this period, the estuary suffered severe eutrophication and extreme weather events with important impacts on the community, impairing system functioning and ultimately the goods and services provided by the estuary (decline in the seagrass bed, decreased community production and/or a boost in the production by opportunistic species, such as Hydrobia ulvae). Following the anthropogenic impacts, management measures were introduced which allowed a gradual recovery of the seagrass bed and a new macrobenthic community structure manifested by production increases of slow-growing species, such as Scrobicularia plana and Hediste diversicolor. There was a gradual re-orientation of energy into population biomass instead of population density but this was not translated into higher community production, mainly due to the decreased production of opportunistic species (H. ulvae and several polychaetes). Several weather extreme events occurred during this post-mitigation phase - floods, heatwaves and droughts, all of which had negative impacts on macrobenthic dynamics and production. The
heatwaves led to the greatest decreases in macrobenthic production, mainly due to *S. plana* perhaps associated with its physiological intolerance of higher temperatures. The prolonged drought that followed the heatwaves maintained low levels of production by *S. plana* and *H. ulvae*. With climate change, the frequency and intensity of extreme weather events are likely to increase worldwide so that the recovery of impacted/disturbed systems from impacts such as eutrophication may be seriously affected by these additional stressors, compromising attempts to improve the ecological quality of estuarine ecosystems.

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

1. **Introduction**

Estuaries provide many goods and services which are essential to society and a balance needs to be struck between human usage and the sustainable use and conservation of these systems. This is recognised and acknowledged in much of the legislation produced to protect and promote the recovery of transitional and coastal areas worldwide (Airoldi and Beck, 2007; Borja and Dauer, 2008). Assessing ecological processes and resources in terms of the goods and services that they provide is attractive to, and resonates with, policy makers and non-scientists (Beaumont et al., 2007; Pinto et al., 2010) and one dimension of this is secondary production which is often a direct measure of food provision delivered by an ecosystem, and which has clear social-economic meaning, especially when a monetary value is attached (Costanza et al., 1997; Pinto et al., 2010). Production is also a measure of ecosystem function and may reveal greater insights into ecosystem change than static parameters such as diversity, density or biomass. Combining production with long-term datasets will increase our level of understating of system functioning (see for instance, Dolbeth et al., 2007; Pranovi et al., 2008). Environmental impacts on the biota, and hence of
the goods and services they underpin, may only be revealed with long-term data series (Boero et al., 2009) and in this period of widespread and rapid global change, it is important to document ecosystems before further changes occur. Thus, the present study documents changes in a well-documented estuarine system, the Mondego estuary, Portugal, over a 14-year period, with a particular focus on macrobenthic community production and seagrass bed dynamics, building on previous studies by Dolbeth et al. (2007) which described some of the changes in the macrobenthic assemblages in relation to various stressors that led to an overall decline in environmental quality. Following this, management measures were implemented to promote recovery of the system although these have been hampered by subsequent extreme climate events. The present study extends that work, adding more data to the long-term series to evaluate other important events: 1) the success of the seagrass beds recovery, following the implementation of management measures in the estuary, and its implications for overall estuarine integrity, and 2) the impact of climatic extremes, such as floods, heatwaves and droughts.

2. Materials and Methods

2.1 Study area

The Mondego estuary, in a warm temperate region on the Atlantic coast of Portugal (40°08’N, 8°50’S), is a small estuary of 8.6 km², comprising two arms, north and south, separated by an island. The north arm is deeper (4-8 m during high tide, tidal range 1-3 m), highly hydrodynamic, is a main navigation channel and hosts the Figueira da Foz harbour. The south arm is shallower (2-4 m during high tide, tidal range 1-3 m) and is characterized by large areas of exposed intertidal flats during low tide. Several human activities led to an ongoing process of eutrophication since the end of the 1980’s, mainly in the south arm. The downstream areas of the south arm support Spartina maritima marshes and a Zostera noltii
(seagrass) bed. In the upstream area, the seagrass community has completely disappeared and blooms of the opportunistic macroalga *Ulva* spp. were common. Until the end of 1998, this part of the estuary was almost silted up, with water circulation mainly dependent on tides and on the freshwater input from the Pranto river (Fig. 1), artificially controlled by a sluice according to rice field irrigation needs in the lower Mondego valley (Dolbeth et al., 2007; Cardoso et al., 2008a).

