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**Patterns in estuarine macrofauna body size distributions: the role of habitat  
and disturbance impact**

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**ABSTRACT**

Schwinghamer's (1981) habitat architecture hypothesis for body mass spectra in marine sediments predicts a single macrofauna mode in response to the bulk nature of the sediment. This proposition was examined for intertidal macrofauna from a well-studied estuarine system, using kernel density estimation to define modality and the locations of peaks and troughs. Three sedimentary environments and habitats were examined along a disturbance gradient related to eutrophication. Our results indicate that bimodality is likely to occur within the macrofauna size range, which weakens the habitat architecture model and casts doubts on the mechanisms behind other modes in benthic size spectra. The location of the modes and intervening trough were not conservative and not apparently related to sediment grain size or habitat structure, but somewhat dependent on the presence of particular species: the presence or absence of large numbers of individuals of *Hydrobia ulvae* and larger-bodied taxa such as *Scrobicularia plana* and *Hediste diversicolor*. Alternative competing hypotheses are explored for the observed results, including Warwick's (1984) phylogenetic explanation, but taking into consideration both species composition and disturbance impact, it seems most likely Holling's (1992) textural discontinuity hypothesis, as a measure of resilience, could be a plausible explanation.

Keywords: Body mass; benthic macrofauna; sedimentary environments; eutrophication; resilience

## 1. INTRODUCTION

The significance of body size in community dynamics has a long history of interest in mainstream ecology from the early writings of Wallace, Darwin and Elton (Woodward et al. 2005), to explorations of the physiological, trophodynamic and behavioural correlates of body size and the broader patterns that arise (Peters and Wassenberg 1983, Peters 1983, Gaston and Blackburn 2003, Brown et al. 2004, Hildrew et al. 2007, O'Gorman and Hone 2012). Presenting information on the distribution of body size within ecological systems has implications for the ways such patterns are interpreted and hence what the underlying causes and processes may be. Representations include a simple scatter plot of body size against abundance (number of individuals or biomass), a constraint space (e.g. Lawton 1990, Brown 1995, Leaper et al. 2001), whilst for marine systems this has typically been as a bar chart of abundance or biomass against body size, the so-called body size spectrum (Warwick 2007). Such spectra are frequency histograms of either the body size of adult body weights of different species (e.g. Warwick 2007) or of all of the individuals present, regardless of their taxonomy (e.g. Schwinghamer 1981). Schwinghamer reported trimodality in such plots from benthic environments, the modes representing micro-, meio- and macrofaunal sized organisms, with a pronounced intervening trough between the meio- and macrofauna that he claimed was consistent in its location at around 0.5 to 1 mm equivalent spherical diameter (the diameter of a sphere the same volume (=biomass) as the organisms, Fig. 1). A similar conservativeness was reported by Warwick (1984, 1989) for frequency histograms of adult body mass of meiofauna and macrofauna, with a trough at a body mass of around 45  $\mu\text{g}$  (Fig. 1). This general bimodal pattern has since been confirmed by many authors (Gerlach et al. 1985, Gee and Warwick 1994), but not all (Duplisea and Hargrave 1996, Parry et al. 1999, Duplisea 2000). Schwinghamer's (1981) explanation for this modality and the conservative location of the trough between meiofauna and macrofauna is as follows: meiofauna predominantly have an interstitial lifestyle inhabiting the spaces between marine sediment particles, whilst macrofauna

are large enough to perceive the sediment as a bulk matrix. Few taxa can occupy the trough where the switch from one kind of habitat structure to another occurs. This “habitat architecture” model of marine benthic systems has at first sight a common sense appeal but has attracted its critics. For instance, a bimodal distribution may also occur in fine muds where an interstitial lifestyle is not feasible (Warwick 1984) or where there is no sedimentary restriction (Gee and Warwick 1994), and the spectrum in freshwater sediments has been reported as unimodal (Strayer 1986, Bourassa and Morin 1995) despite apparently similar physical sediment constraints as marine habitats.

Whilst there is clearly disagreement about the validity of Schwinghamer’s model, and hence his postulates about constraints on body sizes in sediments, all of these discussions are greatly confounded by the lack of rigour in defining and locating modes. For instance, Schwinghamer (1981, 1983) interpreted modality based only on visual inspection of spectra where body sizes had been grouped into bins (size classes) on a logarithmic scale. More objective statistical procedures for detecting modality are now available (Silverman 1981, Manly 1996). Here, we test the generality of Schwinghamer’s claim for a single mode for macrofauna by exploring body size distributions within the macrofaunal component of intertidal sediments from the Mondego estuary, Portugal, for a range of sediments and degrees of disturbance. Specifically, we test the conservatism of the modality in the size distribution within the macrofauna, using a rigorous statistical procedure, kernel density estimation (Silverman 1981, Manly 1996). According to Schwinghamer’s model a single mode should occur, independently of grain size or disturbance impact. If more than one mode is present, this seriously undermines the simple habitat architecture hypothesis, suggesting alternative hypotheses such as phylogenetic and trait differentiation hypotheses. In particular, if the body size spectrum and modality pattern change with disturbance, this may provide insights into the system’s ability to cope with stress. (Holling 1992, Allen et al. 2005, 2006).

## 2. MATERIALS AND METHODS

### 2.1. Study site

The Mondego estuary is located in a warm temperate region, on the Atlantic coast of Portugal (40°08'N, 8°50'W). It is a small estuary (8.6 km<sup>2</sup> in area), with two arms (north and south) of distinct hydrological characteristics, separated by an island (Fig. 2). The north arm is deeper (4-10 m during high tide, tidal range 1-3 m), is a main navigation channel, hosts a harbour, and has the Mondego River as the main freshwater input. The south arm is shallower (2-4 m during high tide, tidal range 1-3 m) and characterized by large areas of exposed intertidal flats during low tide (about 75% of the total area). The downstream areas of the south arm support *Spartina maritima* marshes and a *Zostera noltii* (seagrass) meadow, but in the upstream areas the seagrass community has completely disappeared and blooms of the opportunistic macroalgae *Ulva* spp. were common. Until the end of 1998, 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. 2). The Pranto river was artificially controlled by a sluice, according to rice field irrigation needs in the lower Mondego valley, and has historically contributed to the delivery of large amounts of nutrient to the estuary (Leston et al. 2008, Cardoso et al. 2010).

