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PRIMARY RESEARCH PAPER

Resilience of an isopod population (*Cyathura carinata*) to multiple stress factors in a temperate estuarine system

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Abstract The Mondego Estuary (Portugal) underwent major modifications in the late 1980s, because of eutrophication, for which it was developed a restoration programme that has been effective in recovering seagrass beds. Recently, this system has been affected by successive weather extremes: floods, droughts, and heat waves. The effect of these multiple stressors on a *Cyathura carinata* (Isopoda) population has been evaluated, through a long-term data series (16 years) in a seagrass bed, an intermediate area, and a sand flat. A well age-structured and abundant population of *C. carinata* was observed in the sand flat, in contrast with the seagrass bed and intermediate area. After introducing the restoration measures, *C. carinata*'s abundance increased even in the stations where it was formerly scarce. This recovery was compromised by successive extreme events. *C. carinata* declined severely in terms of total abundance and growth production during the 2003 summer heat wave, at the sand flat, also endangering its reproductive success. Floods and droughts affected dispersion of the individuals, which was reflected in the population's density and production. Nevertheless, this isopod had great resilience, recovering successfully after disturbances. In contrast, the population of *C. carinata* had less resilience in the seagrass bed and intermediate area, being unable to recover after a succession of disturbances, which may threaten the success of this species in the system. Because the frequency and intensity of weather extremes are expected to continue to increase in a scenario of global climate change, their repercussions will affect such populations, which will have difficulty surviving. This will have severe implications on the functioning of the whole ecosystem.

Keywords Isopod · Estuaries · Population dynamics · Eutrophication · Climate change · Long-term study

Introduction

Estuaries are naturally stressed ecosystems that are, at the same time, subjected to anthropogenic impacts

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(Elliot & Quintino, 2007). As a result of human pressure associated with increasing coastal socio-economic development, estuarine systems are not only exploited for their resources, but also function as receivers of organic matter, nutrients, and pollutants (McLusky & Elliot, 2004). Moreover, they are susceptible to the climate variability that is one of the greatest environmental, social, and economic threats menacing the planet nowadays (Harley et al., 2006). Erratic weather patterns, for example precipitation unpredictability (with increased risks of floods and droughts) and temperature variability (reflected on the increasing number of episodic heat waves), are becoming more frequent (IPCC, 2007; Roth et al., 2010). The scale and array of climatic alterations in the physical environment may induce substantial responses in the biota (Harley et al., 2006). Ecologists are confronted with a new challenge: the comprehension of how natural ecosystems will respond to changing environmental conditions in the present and also to unpredicted events that may take place in the future (Harley et al., 2006). Given this period of global change, it becomes crucial to understand the state and functioning of a given ecosystem, before new alterations occur. Biota responses to multiple stressors can be manifested as alterations in the abundance, diversity, and fitness of individuals, populations, and communities (Adams, 2005). A significant approach is to examine the effect of these stressors in terms of population dynamics of key species present in the systems, by use of long-term data series that demonstrate how species behave in both “normal/regular” (absence of stochastic events) and “atypical” years (occurrence of stochastic events).

In the late 1980s the Mondego Estuary went through eutrophication processes. This led to a decline of overall environmental quality and, consequently, to reduction of the beds of the seagrass *Zostera noltii*. In 1998, implementation of a restoration programme improved environmental quality, by ameliorating water transparency, reducing water residence time, and reducing nutrient loading (for more details see Lillebø et al., 2005; Dolbeth et al., 2007; Ferreira et al., 2007; Cardoso et al., 2010). This also resulted in recovery of the seagrass beds. Besides the anthropogenic impact, this estuary, similar to other systems worldwide, is being more frequently affected by extreme climate events. Heat waves, floods, and droughts have additional consequences on the macrobenthic communities that have been recovering from eutrophication. The decline in environmental quality because of anthropogenic effects associated with extreme weather episodes may lead to a slow recovery of the system (Cardoso et al., 2008a, b).

The main objective of this study was to assess the response of the isopod *Cyathura carinata* population to a succession of anthropogenic (eutrophication) and climate events (floods, droughts, heat waves) that occurred during a 16-year period in the Mondego Estuary. This anthurid isopod reaches high abundances in this system and contributes greatly to the overall production of the estuary (Dolbeth et al., 2007; Ferreira et al., 2007). It is a euryokous, tube-dwelling predator, regarded as a key macrobenthic species in estuarine trophic webs (Bamber, 1985; Olafsson & Persson, 1986; Ferreira et al., 2004, 2007). Being a typical estuarine species, it tolerates fluctuating environmental conditions, and is thus capable of succeeding in this naturally variable ecosystem (Jazdzewski, 1969; Burbanck & Burbanck, 1979; Bamber, 1985). Despite this capability, it is important to understand how this population reacts to atypical climate events, because of its important role in the estuarine community. Accordingly, this work focussed on *C. carinata*’s ability to cope with multiple stressors, by surveying its population structure, dynamics, reproductive biology, and secondary production.

