



Dynamic changes in seagrass assemblages under eutrophication and implications for recovery

P.G. Cardoso^{a,*}, M.A. Pardal^a, A.I. Lillebø^a, S.M. Ferreira^a,
D. Raffaelli^b, J.C. Marques^a

^a*Department of Zoology, IMAR-Institute of Marine Research,
University of Coimbra, 3004-517 Coimbra, Portugal*

^b*Environment Department, University of York, Heslington, York YO10 5DD, UK*

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Abstract

Over the last 20 years, loss of seagrass beds, often related with increased eutrophication, became a common problem worldwide. In the Mondego estuary (Portugal), eutrophication has triggered serious biological changes, which led to an overall increase in primary production and to a progressive replacement of seagrass *Zostera noltii* beds by coarser sediments and opportunistic macroalgae.

The effects of this eutrophication on benthic assemblages were studied along a spatial gradient in the Mondego estuary from 1993 to 1995. Over these short temporal and small spatial scales, distinct changes in the structure of the macrobenthic communities were observed. One of the main structural modifications was the decrease in species diversity along the eutrophication gradient and over time, with a marked impoverishment of the most disturbed inner area. Other changes included an increase in detritivores and a decline in herbivores together with a significant increase in small deposit-feeding polychaetes.

In the long term, sustained eutrophication of this estuary is expected to lead to complete replacement of seagrass habitat by unvegetated coarser sediments, occasionally covered by green macroalgal blooms and dominated by opportunistic invertebrate taxa. Recovery from this situation may not only require reduction in nutrient loadings to the estuary, but also active seagrass restoration programmes to reverse the positive feedback processes thought to be presently taking place.

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* Corresponding author.

E-mail address: gcardoso@ci.uc.pt (P.G. Cardoso).

1. Introduction

Declines in seagrass beds have been documented for many areas of the eastern Atlantic (reviewed in [Schramm and Nienhuis, 1996](#)), including much of the Iberian Peninsula ([Niell et al., 1996](#); [Oliveira and Cabecadas, 1996](#)), often associated with increased eutrophication. The mechanisms responsible for seagrass decline under eutrophication are complex and probably involve a suite of direct and indirect effects of changes in water quality, smothering by green macroalgal blooms ([Den Hartog and Phillips, 2000](#)), and competition for light and nutrients with epiphytic microalgae and with phytoplankton ([Nienhuis, 1996](#)). Loss of the seagrass plants leads to changes in the associated biological communities ([Reise et al., 1989](#); [Flindt et al., 1997](#)) and the functions, services and goods that seagrass beds provide ([Duarte, 2000](#)).

The temporal trajectory of the eutrophication-induced ecological changes that take place in seagrass beds with eutrophication is not well-documented. This is partly because the early stages of the process are so gradual that they usually are not recognised until changes are well under way, and partly because, for many locations, the major changes occurred decades ago ([Schramm and Nienhuis, 1996](#)). However, an appreciation of such trajectories is vital if remedial and restorative programmes for seagrass beds are to be successful ([Van Katwijk and Hermus, 2000](#); [Reise, 2002](#)). [Hobbs and Norton \(1996\)](#) provide a framework pointing out that restoration will only be effective if all the processes which have driven the observed ecological changes are understood and addressed, and this may include additional engineered disturbance to replace an ecosystem component, as well as removing the original stressors. For aquatic systems, there is much evidence that nutrient-induced changes in the growth of opportunistic macroalgae and/or phytoplankton are implicated in catastrophic shifts in aquatic communities ranging from freshwater lakes to coral reefs ([Scheffer et al., 2001](#)) because of nonlinearities (hysteresis) in the dynamics of the systems as they change. These systems may be pushed into an alternate stable state by positive feedback processes from which recovery is very difficult to engineer ([Hobbs and Norton, 1996](#); [Scheffer et al., 2001](#)). Such positive feedback dynamics may explain why long-term recovery of seagrass beds throughout much of Europe and Australia has been painfully slow or non-existent ([Kendrick et al., 2002](#)) despite reductions in nutrient loadings. The mechanisms underlying potential hysteresis in seagrass beds are likely to be associated with the positive feedback processes leading to changes in the local physical environment following the loss of plants, i.e. the further loss of sediments, especially fine material, and sediment resuspension, which further accelerates bed decline ([Duarte, 1995, 2000](#); [Reise, 2002](#); [Schramm, 1996](#); [Widdows and Brinsley, 2002](#); [Van Katwijk and Hermus, 2000](#); [Van de Koppel et al., 2001](#)). Clearly, the sediment issues (ecosystem components) need to be addressed as well as the stressors (nutrients). In the present study, we describe the ecological changes that have taken place over relatively short temporal and small spatial scales in a well-documented seagrass habitat experiencing eutrophication, the Mondego estuary, Portugal, and comment on the likely form of the dynamics of this system under change.