In common with other estuaries worldwide, the south arm of the Mondego estuary has suffered from eutrophication over the last 20 years. Changes have been observed in the quality and quantity of primary and secondary production, with huge increases in macroalgal productivity, concomitant with decreases in seagrasses (Cardoso et al. 2010) and general impoverishment of the biotic communities (Leitao et al. 2007, Grilo et al. 2011, Dolbeth et al. 2011). A restoration and management programme was implemented in 1998 to control and reverse eutrophication and its main effects, which included experimental mitigation measures, such as hydrological management to increase circulation and diversion of nutrient-rich freshwater inflow to the estuary. These changes have been monitored over the past 20 years

(e.g. Patrício et al. 2009, Cardoso et al. 2010, Dolbeth et al. 2011 and references therein), providing a large database and comprehensive background information on the eutrophication process and on the efficiency of the measures to control eutrophication and restore the original seagrass community.

For the present study, data on the macrobenthic communities were used from three different habitats along a eutrophication gradient in the south arm (Fig. 2): 1) a seagrass area, characterized by muddy sediments covered with *Zostera noltii*, high organic matter content (mean  $6.2\% \pm \text{s.d. } 1.76$ ) and high water flows ( $1.2 - 1.4 \text{ m s}^{-1}$ ); 2) a mudflat area, with some macrophyte rhizomes in the sediment, physical-chemical conditions similar to those of the seagrass area but with lower sediment organic matter content ( $5.8\% \pm \text{s.d. } 1.3\%$ ); and 3) a eutrophic sandflat area, which has not supported rooted macrophytes for more than 20 years, has a lower organic matter content (mean  $3.0\% \pm \text{s.d. } 1.14$ ), lower water flows ( $0.8 - 1.2 \text{ m s}^{-1}$ ) and was regularly covered seasonally by green opportunist macroalgal blooms before 1998.

This combination of different sedimentary environments – mud vs sand, vegetated vs unvegetated and across a disturbance gradient – provides a range of comparisons for assessing the degree of conservativeness of the macrofauna part of the benthic body size spectrum.

## **2.2. Sampling programme, laboratory procedures and data analyses**

Samples had been taken at low tide, fortnightly from February 1993 to June 1994 and monthly until 2002. On each sampling occasion and at each site, 6 to 10 cores ( $141 \text{ cm}^2$ ) were taken to a depth of 20 cm and washed in  $500 \mu\text{m}$  mesh sieve bags, and one sediment sample was taken for particle size analysis. At the same time, water samples were collected for analysis of dissolved inorganic nitrogen and phosphorus. In the laboratory, the water samples were immediately filtered (Whatman GF/F glass-fibre filter) and stored frozen, until analysis following standard methods as described in (Leston et al. 2008). The fauna from sediment cores was separated and preserved in a 4% buffered formalin solution. Plant material within the

cores was sorted and separated into green macroalgae and *Z. noltii*. For both faunal and plant material, the ash-free dry weight (AFDW) was measured after combustion for 8 h at 450°C. The sediment samples were dried at 60°C for 48 hours and analysed for grain size using the classical methods of sieving for the coarse grained material. Median particle size and sorting coefficient were defined for each site using GRADISTAT software (Blott and Pye 2001).

*Zostera noltii* biomass variation over the years was analyzed using simple linear regression, assuring assumptions were fulfilled after visual inspection of the residuals, using R software (R Development Core Team 2008). Macrofauna diversity was expressed as the number of species (richness) and Pielou's index. Diversity, density and biomass in the pre-mitigation (before 1998) and post-mitigation periods were compared using 1-way ANOSIM within the PRIMER software.

### **2.3. Methods for detecting modality in body size distributions**

The body size (mass) distributions in each sample were explored for modality after Silverman (1981) and Manly (1996). Species weights (mg AFDW) were transformed to  $\log_{10}$  and the degree of smoothing required to produce an n-modal body mass spectrum estimated, having as the null hypothesis that the distribution is unimodal (Manly 1996). This method, Kernel density estimation and smoothed bootstrap re-sampling (based on 1000 randomizations) allows estimation of the number of modes present in the body mass distribution and of the location (body sizes) of any modes and troughs. The procedure tests whether a distribution with k+1 modes fits significantly better than a distribution with k modes, thus determining the optimum modality of the data. The analyses were performed using the software produced by Dr Jim Smart (2005) in R 2.8.1 (R Development Core Team 2008), used here with his permission, coded for the algorithms provided by (Silverman 1981, Manly 1996).

## **4. RESULTS**

Results section is structured as follows. First, we present an analysis of the three main habitats with respect their major environment characteristics and their biological assemblages and how these have changed over time relative to disturbance (eutrophication). Then, having established this context, we present an analysis of the macrofaunal size spectra at those sites for three critical time periods: 1993, 1999 and 2002.

#### 4.1. Nutrients, sediment characteristics and plant dynamics

The N/P ratio showed a decline after 1998 for all study sites (Fig. 3A), reflecting two distinct scenarios for the estuary before and after the implementation of management measures aimed at reducing nutrient input into the system (see Materials and Methods, Study site).

Median grain size (MGS) at the sites indicated fine sands for both seagrass and mudflat areas, ( $MGS = 2.7\phi \approx 1.5$  mm, moderately sorted), and medium sands for the sandflat area ( $MGS = 1.7\phi \approx 1.5$ mm, moderately sorted). The percentage of silts and clay was higher for both the mudflat (varied between 22-45%) and seagrass areas (varied between 20-29%), compared to the sandflat area (between 9-12%).

With regard to *Zostera noltii* biomass, there was a significant annual decline over the pre-mitigation period, from 1993 to 1997 (Fig. 3B, simple linear regression, assumptions verified by inspection of the residuals:  $R^2 = 0.8322$ , d.f. = 41,  $p < 0.001$ ), reaching its lowest areal cover in 1997 (0.7 ha, Fig. 1). After the mitigation measures in 1998, there was a gradual recovery of the seagrass bed until 2002 (Fig. 3B, simple linear regression:  $R^2 = 0.5866$ , d.f. = 42,  $p < 0.001$ ), with significant differences in biomass between pre-mitigation and post-mitigation periods (Student's t-test,  $t_{[43,44]} = 4.7$ ,  $p < 0.001$ ). Almost no green macroalgae were recorded in the *Zostera* area (Fig. 3C).