Materials and methods

Study site

The Mondego Estuary is a temperate coastal system located on the Atlantic coast of Portugal (40°08′N; 8°50′W). It comprises two arms, north and south, separated by the Murraceira Island (Fig. 1). The north arm is deeper (4–8 m during high tide, tidal range 1–3 m), highly hydrodynamic, and is the main navigation channel that supports 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. Until the implementation of the restoration programme in 1998 (for more details see Dolbeth et al., 2007; Cardoso et al., 2008a), the south

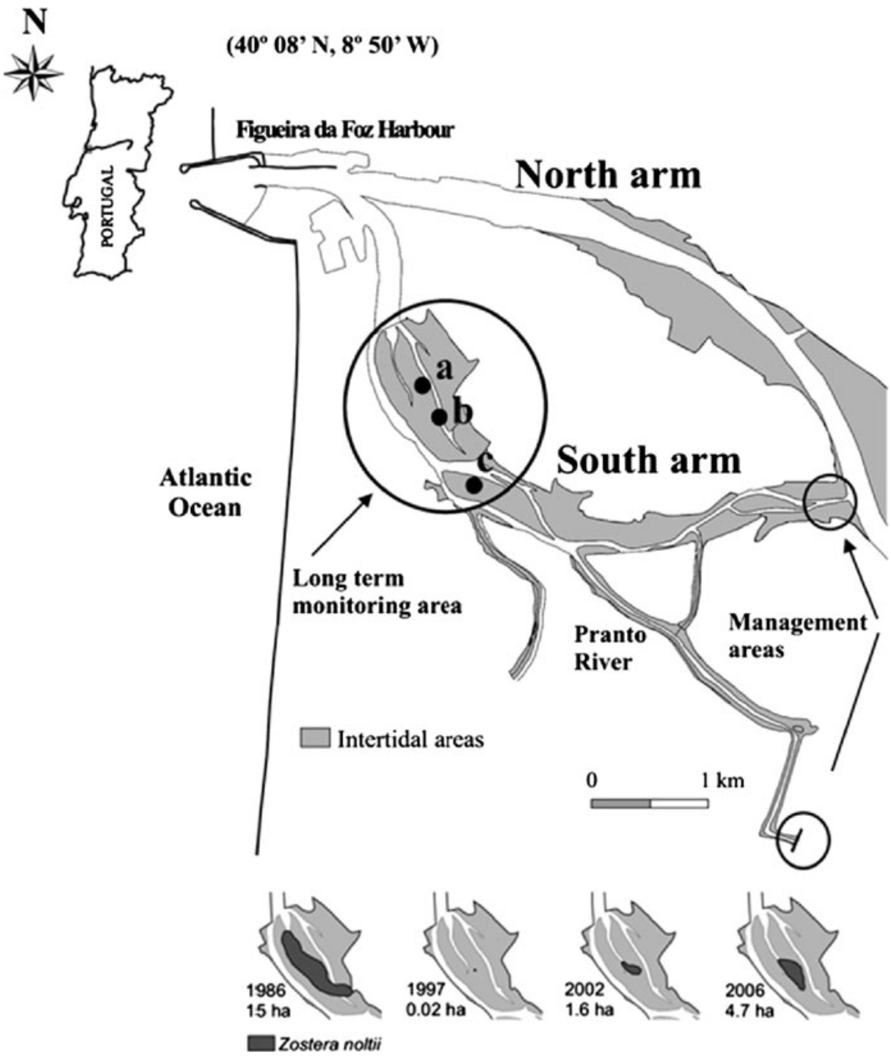

Fig. 1 Location of the Mondego estuary and the sampling stations: **a** *Z. noltii* bed, **b** intermediate area, and **c** sand flat. *Expanded area maps* show evolution of the area of *Z. noltii* beds and cover in the south arm, from 1986 until 2006. Mapping of benthic vegetation is based on field observations, aerial photographs, and GIS methodology (ArcView GIS version 8.2)

arm was almost silted up and as a result the water circulation was mainly dependent on the tides and on the freshwater input from the Pranto river, artificially controlled by a sluice, depending on rice field irrigation needs in the lower Mondego valley.

Macrobenthic sampling was performed in three stations along the estuary's south arm:

1. a *Z. noltii* bed located downstream;
2. an intermediate area, located in the middle section, characterized by a mudflat which is currently being re-colonized by *Z. noltii* after 15 years of absence of this macrophyte; and
3. a sand flat area, located upstream in the inner areas differentiated by the absence of seagrass for more than 25 years, and where seasonal macroalgal blooms frequently occurred before 1998.

The *Z. noltii* bed is characterized by higher salinity (20–30) and higher organic matter content (6.8 ± 0.99% (±SD)). The intermediate area physical–chemical conditions are similar to those of the previous area. The sand flat is characterized by lower salinity (15–25) and a mean organic matter content of 3.7 ± 1.0% (±SD) (Pardal et al., 2004).

Field sampling and laboratory work

Benthic sampling was performed from January 1993 to September 1995 and again from February 1999 to November 2008. Samples were collected fortnightly in the first 18 months and monthly afterwards. On each sampling station and occasion, ten (during the first 18 months) to six sediment cores (each core with

141 cm^2 surface area) were taken randomly to a depth of 20 cm and washed in estuarine water through a 500 μm mesh sieve. The remaining material (sediment, rooted macrophytes, algae, and fauna) was preserved in 4% buffered formalin. For every sampling date, at each station, low water pools temperature, pH, dissolved oxygen, and salinity were measured in situ. Sediment samples were also collected to estimate the organic matter content, which was later determined by loss on ignition (8 h at 450°C).