2. Materials and methods

2.1. Study site and sampling programme

The Mondego estuary is located on the Atlantic coast of Portugal (40°8' N, 8°50' W). It is about 7 km long and is 2–3 km across at its widest part. Wetland habitats occupy about 1072 ha (Lopes et al., 2000). The estuary comprises two contrasting arms, northern and southern, separated by Murraceira island, formed by the deposition of detrital materials transported by the river, as the river floodplain (Fig. 1). The northern arm is deeper (4–8 m during high tide, tidal range 1–3 m) and constitutes the principal navigation channel and the location of the Figueira da Foz harbour. The southern arm is shallower (2–4 m during high tide, tidal range 1–3 m) and is almost silted up in the upper zones, so that the freshwater outflow is mainly via the northern arm. Circulation in the southern arm is mostly dependent on the tides and on the freshwater input from the Pranto River, a small tributary. The discharge from this tributary is controlled by a sluice and is regulated according to the water needs of rice fields in the Mondego Valley. The estuary supports several industrial activities and aquacultures, as well as receiving nutrients from 15000 ha of cultivated land upstream. Green macroalgal mats have appeared regularly over the last 20 years with a concurrent decline in seagrass beds (Marques et al., 1993a,b, 1997; Flindt et al., 1997; Lillebø et al., 1999; Pardal et al., 2000; Martins et al., 2001; Cardoso et al., 2002; Dolbeth et al., in press).

Three different study areas were established along a spatial gradient in the southern arm of the Mondego estuary: (1) the *Zostera noltii* beds, corresponding to a non-eutrophic area, (2) an intermediate area and (3) the most eutrophic area (Fig. 1).

The *Z. noltii* beds are characterised by higher salinity values (20–30 g l⁻¹), lower total inorganic nitrogen concentrations (15–30 μmol N l⁻¹) and higher water-flow velocities (1.2–1.4 m s⁻¹) comparatively to the other areas. The mean organic matter content of the sediment is 6.8 ± 0.99% (± S.D.). (Pardal et al., 2000; Martins et al., 2001; Cardoso et al., 2002). In the 1980s, *Z. noltii* beds occupied a broad expanse along the southern arm (150 000 m²) reaching the inner most parts of the estuary. By the mid-1990s, *Z. noltii* had become restricted to a small patch (200 m²) located downstream, having been replaced elsewhere by blooming, fast-growing green macroalgae (free-floating forms) (Fig. 1). Mapping of benthic vegetation was done based on field observations, aerial photographs and GIS methodology (ArcView GIS version 8.2).

The intermediate area is located just upstream of the *Z. noltii* beds and has no seagrass cover although some rhizomes remain in the sediment. The physical–chemical conditions are otherwise similar to those of the *Z. noltii* beds.

The most eutrophic area is upstream in the inner part of the estuary. It comprises a sandy–muddy sediment characterised by the absence of seagrasses (for more than 15 years) and now covered seasonally by green macroalgae, especially *Enteromorpha* sp. (Pardal et al., 2000; Martins et al., 2001; Cardoso et al., 2002). In contrast to the *Z. noltii* beds, this area has lower salinities (15–25 g l⁻¹), higher total inorganic nitrogen concentrations (30–50 μmol N l⁻¹) and lower water-flows