In the sandflat area, there was a macroalgal bloom in spring 1993 (maximum biomass of 377 to 452 g AFDW  $m^{-2}$  in April), followed by a crash in early summer (Fig. 3C). In 1995,

algal biomass again reached high values, but not enough to be considered a spring bloom (maximum biomass of 111 g AFDW m<sup>-2</sup> in April 1995) (Fig. 3C). Differences were evident in macroalgae biomass between the pre- and post-mitigation periods, since blooms were never recorded again after 1998 (Fig. 3C). This area has not supported seagrasses for more than 20 years. Some algae were recorded in the mudflat, but not enough to be considered a bloom (Fig. 3C).

#### 4.2. The macrofauna community

Eighty-two different taxa were recorded over the 10-year period. The seagrass beds generally supported more species than the other areas, with this difference was more pronounced in the pre-mitigation period (Fig. 4A). Nevertheless, evenness was higher in the mudflat and sandflat areas (Fig. 4B), mainly due to the dominance of *Hydrobia ulvae* in the *Z. noltii* beds (as detailed by Grilo et al. 2011). For all areas, there was a clear decline in the number of species during the pre-mitigation period. Following the introduction of the management plan in 1998, species richness increased, but in 2000/01, during a high rainfall event, there was a further decline in species richness. After this event, species richness only started to recover again in 2002 for all areas. There were significant differences when comparing diversity for the pre- and post-mitigation periods for all areas (ANOSIM,  $p = 0.001$ ), except for Pielou's index in the seagrass area ( $p > 0.05$ ). However Global R was always lower than 0.45 (Global R = 0.45 for seagrass and  $< 0.15$  for the other areas).

The trends in density and biomass are broadly similar to those of diversity. In general, both density and biomass were higher in the seagrass beds than in the mudflat and sandflat areas (Fig. 4C, D). Mean densities showed a clear seasonal pattern in the seagrass and mudflat areas, with higher values in spring/summer throughout the study period, and densities were lower in the post-mitigation period (Fig. 4C). In the sandflat area, mean density and biomass were higher during spring 1993 and spring 1995 (Fig. 4C, D), matching those periods of higher

macroalgal biomass (Fig. 3C). After those periods, there was a general decline in total density throughout the period (Fig. 4C), while mean biomass increased considerably in the post-management period, maintaining similar values for all years, with only a slight decrease in 2001 following a flood event (Fig. 4D). In contrast, in the seagrass beds mean biomass declined at the beginning of the post-management period, after which there was an increase until 2000/01, increasing again after that year (Fig. 4D). The lowest biomass was observed in the mudflat area, but with a gradual increase perceptible during the post-management period (Fig. 4D). For density and biomass, there were significant differences between pre- and post-mitigation periods for all areas (ANOSIM,  $p = 0.001$ ), except for biomass in the mudflat area ( $p > 0.05$ ). Nevertheless, Global R was always lower than 0.27, suggesting that other factors might be influencing the observed variations patterns of density and biomass (e.g. seasonal variations).

### 4.3. Macrofauna size spectra

We selected data (mean individual body mass and abundance) from autumn (September to December) for comparisons between sites and years. Mean individual body mass ranged from  $1\mu\text{g}$  to  $470\text{mg}$  AFDW, equivalent to a  $\log_{10}$  mg AFDW of -3 to +3.

Statistically significant troughs were found in the body mass distributions, indicating bimodality (Table 1), modes corresponding to the highest abundance peaks within the body mass spectra in each habitat and year (Fig. 5). It should be noted that the size spectrum obtained here spans Warwick's (1984) predicted meiofauna/macrofauna trough at  $28\mu\text{g}$  AFDW ( $-1.6 \log_{10}$ , Fig. 1), but the troughs detected here were much larger, within  $0.89\text{mg}$  to  $1.23\text{mg}$  AFDW ( $-0.05$  to  $0.09 \log_{10}$ ) (Table 1). Thus, the bimodality detected here is not a reflection of a meio-macrofaunal trough.

A single mode was observed in the seagrass area, where *Hydrobia ulvae* is the most abundant species, whilst one or two modes were found in the mudflat (which had similar

sediment characteristics to the seagrass area) and sandflat areas (Table 1, Fig. 6A-C). When *H. ulvae* comprised more than 78% of all the individuals present (Table 1) only a single mode was detected, irrespective of sediment grain size or vegetation cover.

Where two modes were recorded, the location of the trough between them was not conservative, varying from 0.89mg to 1.23mg AFDW (Table 1), depending on the habitat (Fig. 6A-C) and the year (Fig. 6D-F).

For our analysis of the effects of disturbance (eutrophication) on macrofaunal modality, we selected three time periods: 1993, the reference condition for the seagrass, with the highest *Z. noltii* biomass values in this year (Fig. 3A), the highest species number for all areas (Fig. 4A), but after the occurrence of a macroalgal bloom in the sandflat; 1999, just after the mitigation measures were introduced when the biomass and spatial extent of *Z. noltii* were at their lowest, as was invertebrate abundance for all study areas; 2002, a recovery period, when *Z. noltii* recovered to occupy the same spatial cover as in 1993, 1.6 ha (Fig. 2), but where seagrass biomass (Fig. 3B) and macrofaunal species richness (Fig. 4A) were 40-50% less than in 1993.

In 1993, a single mode composed mainly of *H. ulvae* (>80% of the community by numbers, Table 1) was recorded for all areas. The mode was at a larger body size in the seagrass compared to the mudflat and sandflat areas (Fig. 6D).

In 1999, there was a single mode in the seagrass samples, dominated by *H. ulvae* (Table 1), but at a slightly lower body mass when compared to 1993 (Table 1, Fig. 6A). In the mudflat two modes occurred (Fig. 6E), a smaller one comprising mainly *H. ulvae* at a similar body size to that in 1993 (Fig. 6B) and a larger one due to *C. carinata* and *S. plana* (Table 1). In the sandflat area, two modes were apparent (Fig. 6F), the smaller mainly due to *H. ulvae* and Oligochaeta and the larger of *S. plana*, *C. carinata* and *H. diversicolor* (Table 1).