In the laboratory, sorted plant material from all the cores (macroalgae plus *Z. noltii* leaves and rhizomes) was dried for 48 h at 60°C and weighed. Afterwards, the ash-free dry weight (AFDW) was determined by loss on ignition (8 h at 450°C). The animals were also sorted, separated by taxa, stored in 70% ethanol, and subsequently identified (Eleftheriou & McIntyre, 2005).

Cyathura carinata individuals were counted, sexed, and their cephalic length was measured. Total body length (mm) and biomass (g AFDW) were determined by use of regression models: total body length = 0.745133 + 9.01010 × cephalic length, $r^2 = 0.97$, $n = 115$ and biomass = 0.0190549 × cephalic length$^{2.71815}$, $r^2 = 0.96$, $n = 800$.

Freshwater inflow, precipitation, and air temperature (from January 1993 to November 2008) and the climatic normal mean precipitation and air temperature values (from 1971 to 2000) were obtained monthly from the Portuguese Water Institute, INAG (http://snirh.pt) and the Portuguese Weather Institute, IM (www.meteo.pt). A climatic normal for a given climate element corresponds to its mean value over an approved 30-year period (IM—Portuguese Weather Institute).

Data analysis

Length–frequency data of *C. carinata* individuals from successive sampling dates were analysed by use of FISAT II software (FAO–ICLARM Stock Assessment Tools), as explained in detail by Gayanillo et al. (2005). Modal progression analysis was used to decompose the length–frequency distributions into separate cohorts. Separation of the length–frequency samples into their likely cohorts (C), complete with their average length (±1 standard deviation; SD), and the number of individuals belonging to each cohort (n_C), were performed by use of Bhattacharya's method. Each representative component with a separation index >2 was assumed to be a single cohort.

Field growth rates were calculated using the equation of Gaschütz et al. (1980). This is expressed as:

$$L_t = L_\infty \left(1 - e^{-[KD(t-t_0)+C(KD/2p)\sin 2p\,(t-t_s)]}\right) 1/D,$$

where L_t is the length of the organism at a given time t; L_∞ the maximum possible length of the organism; t_0 the instant when the organism would have a length equal to zero; t_s the time interval between the start of growth (when $t = 0$) and the first growth oscillation, which is growth expressed by a sine curve with a one-year period; K the growth constant; C a parameter the value of which can range from 0 to 1, depending on the species; and D a parameter that expresses metabolic deviations from the von Bertalanffy's 2/3 rule.

Secondary production was estimated according to the increment summation method, using the cohorts previously recognised, expressed as:

$$P = \sum_{n=1}^{N} P_{cn};$$

where P_{cn} is the growth production of a cohort n. The mean population biomass B was calculated as follows:

$$\overline{B} = (1/T) \sum_{n=1}^{N} \overline{B}_n t;$$

where T is the period of study; N the number of cohorts in the period T; B_n the mean biomass of cohort n; and t the duration of that same cohort. This methodology was used in the sand flat area but could not be used in the data from the other two sampling stations, because of their low abundance.

Variations in *C. carinata* annual density values were explored by use of the Primer v6 software package (Clarke & Gorley, 2006) with regard to spatial (*Z. noltii* bed, intermediate area, and sand flat sampling sites) and temporal (16-year data series) differences. *C. carinata* abundance data were divided in four categories: juvenile, male, ovigerous female, and unreproductive female. We also wished to understand which environmental variables (air temperature (mean and maximum), water temperature, salinity, organic matter, pH, precipitation, runoff, dissolved oxygen, macroalgal biomass, and *Z. noltii* biomass (this last one for the seagrass bed and the intermediate areas)) affected *C. carinata* density the most. At first, a similarity matrix (based on square-root transformed data) was constructed using the Bray–Curtis similarity index (Clarke & Warwick, 2001). Non-metric multidimensional scaling (MDS) was then used for ordination of the data, and analysis of similarity (ANOSIM) was used to statistically test differences in the data, with regard to spatial and temporal differences. Finally, the BIOENV procedure (Clarke & Gorley, 2006) was used to identify the best combination of environmental variables that explained the variation in the *C. carinata* density for each sampling station. Spearman's correlation was performed between the Euclidian distance similarity matrix of environmental variables and the Bray–Curtis similarity matrix from the isopod's density data. Environmental variables were first checked for collinearity using Pearson's product moment correlation coefficient. All variables were preserved, because none had an *r* value >0.95.

Results

Climate characteristics

Temperature varied according to the seasonal pattern of a temperate region, with lower values of mean air temperature in the winter and higher in the summer (Fig. 2A). Mean monthly values were similar to the mean temperatures for the period 1971–2000 ((10°C (winter), 17°C (spring), 21°C (summer) and 14°C (autumn)). Nevertheless, higher values of mean temperature were observed in the spring and summer of 2003 and 2005 compared with the mean temperatures for the period 1971–2000 in the central region (Fig. 2B). In these periods, the maximum temperature reached values higher than 40°C. The summer of 2003 was characterized by one heat wave that lasted 16–17 days, considered an unprecedented event and the longest heat wave recorded since 1941 (Portuguese Weather Institute). In 2005, two heat waves that lasted 8–12 days were recorded.