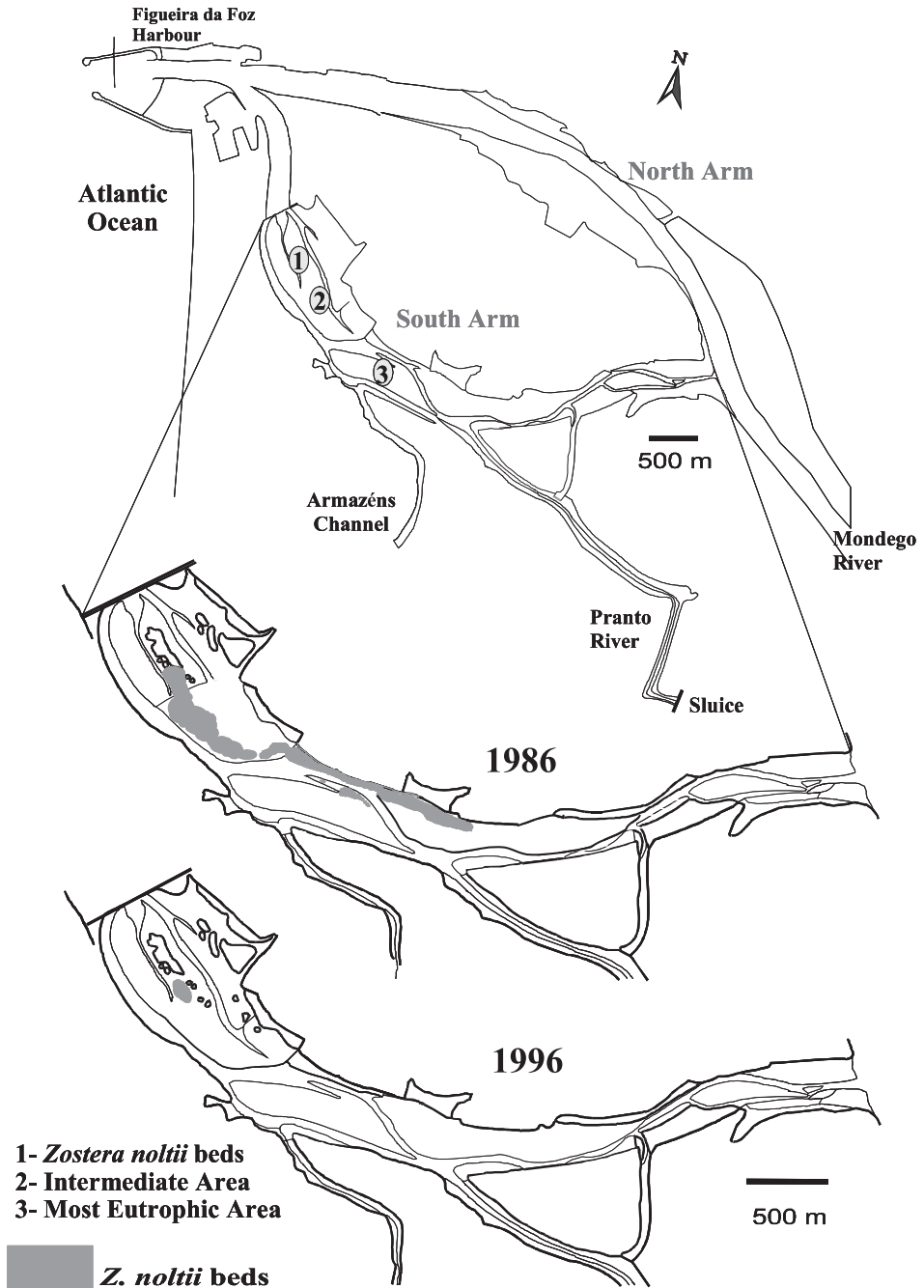


Fig. 1. Location of the sampling areas in the south arm of the Mondego estuary and comparison of the area covered with *Z. noltii* between 1986 and 1996.

(0.8–1.2 m s⁻¹). The mean organic matter content of the sediment is $3.7 \pm 1.0\%$ (\pm S.D.).

Sampling of the macrobenthic community was carried out from January 1993 to September 1995. Samples were collected fortnightly in the first 18 months and monthly during the rest of the study period. On each sampling occasion, 6–10 cores (13.5 cm diameter) were taken to a depth of 20 cm. Samples were washed in estuarine water through a 500- μ m mesh at each sampling station and the fauna retained preserved in 4% buffered formalin. Later, animals were separated and kept in 70% ethanol.

On each sampling occasion (monthly) and at each station, environmental parameters were measured in situ, in low water pools and water sampled for physical and chemical analysis (e.g. temperature, salinity, dissolved oxygen, pH, total inorganic nitrogenic, dissolved inorganic phosphorous).

2.2. Laboratory procedures

All macrofauna were identified to the lowest possible taxon and counted. Seagrass and macroalgal biomass was determined as ash free dry weight (AFDW) after oven drying at 60 °C for 72 h and combustion at 450 °C for 8 h. The same procedure was used to quantify the organic matter content of the sediment.

2.3. Macrobenthic trophic group assignments

Each of the macrobenthic taxa was assigned to a trophic group based on feeding behaviour and food type. Trophic groups used in this study were surface-deposit feeders (SDF), subsurface-deposit feeders (SsDF), suspension feeders (SF), carnivores (C), herbivores (H) and omnivores (O) (sensu Gaston, 1987; Gaston and Nasci, 1988; Gaston et al., 1995, 1997; Brown et al., 2000). Some species could not be confidently classified using the available schemes and these were entered as “unknown”. Preliminary analysis included the snail *Hydrobia ulvae*, but it was also decided to analyse trophic structure omitting this species, since it occasionally occurred in very high numbers and its inclusion masked changes in other species.

2.4. Data analysis

2.4.1. Macrofaunal diversity

The diversity of the macrobenthic communities in the three areas was assessed and represented using rank–abundance curves (Molles, 1999) where the total number of ranks corresponds to species richness and evenness is reflected in the slope of the curve.

2.4.2. Multivariate analysis of the macrofaunal assemblages

The faunal samples were analysed using the nonmetric Multi-Dimensional Scaling (MDS) ordination method (Clarke and Warwick, 2001; Clarke and Gorley, 2001).

Firstly, raw data were square-root-transformed in order to scale down the scores of the abundant species (Clarke and Warwick, 2001).

3. Results

3.1. Seagrass and macroalgal biomass

In the *Z. noltii* beds, total seagrass biomass decreased gradually throughout the study period (Fig. 2), but there was a clear seasonal pattern. During spring and summer, biomass increased substantially due to leaf growth and in autumn and winter, below ground biomass (rhizome and roots) represented about 50% of the total biomass. Green macroalgal biomass was low in this area while red macroalgae (*Gracilaria* sp.) were more abundant (Fig. 3A).