By 2002, both seagrass and mudflat areas had only one mode, similar to 1993 (Table 1, Fig. 6F), but with larger body sizes than in 1993 (Fig. 6A-B). The mode in the mudflat area in

2002 was located within the trough located in 1999 (Fig. 6B). In the sandflat area, green macroalgae biomass was practically zero, and species number and density were similar to those obtained for the whole post-mitigation period (Fig. 3A, C), with slight lower values for biomass (Fig. 3D). A similar pattern to that for 1999 was seen in the body size spectra: the presence of two modes (Table 1, Fig. 5C), yet the smaller mode defined in 2002 was at a larger body size than in 1999 (Fig. 6F), with more species present than in 1999 (Table 1).

A comparison of the three years shows that modes were in general at smaller body sizes in 1993 than in 1999 and 2002 for all areas (Fig. 6, Table 1), suggesting an overall increase in the body sizes of the main species in the post-mitigation period.

## 5. DISCUSSION

The technique used here used to investigate modality - kernel density estimation combined with smoothed bootstrap re-sampling - is a powerful approach that produces objective statistical tests for the presence of modes and their location, and is more rigorous than previous approaches such as “eye-balling” of distributions which is highly dependent on the bin-sizes used. It is more conservative than Holling’s Body Mass Difference Index, distribution mixtures or other techniques with a priori defined weight classes (Manly 1996, Raffaelli et al. 2000); when Manly (1996) used kernel density estimation on Holling’s original data, he found fewer modes and troughs. The method has been used before successfully to determine modality patterns in body size spectra for several taxonomic groups (e.g. Leaper et al. 2001, O’Gorman and Hone 2012). We are therefore confident that our analyses reflect the most likely modality found in the benthic body size spectra analysed.

The habitat architecture hypothesis proposed by Schwinghamer (1981) for the location of trough and modes in benthic body size spectra predicts a single macrofauna mode in response to the bulk nature of the sediment habitat. Our analyses indicate that bimodality may occur within the macrofauna size range and that the location of the modes and intervening trough are

not conservative and therefore cannot be easily related to sediment grain size or habitat structure, but are somewhat dependent on the presence of particular species: the presence or absence of large numbers of individuals of *H. ulvae* and the effects of larger bodied taxa such as *S. plana* and *H. diversicolor*. It is clear that the meiofauna-macrofauna two-modes model for body sizes in marine sediments in relation to underlying habitat architecture, is over-simplistic and that the macrofaunal modality may be expected to vary. If this is true for the macrofauna, where no obvious architectural structuring processes seem to be present, then the location of the meiofauna-macrofauna trough may be equally well explained by non-architecture hypotheses, such as the phylogenetic explanations. For example, polychaetes and bivalves are typically large and nematodes and other meiofauna are typically small, perhaps for the reasons suggested by Warwick (1984). He proposed that the meio- and macrofaunal modes represented fauna with different size-related biological traits that switch at the location of the meiofauna/macrofauna trough (45 $\mu$ g), each mode presenting optimized traits for feeding behavior, life history and reproductive mode (e.g. direct benthic vs planktonic development) in order to avoid predation and competition (Warwick 1984). Whilst this could account for the meio-macrofaunal trough, such explanations are unlikely to apply to the macrofaunal distributions reported here. In our study, whenever two modes were detected, the larger included always at least one of the species *C. carinata*, *H. diversicolor* and *S. plana*, while the smaller mode was composed by *H. ulvae* and small opportunist annelids. Also, the location of trough was not conservative, nor within the expected weight according to Warwick's hypothesis. Apart from size that changed considerably over time and habitat, similar traits (e.g. life span, mobility, burial depth) could occur in both of the macrofauna modes (Dolbeth et al. 2013). However, the smaller species were mainly strictly deposit feeders with shorter life spans and dominant in habitats with a higher percentage of organic matter, while the larger species had more diverse feeding behaviors (i.e. higher percentage of omnivore species) and longer life spans. So, size range patterns probably result from a mixture of several effects (Allen et al.

2005), including availability of resources, which might condition the presence of specific traits in certain years (Dolbeth et al. 2013) or species behavioral changes (e.g. diet shifts for *S. plana* (Baeta et al. 2009) and energy allocation. This was especially evident during the disturbed conditions, which presented a single mode produced by smaller r-strategist species.

With regard to the meiofaunal size range, Raffaelli et al. (2000) were unable to clearly differentiate between a single or two modes for the meiofauna of an estuarine benthic assemblage, using the same kernel density procedures as performed here. Similarly, Yamanaka (2010) recorded several modes in both the meiofaunal and macrofaunal body size range in a number of estuarine benthic communities in the UK. Taken together with the results presented here, it would seem that explanations which appear plausible for the meiofaunal-macrofaunal trough are unlikely to be able to be extended to troughs between modes within the meiofaunal or macrofaunal size range. (Allen et al. 2006) review the possible processes generating body size modality in assemblages, including community interactions, phylogenetic, biogeographic and Holling's textural discontinuity hypothesis, whereby gaps in body size distributions may represent equivalent discontinuities in different dominant ecological processes operating at different spatial and temporal scales. What those dominant processes might be for the Mondego estuary is unknown, but an intriguing corollary of Holling's (1992) theory is that such discontinuities reflect heterogeneity in the system which promotes community resilience. Discontinuities should persist until the system is pushed beyond the limits of its resilience, when a different pattern should emerge (Allen et al. 2005). Our findings are consistent with that proposal. The sandflat area displayed a bimodal pattern in the post-mitigation period, perhaps indicating greater resilience than the mudflat and seagrass areas, which had a unimodal pattern. Dolbeth et al. (2007, 2011) suggested that the sandflat area, following disturbance by macroalgal blooms and following mitigation measures, might have reached a new stable state whilst the seagrass and mudflat areas are still recovering, consistent with the present results. Also, when comparing the location of the modes for the 3 areas, the sandflat area in the post-

mitigation period presented larger body sizes than for the other areas, which is consistent with a recovery of the system due to the presence of slow-growing species that can attain higher body mass, such as *S. plana*, *H. diversicolor* or *C. carinata*, a pattern also noted by Dolbeth et al. (2011, 2013).