The mean precipitation values in the central region, for the period 1971–2000 were 283 mm (winter), 204 mm (spring), 79 mm (summer), and 339 mm (autumn). Some atypical weather events occurred during the study period: in the winters of 1993/1994, 1995/1996, and 2000/2001 precipitation was greater than expected (593, 670, and 767 mm, respectively); this led to flooding of the estuary, particularly in the winter 2000/2001 (regarded as the 3rd rainiest of the last 30 years) (IM), which was reflected in the elevated freshwater runoff value (Fig. 2B). Precipitation was also above the mean value in the autumn months in 2003 and 2006 (Fig. 2B). In contrast, a period of severe drought occurred in the winter of 2004/2005, when precipitation did not exceed 40 mm (Fig. 2B). This hydrological year was regarded by the IM as the driest since 1931, followed by the years 2007 and 2008, for which lowest autumn precipitation was registered. As a result, river runoff decreased drastically in these years, with lower numbers than the ones observed in other years (Fig. 2B). Weather extremes are being observed more frequently, and there is a tendency for a progressive increase in temperature. The decade 2000–2009 was, indeed, characterized by

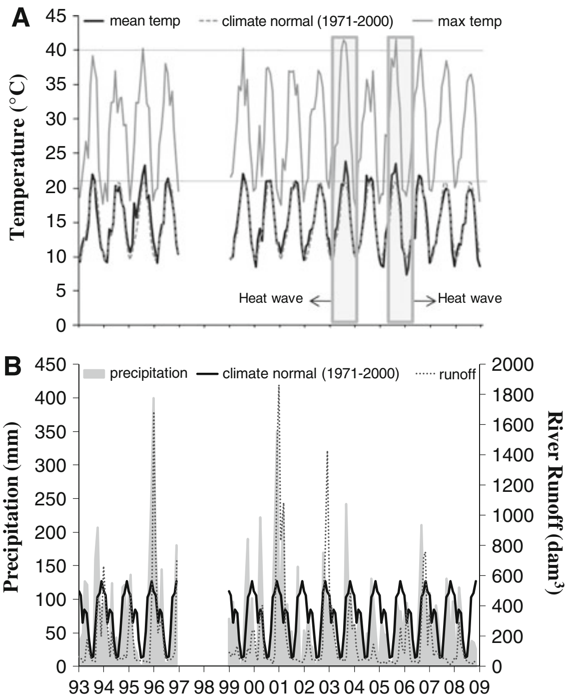

Fig. 2 Monthly variation of **A** atmospheric temperature (mean and maximum values registered and mean for the period 1971–2000) and **B** precipitation (total cumulative per month and mean for the period 1971–2000) and river runoff. The climate normal of 1971–2000 is regarded as a reference (Portuguese Weather Institute, httw://meteo.pt)

higher temperatures and drier years than the decade 1990–1999 (IM).

Seagrass and macroalgal biomass

In the sand flat, green macroalgal blooms were only present before the restoration programme. Biomass was extraordinarily high in the spring of 1993 (342 g m^{-2} AFDW), but was also significantly high in the autumn of 1994 and spring of 1995. After the restoration measures, macroalgal biomass decreased substantially throughout the study period reaching values in general below 10 g m^{-2} AFDW (Fig. 3A). Nevertheless, small amounts of macroalgae biomass were present in 2003, 2005, 2007, and 2008, which corresponded to dry periods.

In the seagrass bed, *Z. noltii* biomass declined dramatically in the first years of the study, and started to increase after the restoration measures in 1998 (Fig. 3B). Recently, this seagrass started to re-colonize the intermediate area, as is apparent from the increase in plant biomass in the last five years (Fig. 3B).

Cyathura carinata spatial and temporal variation

Cyathura carinata population was more abundant in the sand flat than in the other sampling stations (Fig. 4). The population in this area was well age-structured and its density followed similar patterns throughout the years of the study, increasing during summer, peaking in autumn, then decreasing until late spring. Maximum density (autumn of each year) was below the average during and after the occurrence of stochastic events, being most evident in 1993 (after the major macroalgal bloom and during autumn floods), 2003 and 2004 (during and after the warmest and longest heat wave recorded in this study, followed by a rainfall period), and in 2007 and 2008 (corresponding to dry years). For the period corresponding to 2003 and 2004 density values were well below average. In the subsequent year the population recovered, the maximum density peak in July 2005, was the highest observed during the study period (Fig. 4).

In the intermediate and *Z. noltii* bed areas, very low densities were recorded before the restoration measures (Fig. 4), in particular in the seagrass bed, where the population was practically non-existent. The population in both areas then seemed to increase slightly, particularly in the intermediate area where two abundance peaks were observed (1,277 ind m^{-2} in 1999 and 3,546 ind m^{-2} at the end of 2000). Despite this apparent resurgence, the population in these areas started to decline again in 2003, reaching very low values, generally less than 100 individuals per m^2. This situation coincided with a succession of extreme weather events, particularly the heat wave in 2003 and the drought period from 2004/2005 onwards.