In the intermediate area, only small biomasses of green and red macroalgae were recorded all over the 3-year period (Fig. 3B).

In the most eutrophic area, there was a typical spring algal bloom (maximum of 452 g AFDW m⁻², April 1993) during the first 6 months, followed by its sudden disappearance (crash) in late June (Fig. 3C). In contrast, in 1994, the biomass of green macroalgae was minimal, but in 1995, biomass was higher than the previous year (111 g AFDW m⁻², April 1995).

3.2. Diversity of the macrofauna

The rank–abundance curves clearly show that the *Z. noltii* beds always had greater species richness than the most eutrophic area, with the intermediate zone having intermediate diversity (Fig. 4). Evenness increased from the *Z. noltii* beds to the most

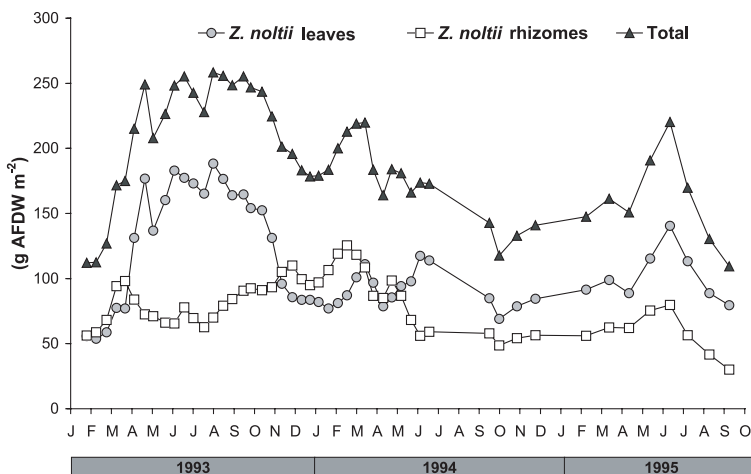


Fig. 2. Variation of *Z. noltii* biomass from January 1993 to September 1995.

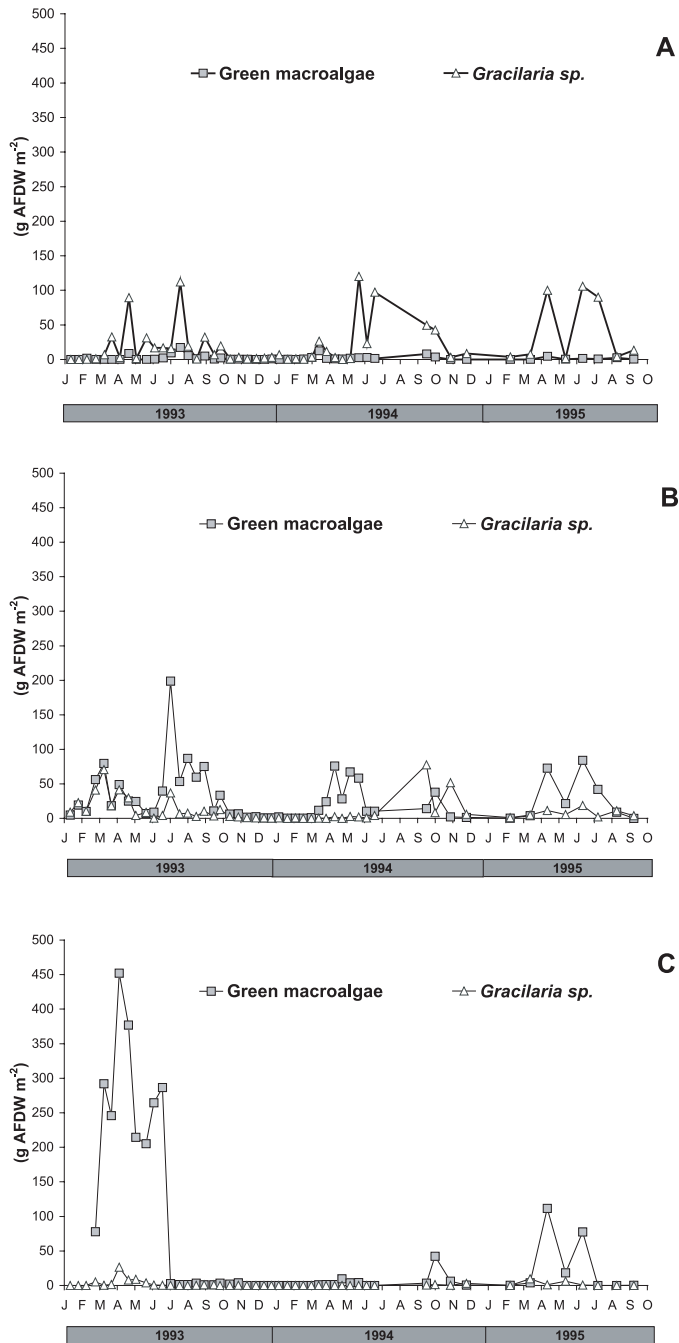


Fig. 3. Variation of algal biomass from January 1993 to September 1995. (A) *Z. noltii* beds; (B) intermediate area; (C) most eutrophic area.

eutrophic area, due to the dominance of *H. ulvae* in the *Z. noltii* beds (see also Cardoso et al., 2002), reflected in the much steeper rank–abundance curve for the *Z. noltii* beds. If *H. ulvae* is omitted from the analysis, evenness appears higher in the *Z. noltii* beds.