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

2.2 Sampling and biological material processing

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

On each sampling occasion and at each site, ten (during the first 18 months) to six sediment cores (141 cm\(^2\) core sectional area) were taken randomly to a depth of 20 cm by using a manual corer. Samples were collected in the morning, during low tide, fortnightly for
the first 18 months and monthly thereafter. Each sample was sieved through a 500 µm mesh using estuarine water, the organisms retained identified to the species level, counted and measured. Plant material was sorted and separated into green macroalgae and Zostera noltii. For both faunal and plant material the ash-free dry weight (AFDW) was estimated after combustion for 8 h at 450ºC (shells of molluscs included). Additionally, temperature, oxygen, pH and salinity were measured in situ in intertidal pools, and water samples were collected to determine nutrient content (for further details see Cardoso et al., 2010).

2.3 Secondary production

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

\[ P_{cn} = \sum_{t=0}^{T-1} \left( \frac{N_t + N_{t+1}}{2} \times (\overline{w}_{t+1} - \overline{w}_t) \right) \] equation 1

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

Brey’s (2001) method, version 4-04 (worksheet for model computation provided in Brey 2001, http://www.awi-bremerhaven.de/Benthic/Ecosystem/ FoodWeb/Handbook/main.htm.) was used as an alternative empirical method for secondary production estimation (after Dolbeth et al., 2005) for other abundant species - Carcinus maenas (Decapoda), Alkmaria romijni, Capitella capitata, Chaetomatus setosa, Hediste diversicolor, Heteromastus filiformis, Streblospio shrubsolii (Polychaeta), Tubificoides sp., Oligochete sp. (Oligochaeta), Cerastoderma edule, Scrobicularia plana (Bivalvia), Haminoea hydatis, Littorina littorea
(Gastropoda), Dipteran larvae (Insecta). The weight-to-energy ratios needed for the application of the empirical method are also provided in Brey (2001). For those species with lower densities and biomasses, production was estimated by summing the increases in biomasses from one sampling date to the other, using the cohort increment summation equation, but without following the cohorts.

Mean biomass and $P/B$ ratios (annual production divided by the annual mean biomass) were also computed for the main species.

2.4 Data analysis

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

For each area, the relationship between the species production identified with SIMPER and environmental variables were explored using CANOCO v 4.5 software. Initially, a detrended correspondence analysis (DCA) was performed with the biotic data (species production) to evaluate the type of model response. Since a linear response was detected, a redundancy analysis (RDA) was applied to examine the relationships between biotic and abiotic parameters. Prior to the analyses, the species production data were square root transformed, in order to scale down the scores of the very productive species. Several environmental variables
were analysed and their significance evaluated with the forward selection procedure (Monte Carlo permutation tests) after checking for and removing the collinearity.

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

3. Results

3.1 Anthropogenic impacts on macrophyte and macroalgal dynamics

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

In the eutrophic area, there was a spring macroalgal bloom in 1993 (maximum biomass of 415 g AFDW m$^{-2}$ / 508 g DW m$^{-2}$ in April 1993), followed by a crash in early summer (Fig. 2B), reported by Leston et al. (2008). In 1995, macroalgal biomass again reached high values, but not sufficient to be considered a spring bloom (maximum biomass of 111 g AFDW m$^{-2}$ / 142 g AFDW m$^{-2}$ in April 1995). Macroalgal blooms in the eutrophic area were present throughout the pre-mitigation period, particularly during dry years, but blooms were never
recorded after the post-mitigation measures were implemented (Fig. 2B) (Wilcoxon two
sample test, W= 3138, p< 0.05).