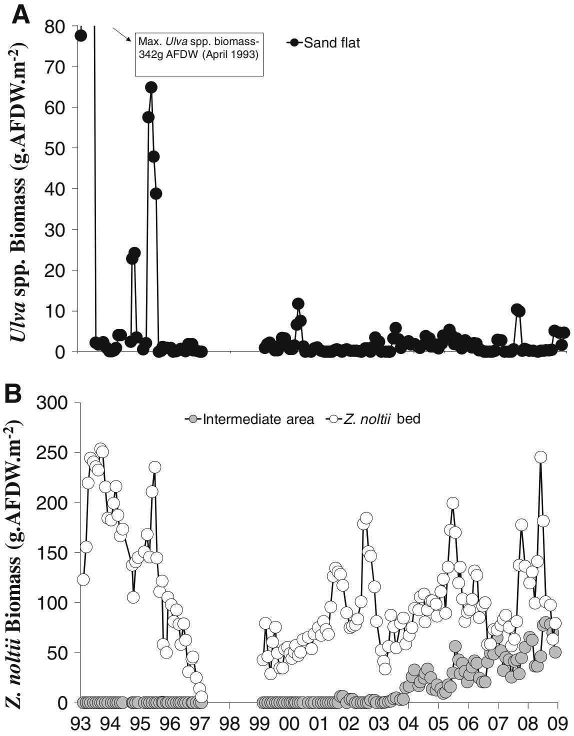

Fig. 3 Monthly variation of plant biomass (g AFDW m^{-2}), from 1993 to 2008. **A** *Ulva* spp. at the sand flat, **B** seagrass at the *Z. noltii* bed and intermediate area

The ANOSIM procedure demonstrated different overall abundance of *C. carinata* between sites ($R = 0.603$; $P = 0.001$). Pairwise comparisons revealed that the sand flat was significantly different from the *Z. noltii* bed ($R = 0.853; P = 0.001$) and from the intermediate area ($R = 0.817$; $P = 0.001$). Significant differences were not detected between the *Z. noltii* bed and the intermediate area ($R = -0.014$; $P = 0.509$). The MDS plots for both the seagrass bed and the intermediate area revealed differences between the samples from the pre and post-2003 heat wave periods, except for the 1993 (extensive macroalgal bloom) sample,

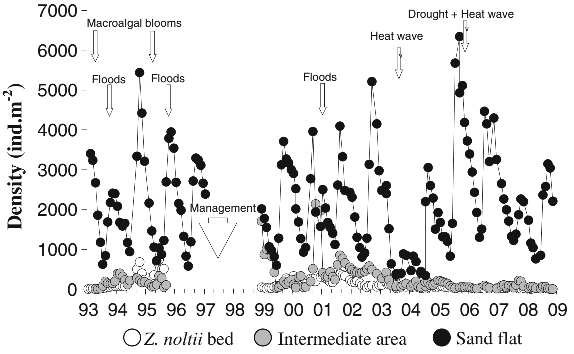

Fig. 4 Variation of *C. carinata* density from 1993 to 2008, at the three sampling stations: *Z. noltii* bed; intermediate area; sand flat

which was close to the post-heat wave samples (Fig. 5). In 1993, the density verified in these two areas was extremely low, and close to the values found in recent years, especially in the *Z. noltii* bed. This situation was confirmed by ANOSIM, which identified significant differences between the pre and the post-2003 heat wave periods for the seagrass bed and the intermediate area ($R = 0.538$; $P = 0.003$ and $R = 0.517$; $P = 0.003$, respectively). In contrast, in the sand flat plot, only the 2003 sample was separated from the others, and 2004 was the only year close to this sample, reflecting the atypical situation verified in this period (Fig. 5). Accordingly, no differences were detected in this area between the pre and post-heat wave periods ($R = -0.041$; $P = 0.563$).

The BIOENV procedure revealed that the suite of environmental variables that explained the *C. carinata* density variation varied slightly depending on the sites. In the *Z. noltii* bed, salinity and organic matter constituted the combination of conditions which gave the highest rank correlation value ($\rho_r = 0.406$). In the intermediate area, the variables *Z. noltii* biomass, dissolved oxygen, pH, and water temperature were responsible for a correlation of 0.572 with the abundance variability. In the sand flat, the analysis resulted in a maximum correlation of 0.478 for three variables (precipitation, water temperature, maximum air temperature).

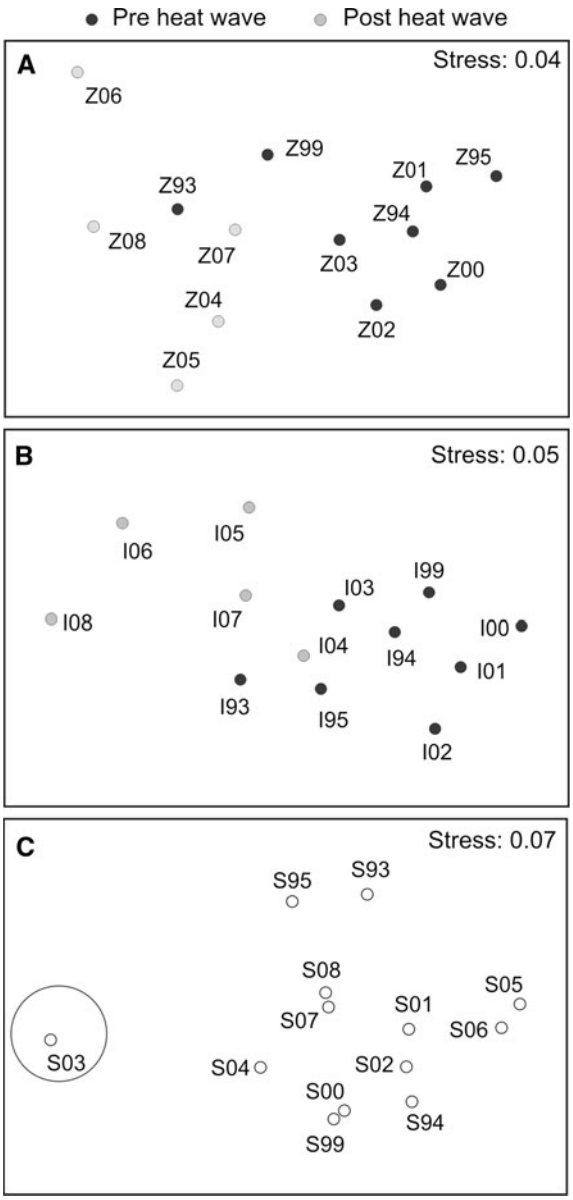

Fig. 5 Two-dimensional MDS ordination plot of *C. carinata* annual density. **A** *Z. noltii* area, **B** intermediate area, and **C** sand flat