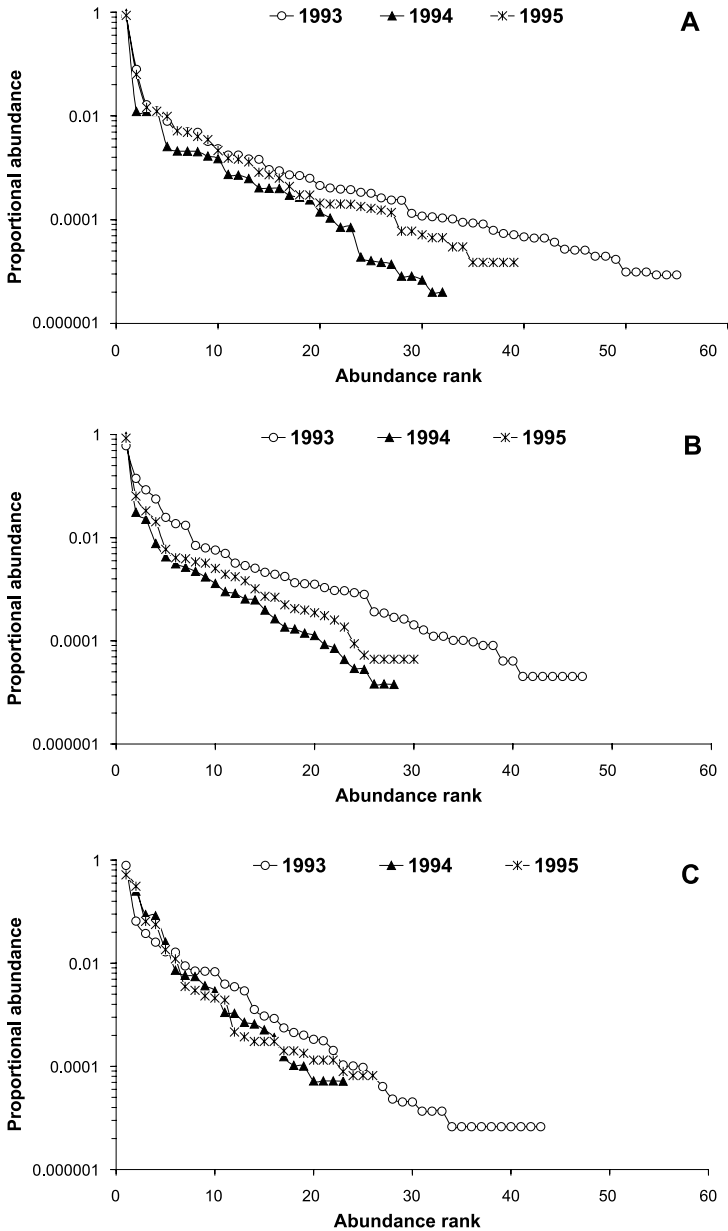


Fig. 4. Rank–abundance curves for three macrozoobenthic communities in the Mondego estuary. (A) *Z. noltii* beds; (B) intermediate area; (C) most eutrophic area.

Species diversity declined throughout the 3 years of study in all three areas (Fig. 4). At the end of the study period, species richness in the *Z. noltii* beds (39 species) was similar to that observed in the most eutrophic area during the algal bloom (1993) (43 species), indicating a rapid deterioration of the seagrass habitat.

3.3. Multivariate analysis of the macrofaunal assemblages

The macrobenthic communities of the three study areas are spatially separated in the MDS plot, with the *Z. noltii* samples separated from those in the most eutrophic area by samples from the intermediate area (Fig. 5). Closer inspection shows that in the autumn of 1994 and the following winter (1995), the community of the *Z. noltii* beds was similar to that of the most eutrophic area (1993), consistent with the contention that the *Z. noltii* community is in decline. In addition, samples from the intermediate and most eutrophic areas showed the greatest scatter in the MDS plot, reflecting perhaps a greater instability of the environmental conditions of these areas.

Significant differences were detected by ANOSIM between the three sites. *Z. noltii* beds were significantly different from the intermediate area and from the most eutrophic area at the 5% level ($R=0.387$; $P=0.001$; $R=0.273$; $P=0.001$, respectively). ANOSIM was also used to detect any differences between the 3 years. Significant differences were obtained between 1993 and 1994 ($R=0.192$; $P=0.02$) and also between 1993 and 1995 ($R=0.206$; $P=0.016$), but not between 1994 and 1995 ($R=-0.03$, $P=0.567$).