Analysing each area alone, the location of the modes are also consistent with a possible gradual recovery of the system and higher resilience in later years, which were at a higher body mass in 2002 for the seagrass and in 1999 and 2002 for the mudflat and sandflat areas. This is indicative of more individuals with larger body mass. In the seagrass, body mass was associated mainly with *H. ulvae*, which in later years presented more structured populations, with a higher percentage of adults and less domination by juveniles (Grilo et al. 2012). In the mudflat in 1999 and sandflat areas in both 1999 and 2002, this was due to the K-strategists mentioned above with a higher investment in body mass. So, although *Z. noltii* biomass was highest in 1993, the severe effects of eutrophication (including the macroalgal blooms) were noticeable in the three study areas, confirmed by the lower body mass, i.e. small opportunist species, whose abundance was mostly subsidised by the macroalgae (Dolbeth et al. 2007).

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**Table 1.** Significant modes and troughs (in mg AFDW and  $\log_{10}(\text{mg AFDW})$  between brackets,  $p < 0.05$ , ns = non significant) found in body mass distributions for benthic communities of the Mondego estuary, with indication of the main species within the mode and their density percentage relative to the community total density.

		1993	1999	2002
SEAGRASS	Mode weight Species %	<b>0.62mg (-0.21)</b> <i>H. ulvae</i> : 86%, <i>H. filliformis</i> : 1%	<b>0.39mg (-0.41)</b> <i>H. ulvae</i> : 85%	<b>1.91mg (0.28)</b> <i>H. ulvae</i> : 90%
	Trough	ns	ns	ns
MUDFLAT	Mode(s) weight Species %	<b>0.11mg (-0.97)</b> <i>H. ulvae</i> : 87%, <i>C. edule</i> : 1%	<b>0.067mg (-1.18)</b> <i>H. ulvae</i> : 47%; <b>6.01mg (0.78)</b> <i>C. carinata</i> : 3%, <i>S. plana</i> : 30%	<b>0.51mg (-0.29)</b> <i>H. ulvae</i> : 78%
	Trough	ns	<b>0.89mg (-0.05)</b>	ns
SANDFLAT	Mode(s) weight Species %	<b>0.14mg (-0.86)</b> <i>H. ulvae</i> : 82%	<b>0.14mg (-0.86)</b> <i>H. ulvae</i> : 43%, Oligochaeta: 1%; <b>7.62mg (0.88)</b> <i>C. carinata</i> : 21%, <i>H. diversicolor</i> : 1%, <i>S. plana</i> : 25%	<b>0.28mg (-0.55)</b> <i>A. romijni</i> : 4%, <i>H. ulvae</i> : 32%, <i>C. capitata</i> : 1%; <b>4.06mg (0.61)</b> <i>C. carinata</i> : 31%
	Trough	ns	<b>1.23mg (0.09)</b>	<b>1.05mg (0.02)</b>

**Figure captions**

**Fig. 1.** Theoretical benthic biomass size spectrum, with indication of the modes and trough body mass in spherical equivalent diameter as proposed by Schwinghamer (1981), dry weight (DW) by Warwick (1984) and the equivalent in ash free dry weight (AFDW) and  $\log_{10}$  (mg AFDW) units. Body mass was converted to AFDW using Brey (2001) conversion factors.

**Fig. 2.** Location of the Mondego estuary showing sampling stations. Expanded maps show the evolution of the *Zostera noltii* bed's area extension, since 1986 until 2002.

**Fig. 3.** Long-term variation of: (A) N/P atomic ratio for all study areas; (B) *Z. noltii* biomass in the seagrass area; and (C) macroalgal biomass for all study areas, with indication of the selected sampling periods. In x-axis: J, January; M, May; S, September.

**Fig. 4.** Long-term variation of: (A) species richness; (B) evenness; (C) mean biomass; and (D) mean density, for all study areas, with indication of selected studied sampling periods. In x-axis: J, January; M, May; S, September.

**Fig. 5.** Abundance – body size spectrum for benthic communities from the Mondego estuary, considering the 3 habitats, seagrass, mudflat and sandflat and years. Abundance data have been square-root transformed for illustrative purposes.

**Fig. 6.** Superimposed significant kernel density distribution curves ( $p < 0.05$ ) per habitat (A) seagrass, (B) mudflat and (C) sandflat; and per year: (D) 1993, (E) 1999 and (F) 2002.