Cyathura carinata population structure, growth and production

During the 16-year period, eighteen cohorts were identified and followed in the sand flat area. In each year, two cohorts coexisted at the same time. The oldest cohort died at the same time a new one was recruited, which occurred in June of each year. Males were only observed during the reproduction season. *C. carinata* was able to reproduce in its first year of life and each cohort could produce two separate sets of males on distinct occasions, relating to the first and second year of life, because of protogynous hermaphroditism (Fig. 6). The pattern of cohort linear

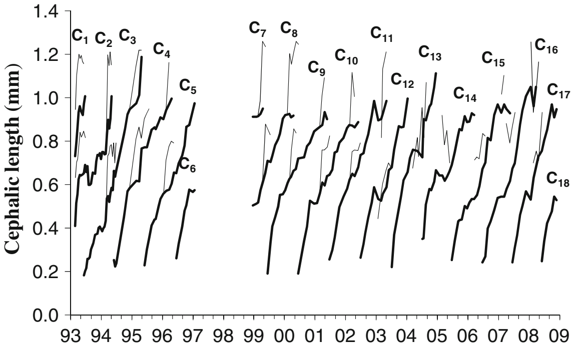

Fig. 6 Linear growth of the cohorts identified in the sand flat area from 1993 to 2008. (*thick lines* females; *thin lines* males) (The methodology used was not able to assess the population structure at the other sampling stations because of low abundance of the individuals.)

growth was maintained approximately the same throughout the years, with few exceptions (Fig. 6): C_{12} and C_{13} disappeared earlier than others lasting only 18 and 19 months, respectively, in contrast with the normal life span of 23–24 months (Table 1).

The growth constants (K) for females from cohorts C_3 (0.58) (recruited in 1993 during the massive algal bloom) and C_{13} (0.56) (recruited in 2003, during the severe heat wave) were higher than those the others (approx. 0.4) whereas those for cohorts C_9, C_{10} (occurring during flooding periods of 2000/2001) and C_{14} (recruited during the severe drought period) were the lowest (0.32, 0.35, 0.33) (Table 1).

The relative frequency of ovigerous females was higher in the pre-restoration period, ranging from 82.9% in 1995 to 56.4% in 1994, in contrast with the post-management period in which the highest percentages were found on two occasions in 2000 and 2004 (60.2 and 63.0%, respectively). The lowest values were found in 2003 (17.1%) and 2007 (15.8%), and were below 40% in most years (Fig. 7A). The percentage of juveniles seems to be increasing from 2005 onwards, after a period of extremely low values in 2003 and 2004. Percentages were also low in 1996, 1999, and 2000 (Fig. 7B). Sex ratio was not constant through the years, ranging from 0.07 in 1999 to 0.33 in 2004, decreasing in the following years, and increasing again in 2008 (0.31). In 2003 the sex ratio attained a median value of 0.19 (Fig. 7C).

Growth production varied with time (Table 2). The lowest values were recorded in periods when macroalgal blooms (1993, 1995), floods (1993, 1995/1996, 2000/2001), droughts (2005, 2007, 2008), and heat waves occurred (2003, 2005), with the lowest value ever in 2003 (7.2 g m^{-2} $year^{-1}$). The population seemed always to recover after these events, achieving higher values afterwards (1994, 2002, and 2006). The highest growth production (29.2 g m^{-2} $year^{-1}$) was observed in 1994, the year after the massive algal bloom. Mean population biomass was lowest in 2003 and 2004 (5.6 and 5.9 g m^{-2} $year^{-1}$, respectively), recovering in the following year, when the values were highest (14.3 g m^{-2} $year^{-1}$) (Table 2). *P*/*B* ratios were highest in the first two years of the study (2.9 and 3.4) being only close to the values in 2002 (2.8) and 2004 (3.0). For other years the turnover was ∼2, with exception of 2003 (1.3) and 2005 (1.2), which were the lowest values.

Discussion

During 16 years, the Mondego Estuary experienced a series of impacts, initially an eutrophication process (caused by anthropogenic action, whose consequences are still ongoing) and later climate-related episodes.