3.4. Trophic groups

In the preliminary analysis, which included *H. ulvae*, we were unable to detect any significant modifications in community trophic structure, for either the spatial or

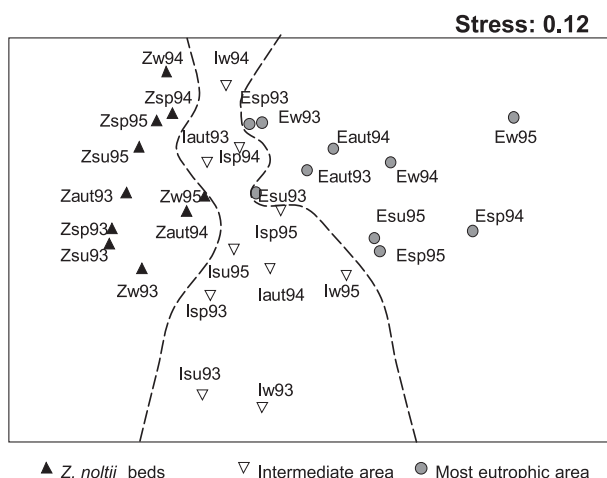
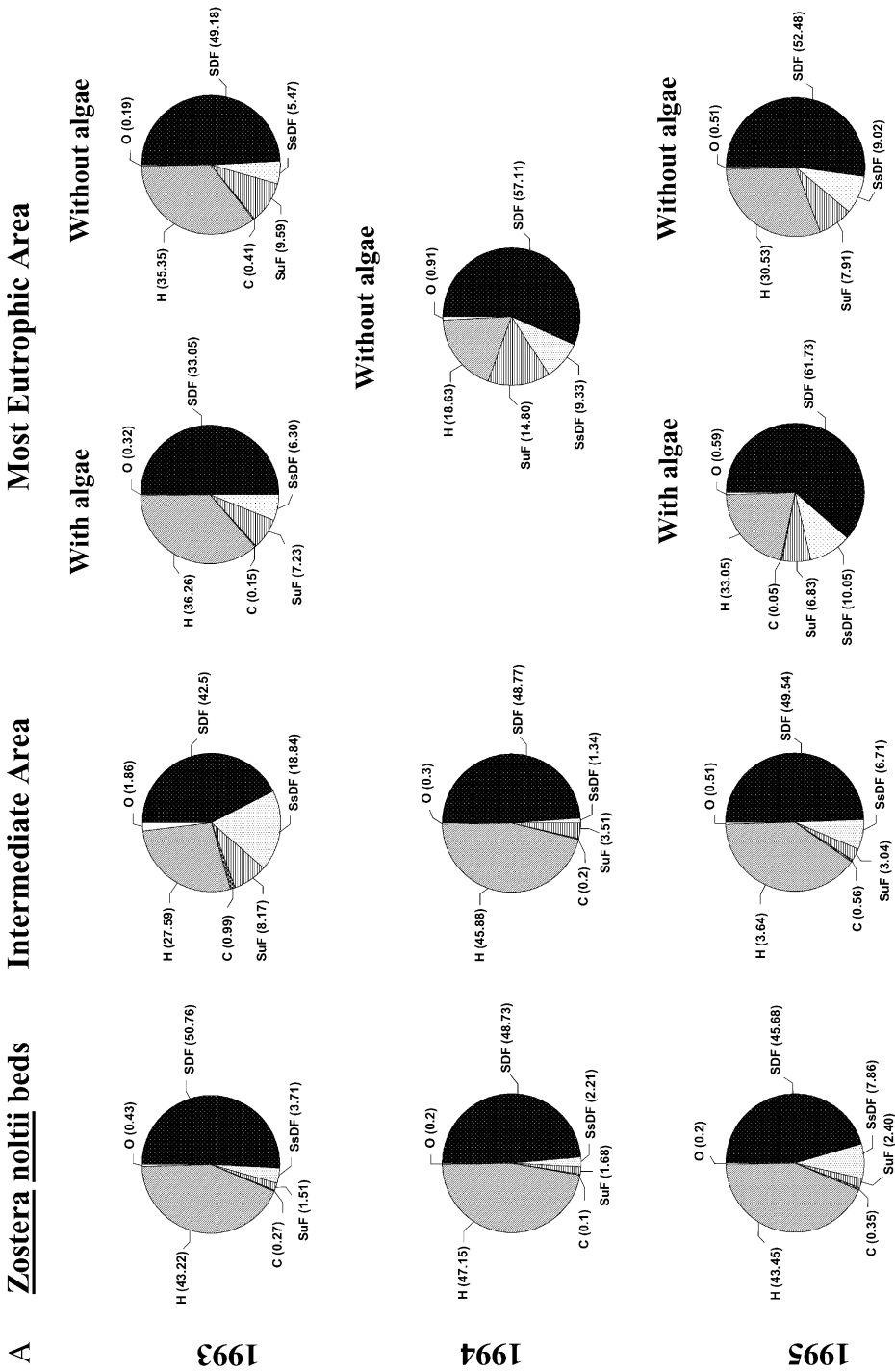


Fig. 5. Two-dimensional MDS ordination plot of macrobenthic communities. (Z) *Z. noltii* beds; (I) intermediate area; (E) most eutrophic area; (sp) spring; (su) summer; (aut) autumn; (w) winter.