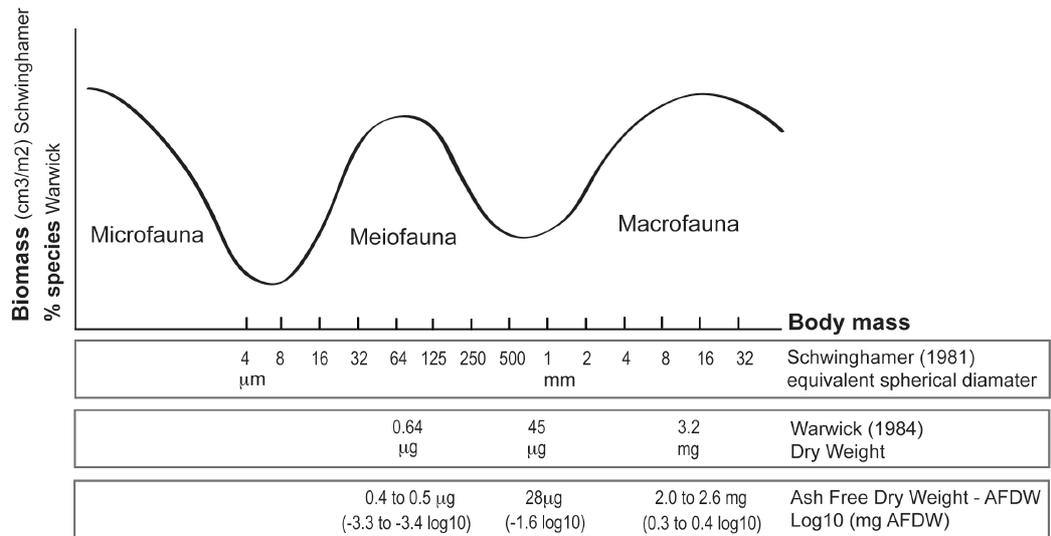


Fig. 1

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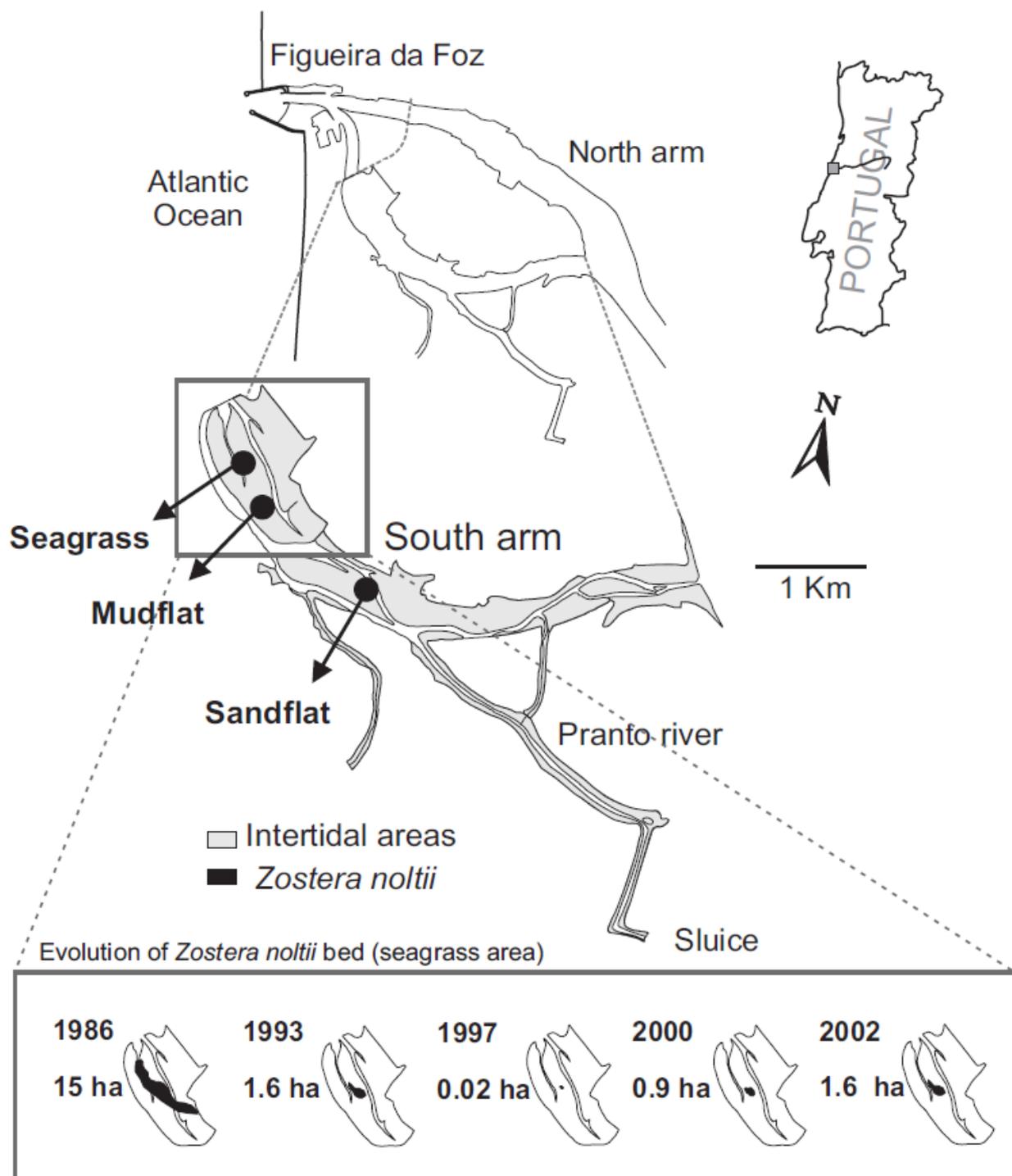