3.2 Climate

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

Air temperature variation was typical of temperate systems, with increasing values in the
spring (March-June), reaching highest values in the summer (July-September) and lowest
values in the winter (December-February) (Fig. 2C). Mean monthly values were within those
of the 1971-2000 mean (range between maximum and minimum means). In the spring and
summer of 2003 and 2005, higher mean monthly temperatures were recorded (Fig. 2C) when
the maximum temperature was above 40ºC on several occasions. In fact, in most of the
Portuguese territory, one heatwave was recorded in July-August (lasting for 16-17 days) in
2003, two in June 2005 (lasting for 8 to 12 days), and three in June, July and August 2006
(lasting for 6 to 7 days). A heatwave occurs when the maximum air temperature increases by
5ºC relative to the mean daily value of the reference period (in this case the climatic normal
1971-2000), for at least 6 consecutive days (IM - Portuguese Weather Institute). The
heatwaves did not extend to the Mondego estuary, but translated into much higher
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 a 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
Secondary production was in general higher in the *Zostera* bed than in the sandflat area (Fig. 4A, B), and these differences were significant (ANOSIM, $R = 0.886$, $p = 0.001$), with the species responsible for that production clearly separated in the MDS plot (Fig. 5). Relatively few species were responsible for more than 97% of the whole community production in both areas, although the dominant species differed in the two areas (Table 1). Of the 75 species recorded over the whole study period, only 13 were associated with the production of the *Zostera* bed macrobenthos (Table 1), and 8 for the sandflat area (Table 1). Even so, the major contributor to the annual production of the *Zostera* bed (and to the differences found between areas) was the gastropod *Hydrobia ulvae*, accounting for more than 57% of the total production (Table 1). Other relevant taxa with higher production in the *Zostera* bed were *Melita palmata*, *Cerastoderma edule*, *Carcinus maenas*, *Littorina littorea*, *Tubificoides* sp., *Hediste diversicolor* and *Heteromastus filiformis* (Table 1). In the sandflat area, *H. ulvae* was also an important species, but a higher percentage of the production was accounted for by the isopod *Cyathura carinata* and the bivalve *Scrobicularia plana* (Table 1). The small polychaetes *Alkmaria romijni* and *Streblospio shrubsolii* attained higher production levels in the sandflat area (Table 1). The mean $P/B$ ratios over the study period were generally higher for species inhabiting the sandflat area (Table 1). More than half of the community production was due to detritivores (Table 1). In the seagrass bed, grazers also contributed a high proportion of the production, mostly due to the *H. ulvae*, while in the sandflat area omnivores made up a higher proportion (Table 1). Since *H. ulvae* was a highly dominating species, especially in the *Zostera* bed, production was also estimated without this species, resulting in higher annual production of the remaining species in the sandflat area over the study period (Fig. 4C, D).

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

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

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

When *H. ulvae* is excluded from the analysis, there are similar production values over the entire period in the *Zostera* bed (Fig. 4C); clearly, *H. ulvae* is responsible for the high variability observed (see also Table 1). In the sandflat area production of the remaining
community tended to increase after the mitigation measures were put in place, though there was a slight decrease in the 2nd recovery phase from 2003 onwards (Fig. 4B).

3.4 Macrobenthic production and environmental variables

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

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

In the sandflat area, only *Ulva* spp. annual mean biomass and pH were statistically significant, with the resulting constraint ordination explaining 64% of the variability. 1993 was clearly differentiated from the remaining samples (Fig. 6B), confirming MDS results (Fig. 5). 1993 had the highest macroalgal biomass, with which *H. ulvae, C. edule* and the
small polychaetes *H. filiformis* and *A. romijni* were associated (Fig. 6B); the last two species had the highest P/B ratios (Table 1). After the bloom in 1993 and associated with higher pH values (within the range 8.4-9.0), *C. carinata* attained the highest production values (1994-1996). This production was also associated with the post-mitigation period, but only with 2005 and 2006. For the remaining post-mitigation period, *S. plana, H. diversicolor and S. shrubsolii* co-occur having higher production values from 1999 to 2004 (Fig. 6B).