C. carinata presented different population dynamics according to the study area; they were progressively less abundant from upstream areas toward the *Z. noltii* bed. The population was much more abundant and well age-structured at the sand flat. Despite the increasing environmental quality verified in the system in recent years, as a result of the restoration programme, the *C. carinata* population could not settle successfully in the vegetated areas. This does not agree with information found in the literature, which describes this species as being present at higher densities in areas with vegetation (Olafsson & Persson, 1986; Sola & Arzubialde, 1993). In fact, Sola & Arzubialde (1993) verified a decrease in the density of the isopod related to the regression of the vegetation cover. In addition, Olafsson & Persson (1986) revealed a density increase in areas that had been re-vegetated. In the Mondego estuary, *Z. noltii* biomass was considered to be a factor influencing *C. carinata* density in the intermediate area, a location where the seagrass has been progressively increasing, in terms of biomass and extension, which could have negative

Table 1 Field growth data (Gaschütz et al. 1980) for females from cohorts C_3, C_4, C_9, C_{10}, C_{11}, C_{12}, C_{13}, C_{14}, and C_{15}

	C_3 jun93–apr95	C_4 jun94–apr96	C_9 jun99–may01	C_{10} jun00–may02	C_{11} jun01–apr03	C_{12} jun02–jan04	C_{13} jun03–dec04	C_{14} jun04–mar06	C_{15} jun05–may07
K	*0.58*	0.43	0.32	0.35	0.41	0.43	*0.56*	0.33	0.43
t_0	−0.01	−0.42	−0.76	0.55	−0.5	−0.41	−0.39	−0.9	−0.36
t_s	−0.05	0.04	0.27	0.19	0.16	0.1	0.22	0.11	0.12
C	0.67	0.31	0.46	0.64	0.75	0.82	0.8	1.26	0.93
r^2	0.95	0.98	0.97	0.98	0.98	0.97	0.97	0.98	0.97
Events	Macroalgae floods	Macroalgae floods	Floods	Floods		Heat wave	Heat wave	Severe drought	

Males were disregarded

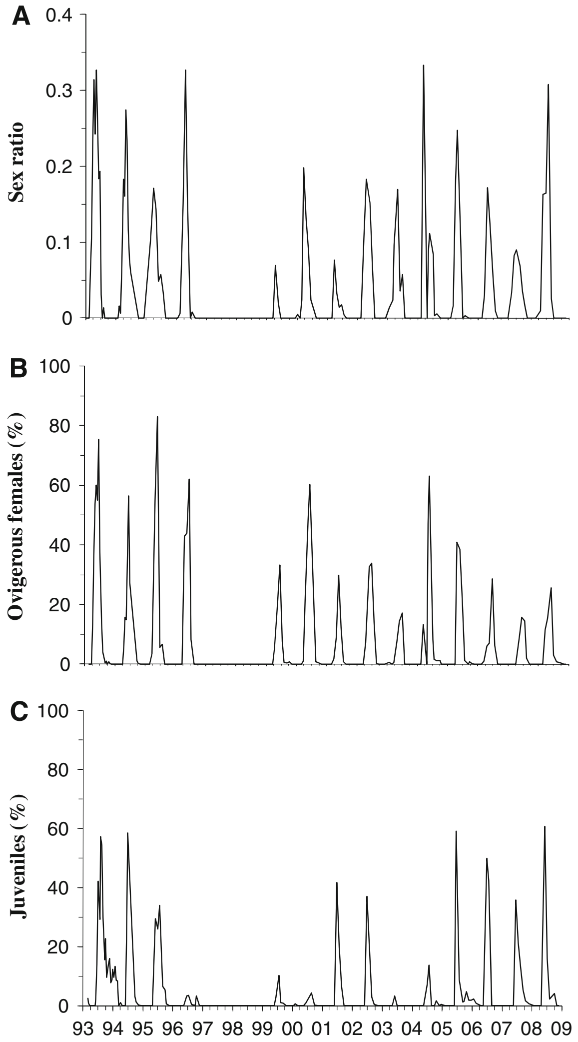

Fig. 7 Biological features of *C. carinata* in the sand flat. **A** sex ratio variation (males/females); **B** relative frequency of ovigerous females (%); **C** relative frequency of juveniles (%)

implications for the successful establishment of this isopod. Hypotheses have been proposed to explain this situation: on the one hand, the seagrass may provide protection for this isopod, reducing predation pressure (Blanchet et al., 2004); on the other hand, it may act as a physical barrier for its own ambush-like predatory behaviour (Ferreira et al., 2007). Moreover, a high prevalence of trematode parasites in these areas, that are known to inflict serious damage on their hosts, may be a strong determinant in their low abundances (Jensen et al., 2004; Ferreira et al., 2007). Taking this into account, the bare sand flat area may encompass ecological niches that are more favourable to *C. carinata* populations. Accordingly, the restoration programme and the associated recovery of the seagrass beds had no effect to the successful establishment of this isopod species in these areas.

The *Z. noltii* bed and the recently re-vegetated intermediate area yielded a scarce population, with much lower abundance than the bare sand flat. At the beginning of the study, *C. carinata* was practically absent from the seagrass bed, and only few individuals were found in the intermediate area. In the post-restoration period, the population recovered slightly in terms of abundance at these two sampling stations. Notwithstanding, since 2003 the population in these areas declined substantially, being unable to recover until the end of the study period. It was mostly related with a succession of extreme weather events, droughts and heat waves, which negatively affected this population. It is important to consider that it is difficult to dissociate the effect of the restoration programme from the climatic extremes; this impedes prediction of how the population in these areas would

Table 2 Growth production estimates for the *C. carinata* population at the sand flat area, from 1993 to 2008

Year	P (g m^{-2} year^{-1})	$\bar{B}$ (g m^{-2} year^{-1})	$P/\bar{B}$ (year)	Events
1993	19.8	6.9	2.9	Algal bloom, floods
1994	29.2	8.5	3.4	
1995	14.8	8.8	1.7	Algal bloom, floods
1996	16.4	8.5	1.9	
1997	Restoration measures			
1998				
1999	17.5	11.2	1.6	Floods
2000	14.8	9.9	1.5	
2001	15.7	7.9	2.0	
2002	21.6	7.9	2.8	
2003	7.2	5.6	1.3	Heat wave
2004	17.7	5.9	3.0	Drought + Heat wave
2005	17.6	14.3	1.2	
2006	21.2	9.8	2.2	
2007	13.7	9.1	1.5	
2008	15.8	8.2	1.9	

react to the restoration measures if the climatic disturbances did not occur.