Fig. 2

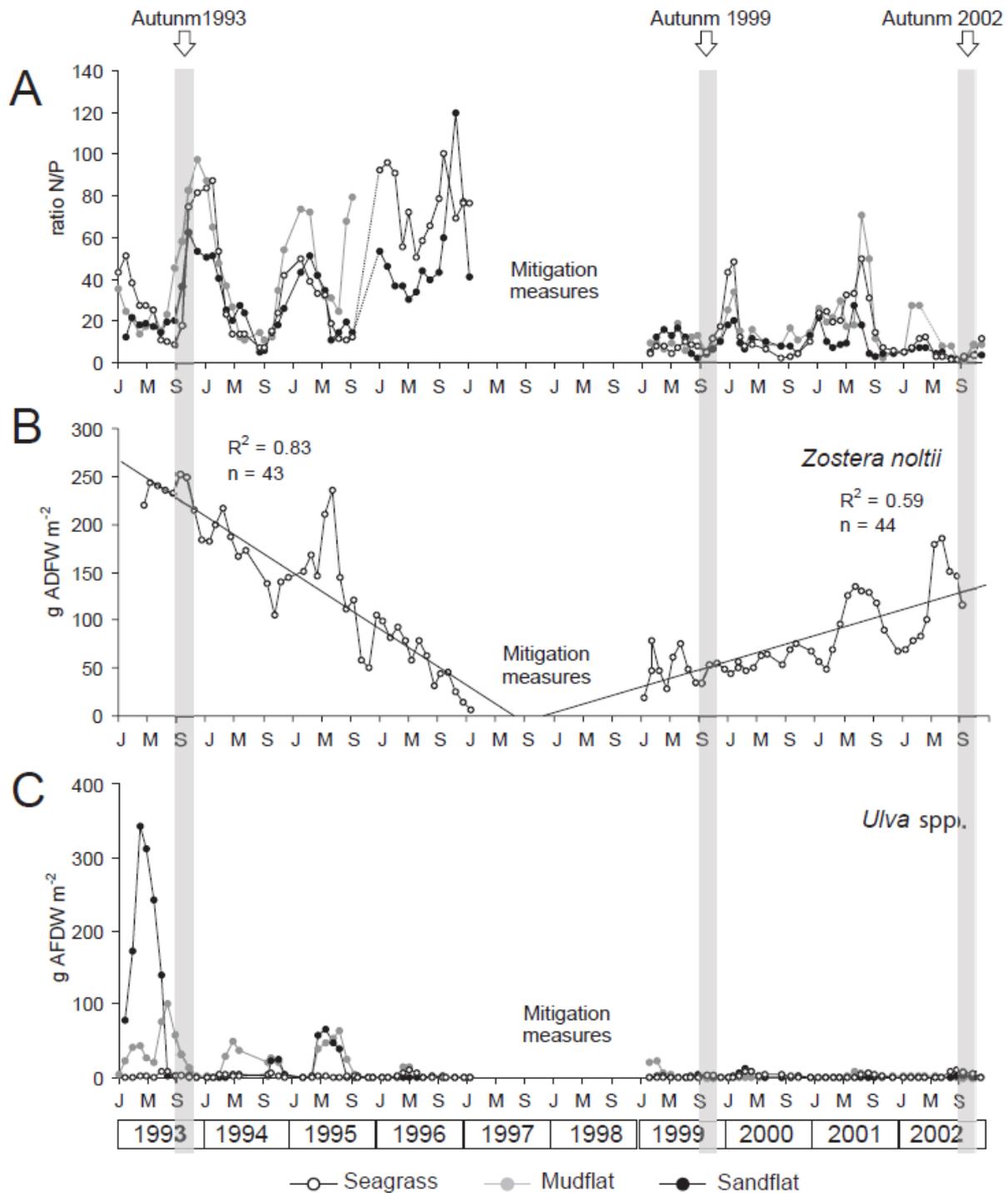


Fig. 3

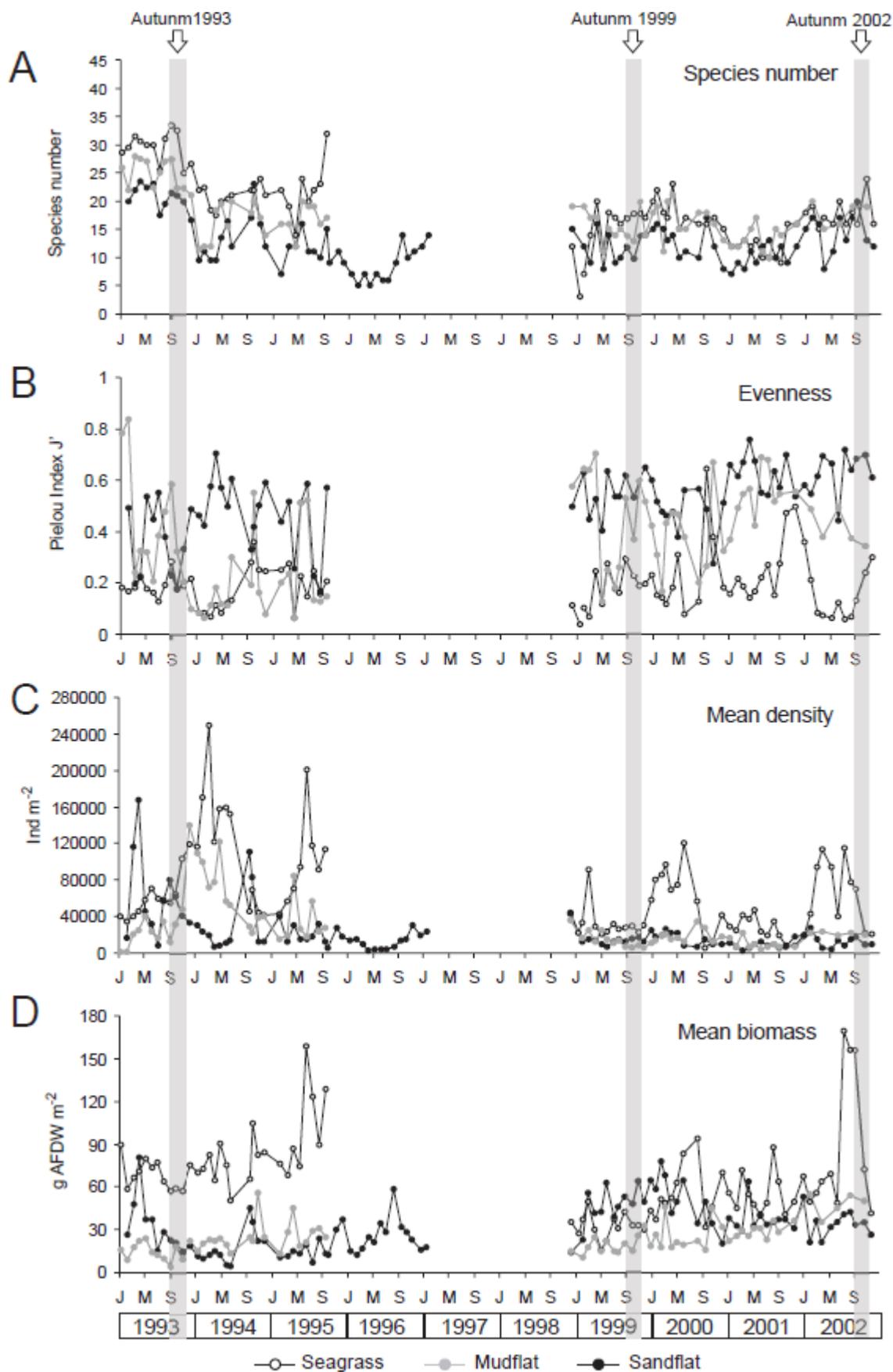


Fig. 4

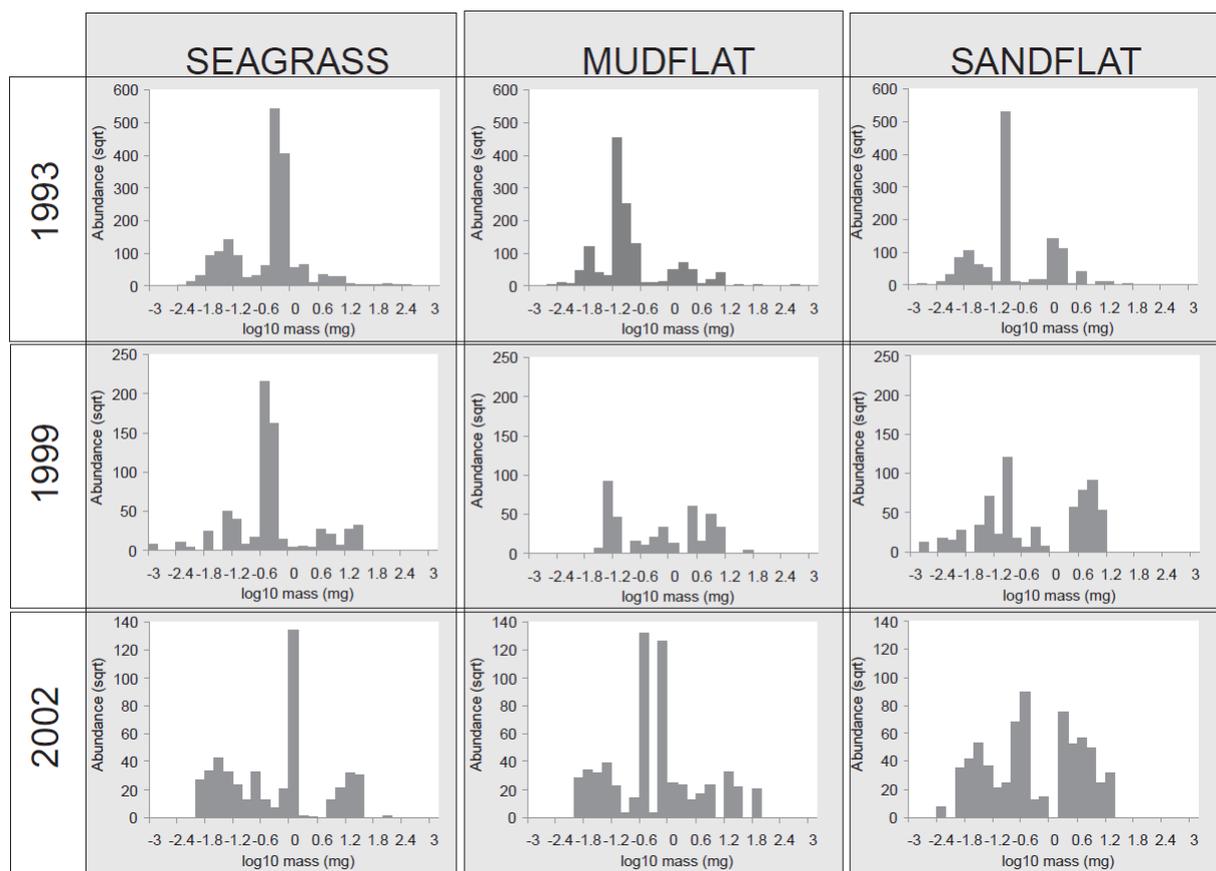


Fig. 5

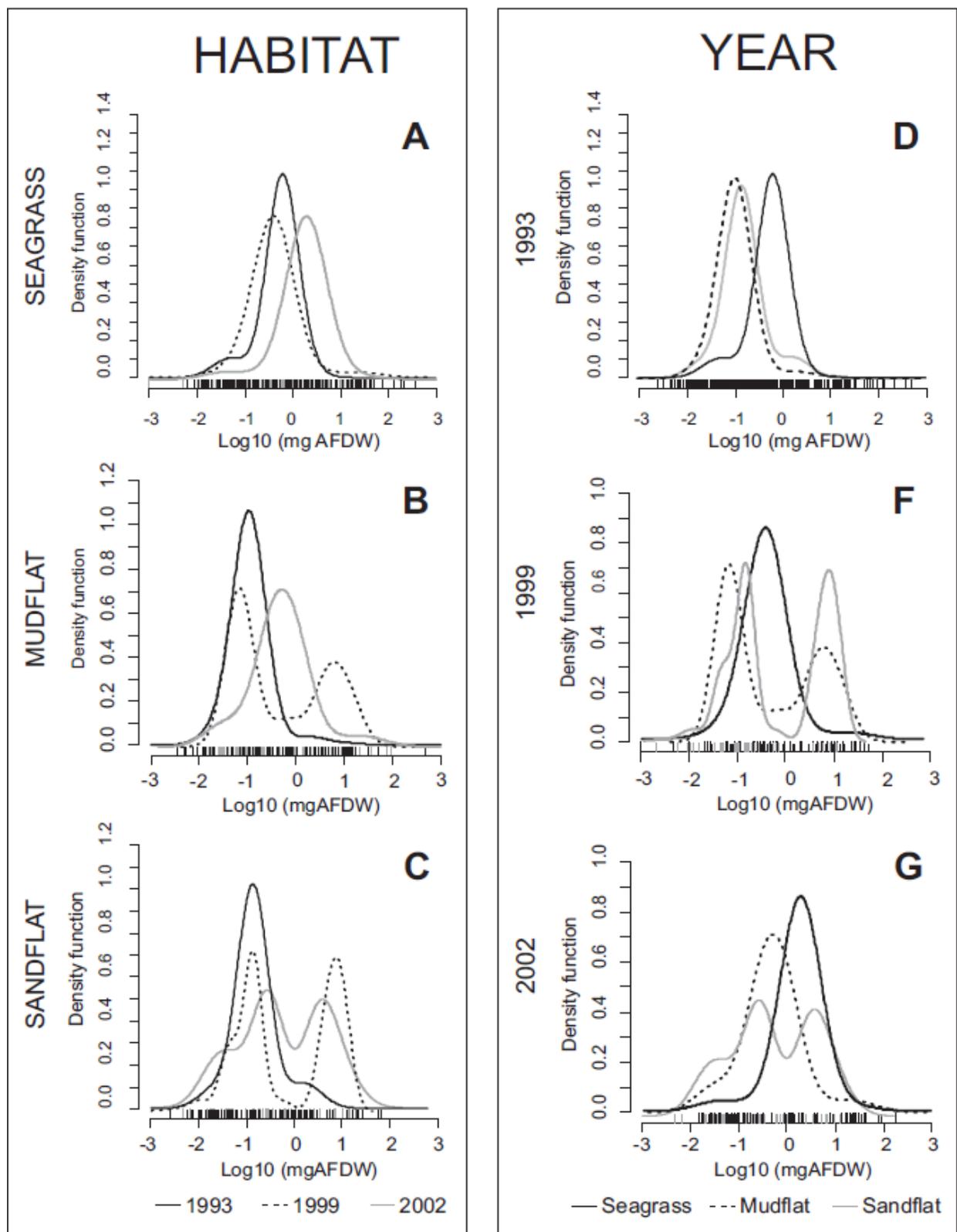


Fig. 6

**Highlights**

Body size spectra of estuarine intertidal macrofauna were examined

Three sedimentary environments and habitats were studied along an eutrophication gradient

Results showed that one or two modes could occur within the macrofauna size range

Body size spectra were apparently not dependent on the bulk nature of the sediment

Bimodality was considered as a measure of resilience towards disturbance events

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