**Discussion**

**Spatial comparisons**

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

The benefits of seagrass beds for both invertebrates and fish are well known, with habitat heterogeneity, shelter and higher food resources all important in this respect (Duarte, 2002; Blanchet et al., 2004; Baeta et al., 2009). In the present study, higher production levels were observed in the seagrass bed, as also reported in other transitional ecosystems (Sprung, 1994; Heck et al., 1995), and there were generally higher levels of diversity (Dolbeth et al., 2007;
Close inspection of the production dynamics of this habitat showed that the greater part was due to *Hydrobia ulvae*, similar to other studies where this species dominates seagrass areas (Asmus and Asmus, 1985; Blanchet et al., 2004). The production of the community with *H. ulvae* production excluded was higher in the sandflat area, especially in the post-management period. In the Mondego estuary, *H. ulvae* production has been considerably boosted after disturbance events, turning the production dynamics more erratic in the *Zostera* bed. Thus, production increased in the years that followed the bloom and the flood (1994 and 2002 respectively, more detail in Dolbeth et al., 2007), but decreased after the heatwaves and drought, showing that benthic responses can vary significantly depending on the frequency and intensity of disturbance (Whomersley et al., 2010). Although benthic community production was higher in the seagrass area, the dominance of *H. ulvae* could compromise its resilience to disturbance, following the idea that higher functional diversity would increase resilience (Peterson et al., 1998; Wardwell et al., 2008).

When *H. ulvae* is excluded, the mean annual production for the 14-year period was much less variable, although different species were responsible at different times. *Z. noltii* biomass was one of the major components influencing the overall macrobenthic production, and several amphipods and the molluscs *C. edule* and *L. littorea* had higher production in the pre-mitigation period. Although *Z. noltii* seems to be recovering in recent years, the species contributing to production have changed, with an increase of *S. plana* and *H. diversicolor* production in the post-mitigation period and a gradual decrease of *H. ulvae* production dominance. In this period, silica has increased, probably related to changes in microphytobenthos communities (diatoms) (Laruelle et al., 2009), an important component of the diet of these species (Baeta et al., 2009, personal communication). A new community structure is becoming evident in the *Zostera* area, with a gradual increase of slow-growing species and omnivore species contributing to production. Nevertheless, these community
changes did not lead to an overall increase in community production, mostly because of the decline in *H. ulvae*.

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

Estuaries are characterized by relatively few species with abundant populations that can attain high production levels in natural conditions, making it difficult to dissociate anthropogenic from natural stress, the estuarine quality paradox of Elliott and Quintino (2007). Overall, production was distributed more evenly in the sandflat area across three or four species, while in the seagrass bed more than 60% of the production was due to a single species. From 2003 onwards, production was more evenly distributed among three species. For both areas, there was a higher investment in individual body mass, instead of growth, consistent with a shift from r-strategists to K-strategists following management, as also observed by Marquiegui and Aguirrezabalaga (2009). From an economic perspective, the recovery measures have increased an economic resource, for example *S. plana* and *H.*
diversicolor, which has also increased, are heavily predated by several important commercial
fish in the estuary (Dolbeth et al., 2008a).

Post-mitigation period and climate events impact

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

The ongoing human impacts (eutrophication) cannot be separated from climate impacts
(Cardoso et al. 2008a, Dolbeth et al. 2007, Lloret et al. 2008, Whomersley et al. 2010), but
macrobenthic production in the recovery period (post-mitigation) was clearly compromised
by extreme weather events. Relationships between climate variables and selected species were
not clearly revealed in the multivariate analyses, probably because of indirect effects (e.g.
climate affected seagrass bed dynamics, which in turn affected the associated fauna) or
because for certain variables only mean annual values (salinity, water temperature) were used,
not the extremes. However, in addition to the seagrass dynamics, the flood, heatwaves and
drought might have impacted the macrobenthic community more directly due to the
physiological tolerances of species to higher temperatures, osmotic stress and physical
resistance to changes in water flow (e.g. Wilson, 1981; Kimmerer, 2002; MarLin database -
http://www.marlin.ac.uk/), which may also affect species interactions (e.g. Freitas et al., 2007), and indirectly through changes in allochthonous material from terrestrial sources and changes in turbidity, both of which are driven by precipitation, runoff and water management plans. Macrobenthic food resources are a mix of terrestrial organic matter, microalgae and macroalgae (Baeta et al., 2009), and the terrestrial component is likely to be lower during drought events (see also Attrill and Power (2000) and Salen-Picard et al. (2002, 2003)).