B Zostera noltii beds

Intermediate Area

Most Eutrophic Area

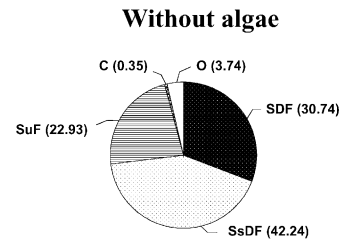
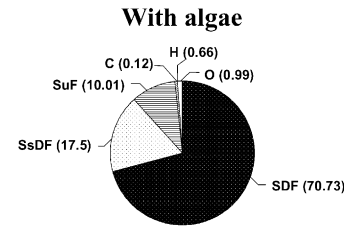
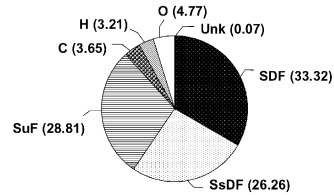
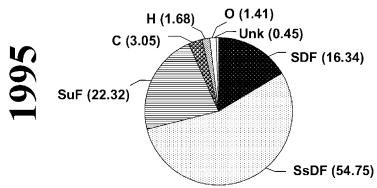
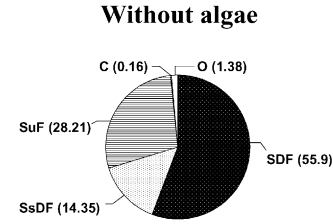
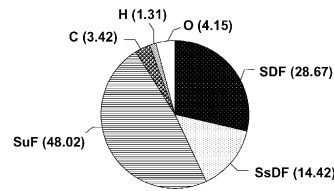
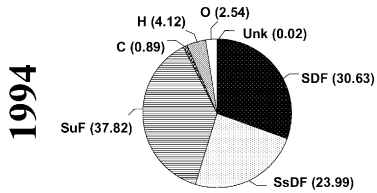
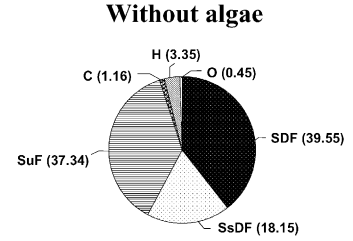
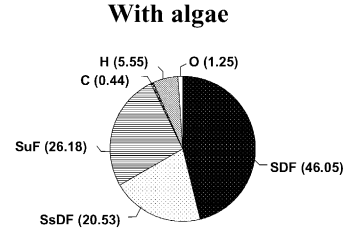
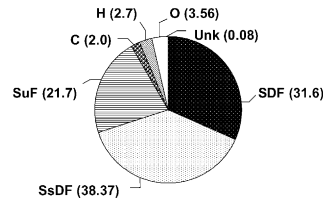
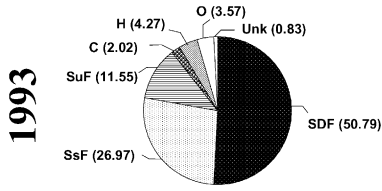


Fig. 6. Benthic assemblages of the Mondego estuary represented by trophic groups: surface-deposit feeders (SDF), subsurface-deposit feeders (SsDF), suspension feeders (SuF), carnivores (C), herbivores (H) and omnivores (O). Values are percentages of total individuals. (A) In the presence of *H. ulvae*; (B) in the absence of *H. ulvae*.

temporal gradient. The most representative groups are the surface-deposit feeders and herbivores due to the dominance of *H. ulvae*, with other groups comprising a small fraction of the community (Fig. 6A).

Omitting *H. ulvae* revealed that the percentage of different trophic groups at the three sites changed considerably along the eutrophication gradient and also over the study period (Fig. 6B). Macrofaunal communities were dominated numerically by detritivores (surface-deposit feeders, subsurface-deposit feeders and suspension feeders), which together accounted for more than 90% of total macrobenthic abundance (Fig. 6). There was evidence of a gradual decline in the percentage of herbivores and subsurface-deposit feeders from the *Z. noltii* beds to the most eutrophic area, while the surface-deposit feeders and suspension feeders were more abundant in the upstream areas. Suspension feeders were more abundant in the intermediate area.

The trophic structure of the *Z. noltii* beds also changed over the 3-year period. Herbivores and surface-deposit feeders declined, followed by an increase in subsurface-deposit feeders. Carnivores increased over the 3 years whereas omnivores declined (Fig. 6B).

In the most eutrophic area, trophic structure showed greater variability over time probably due to the temporary occurrence of algal cover. Given that the presence of macroalgae can have a dramatic effect on macrofaunal trophic structure (Pearson and Rosenberg, 1978; Norkko and Bonsdorff, 1996a,b), a separate analysis was carried out for the years 1993 and 1995 (both of which experienced blooms) for periods with and without algal cover. This analysis indicated that the trophic structure of the most eutrophic area is more impoverished compared to that of the *Z. noltii* beds. Surface-deposit feeders represented the dominant group in all years, except in 1995 during the period without algae. Suspension feeders, which fluctuated widely with macroalgal events, were more abundant during the periods without macroalgae, when the available suspended organic matter was presumably higher.