Similarly to the changes in Z. noltii biomass, the greatest decrease in macrobenthic production followed the high temperatures of 2003 and this lower production continued in the following drought period of 2005. Macrofauna mass mortalities following the 2003 heatwave were also observed in the NW Mediterranean (Garrabou et al., 2009) with H. ulvae in the seagrass area and S. plana in both areas suffering the highest decline during these events. Since the production of H. ulvae increased at the sandflat area, its decline may be related to the Z. noltii decline. High temperatures, which in the intertidal pools could reach 40°C, were probably responsible for decline in S plana, which has a lethal temperature of 27.5°C in summer conditions (Wilson, 1981). The response to the heatwaves varied between species: some, such as H. diversicolor and some amphipods (for more detail see Grilo et al., 2009), seemed not to be strongly affected. The following prolonged drought contributed to the lower levels of production, possibly due to decreased food sources since freshwater runoff was severely reduced (see above). The effects of floods are also expected to vary between species, depending on feeding habits and the habitat itself (Norkko et al., 2002, Salen-Picard et al., 2003). Production decreased after the flood, but it recovered relatively quickly in the following year, mostly due to H. ulvae, consistent with Salen-Picard et al. (2003), who found that communities dominated by opportunistic or tolerant species could be favoured by floods. The tendency for production levels to be lower after weather extremes was also seen in the fish production of the estuary which decreased considerably following the drought (Dolbeth et
Extreme weather events have implications for the food provision services of estuary, since the production of commercially important species (e.g. the shellfish *S. plana* and *C. edule*, in the present study; and fish, *Dicentrarchus labrax*, *Solea solea*, *Platichthys flesus*, in Dolbeth et al. (2008b)) declined after these events. In addition to food provisioning services, changes in community composition and structure may also have repercussions for other ecosystem services and functions, such as nutrient cycling or carbon fluxes (Beaumont et al., 2007).

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

Acknowledgments

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References


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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, $P/B$ 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).

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Species</th>
<th>Trophic group*</th>
<th>ZOSTERA BED AREA</th>
<th>SANDFLAT AREA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphipoda</td>
<td>Melita palmata</td>
<td>Grazer</td>
<td>1.3</td>
<td>0.1</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Cerastoderma edule</td>
<td>Grazer/Detritivore</td>
<td>6.0</td>
<td>0.7</td>
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<tr>
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<td>Scrobicularia plana</td>
<td>Detritivore</td>
<td>3.6</td>
<td>11.8</td>
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<td>Decapoda</td>
<td>Carcinus maenas</td>
<td>Omnivore</td>
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<td>1.0</td>
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<tr>
<td>Gastropoda</td>
<td>Hydrobia ulvae</td>
<td>Grazer/Detritivore</td>
<td>145.8</td>
<td>87.8</td>
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<td></td>
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</tr>
<tr>
<td>Insecta</td>
<td>Diptera (larvae)</td>
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<td>0.4</td>
</tr>
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<td>Cyathura carinata</td>
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<td>Polychaeta</td>
<td>Alkmaria romijnii</td>
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<td>Hediste diversicolor</td>
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<td>Heteromastus filiformis</td>
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<td>Streblospio shrubsolii</td>
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<td>0.1</td>
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<tr>
<td>Oligochaeta</td>
<td>Tubificoides sp.</td>
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<td></td>
<td>Detritivore</td>
<td>51%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Grazer</td>
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</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Omnivore</td>
<td>2%</td>
</tr>
<tr>
<td></td>
<td>Simper species production</td>
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<td>164.8 (97%)</td>
<td>112.6 (98%)</td>
</tr>
<tr>
<td>Whole community production</td>
<td></td>
<td>170.6</td>
<td>114.3</td>
<td>62.6</td>
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</table>
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 simper 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.
Zostera noltii

- Ulva spp
- Gracilaria sp

Sandflat area

Macrophage (g AFDW m\(^{-2}\))

Atmospheric temperature (ºC)

Precipitation (mm)

River runoff (dam\(^3\))
**Impact source:**
- Climatic
- Anthropogenic

**Study periods**
- PRE (Decline)

- 1980
- 1993
- 1994
- 1995
- 1996

- Eutrophication
- Decreasing Zostera noltii
- Ulva spp. Bloom
- Flood
Zostera bed
Sandflat area

1993 1994 1995
1996 1999 2000
1997 2002 2004
1998 2003

Stress: 0.07