The trophic structure of the intermediate area was much more erratic over time. Surface-deposit feeders were the only consistent group throughout the study. Carnivores and omnivores were more consistent over time in this area.

4. Discussion

Over the last 20 years, eutrophication of the south arm of the Mondego estuary has promoted major biological changes. Seagrass beds declined rapidly throughout the 1980–1990 period, macroalgal blooms increased and there have been marked changes in the macroinvertebrate assemblages, principally a progressive impoverishment of the most impacted, inner area (Marques et al., 1997; Lillebø et al., 1999; Lopes et al., 2000; Martins et al., 2001; Pardal et al., 2000; Cardoso et al., 2002). These estuary-scale, temporal trends are mirrored in the present, relatively small-scale (1–2 km) eutrophication gradient documented here over a 3-year period.

With respect to trophic groups, the invertebrate assemblages were dominated (90%) by deposit-feeding species, indicative of the major role of detritus throughout the three sites. However, seagrass beds had more carnivores, herbivores and omnivores (8%) than the most eutrophic area (4%), and the percentage of herbivores and subsurface-deposit

feeders decreased from seagrass beds to the most eutrophic area. In contrast, surface-deposit feeders and suspension feeders increased from seagrass beds to the inner eutrophic area.

Interpreting these patterns is not straightforward. Seagrass beds provide a heterogeneous and complex habitat and thus support a higher diversity of both species and trophic groups, as reflected in our data. However, macroalgal blooms also create structural heterogeneity (Norkko and Bonsdorff, 1996a,b; Raffaelli et al., 1998) and may function as an enriched trophic resource, which can result in invertebrate assemblages of eutrophic areas being similar in structure to those of seagrass beds, as seems to have occurred in 1995. However, the benefits algae bring to the benthic fauna (habitat enhancement, food, refuge) are only temporary, because algal mats can shift position on the flats and they are highly seasonal. Also, macroalgal blooms have well-documented effects on the sediment physico-chemical environment and hence on invertebrate assemblages, but these may not be dose-dependent or monotonic (Raffaelli et al., 1998). A further complication is that over the 3-year period, there was a general decline in species diversity, especially in the seagrass beds.

Notwithstanding the above, there was a consistently higher proportion of subsurface-deposit feeders in finer sediment habitats of the seagrass bed, while surface-deposit feeders were more abundant in the more erosive sandy sediments of the eutrophic area. This coarse sediment area occasionally accumulated superficial detritus, but periodic scouring by currents removed this fine material (Gaston, 1987). Suspension feeders tended to be more abundant at the intermediate and most eutrophic areas, where, in the absence of vegetation cover, sediment resuspension and bedload transport are significant. Our results are broadly consistent with those of Bachelet et al. (2000) for French lagoons, although the trophic structure of the Mondego assemblages was much more dynamic through time. This probably reflects the progressive disappearance of seagrass at our site, which was relatively constant in the French study.

Our data are consistent with other, general eutrophication scenarios, viz. a replacement of one type of primary producer (seagrass) by another (macroalgae), declines in species diversity, and increase in detritivores and decline in herbivores and large increases in small deposit-feeding polychaetes (mainly *Alkmaria romijni*, *Capitella capitata*). Continued eutrophication is likely to lead to complete replacement of seagrass habitat in the Mondego by coarser sediments, mostly unvegetated except for occasional macroalgal blooms, and a variable invertebrate assemblage characterised mainly by opportunistic species. A central question that arises from this study is whether these changes are easily reversed. There is no shortage of policy instruments from the EC or nationally for addressing eutrophication in coastal areas and, although these are challenging to enact for socio-economic reasons, it would be technically possible to reduce nutrient enrichment in the Mondego. However, would the seagrass beds and their associated assemblages return? From the compelling evidence to date for seagrass beds in Australia (Kendrick et al., 2002) and northern Europe (e.g. Den Hartog, 1996; Van Katwijk and Hermus, 2000; Reise, 2002), we are not optimistic. The loss of seagrass from the eutrophic area of the Mondego and much of the intermediate area is associated with marked changes in the sediments of those areas, which have become coarser and more mobile, making re-colonisation by *Z. noltii* very difficult. The dynamics of this

system may well contain the hysteresis described by Scheffer et al. (2001) for a range of ecological systems and by van de Koppel et al. (2001) for intertidal flats. Re-establishment of seagrasses under such conditions may require additional active restoration initiatives such as coastal engineering to modify the sediment regime and transplantation of seagrasses (Van Katwijk and Hermus, 2000; De Jonge et al., 2000), rather than relying on natural re-colonisation. In other words, by replacing lost ecosystem components as well as removing the key stressors (Hobbs and Norton, 1996).

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