In the upstream sand flat, *C. carinata* was affected by the 2000/2001 massive floods which had a negative outcome in terms of population density, although a more dramatic effect had been expected because of the strong water currents. The event which seemed to have affected the population the most was the 2003 heat wave, the warmest and longest of the study. On no other occasion was the recorded population density in this area so low for such a long period of time. Actually, temperature (both water and air maximum) was shown to be an important factor regulating this isopod density variation in this study area. Moreover, during the period from 2003 to 2004, both ovigerous females and juveniles were present in very low numbers, revealing very low recruitment success that contributed to a decrease of the total density. Temperature was regarded as a crucial factor controlling both the process of sex reversal and reproduction (Jazdzewski, 1969). Roth et al. (2010) proved that temperature extremes were associated with metabolic stress and reduced immunocompetence of the isopod *Idotea baltica*; accordingly, the response of *C. carinata* may be similar. Together with the hypothesis of reduced survival of these individuals, it is also possible that cyathurans facing adverse conditions migrate to locations where the conditions are more favourable (Burbanck & Burbanck, 1967), for example the subtidal environment. These two hypotheses would explain why the cohorts C_{12} and C_{13} lived less than expected at the sand flat. The life span and the pattern of cohort linear growth was similar throughout the years, except for these cohorts, which went through the severe heat wave, a period of great decline in the population density of *C. carinata*. Cohort C_{13} was particularly affected, because the heat wave occurred during recruitment, which was reflected in the lowest relative frequency of juveniles ever recorded in this system. Because only 10% of the individuals of a given cohort survive their first reproduction season (Ferreira et al., 2004), the low recruitment of 2003 was reflected not only in the low population abundances at the sand flat during that year but also on the number of juveniles recruited in the following year. Temperature has a great effect on the growth rate of this isopod (Bamber, 1985; Olafsson & Persson, 1986); rapid growth occurs when the temperature increases, decreases when the temperature diminishes, and is suspended when temperatures are extremely low. This was shown by the higher intrinsic growth constant (K): individuals from the C_{13} had faster growth, achieving the highest cephalic length observed, and disappeared earlier than the isopods from other cohorts. A high K value was also observed for individuals that were recruited in the period of the massive spring bloom and lived through three periods when macroalgal biomass abounded (spring 1993, autumn 1994, and spring 1995). The availability of food resources and the temporary advantages that algal mats provided, for example alternative habitats and protection against predators (Norkko et al., 2000) led to an increase in the growth rate of *C. carinata* (Martins et al., 1997; Ferreira et al., 2004, 2007). On the other hand, excessive amounts of algal biomass and its consequent decay strongly affected the survival of this species; juveniles, especially, with their interstitial behaviour, are more sensitive to hypoxia conditions (Burbanck & Burbanck, 1975). Cohorts that went through great disturbances as the heat wave of 2003 and the massive algal bloom of 1993 have higher *K* values. In contrast, strong floods and severe droughts seem to have the opposite effect, reducing the *K* value; hence the growth rate seen for C_9, C_{10}, and C_{14}. Accordingly, it can be assumed that the normal *K* for this species in this system is approximately 0.4.

The heat wave in 2003 was followed by a rainy autumn that added one additional stress factor to the population's capability to recover, by contributing to the dispersal of individuals elsewhere. Nevertheless, after the drastic population decline in the sand flat during the 2003–2004 period, *C. carinata* was able to recover during the subsequent year. A significant increase in density occurred after the reproduction period in 2005, with most of the population being young individuals from the smaller size classes, demonstrating that favourable conditions for successful recruitment had been re-established. Later, during the summer of that year, the population was affected simultaneously by a heat wave and a drought. The synergistic effect of these events did not have such a harmful impact as the heat wave alone in the summer of 2003. In fact, after these disturbances in 2005, the population was able to recover, mainly because of precipitation that was close to the normal climatic mean, enabling influx of individuals dispersing from upstream without being flushed elsewhere because of strong water currents of floods. These upstream areas act as standing reservoirs of newly recruited specimens that will colonise stressed areas of the estuary. The ability of this isopod population to overcome these adversities is dependent on this migration of upstream individuals, which is apparent from increased abundance each year after the end of the reproduction period.

Growth production and population biomass seem to be affected by the occurrence of all the stress factors mentioned above. The lowest values were recorded in periods of extreme events, for example macroalgal blooms, floods, droughts, and heat waves, with the lowest value ever during the extensive heat wave in 2003. In 1993, the production estimate is a combination of the seasons favoured by the presence of some algae and the period corresponding to the algal crash. The population succeeded in recovering, achieving higher values after each stress event. In 1994, the year after the massive algal bloom, growth production was the highest observed. Mean population biomass was lowest in 2003 and 2004, in contrast with the subsequent year, in which values were the highest for the whole study period, revealing strong recovery in terms of biomass.

Extreme weather events seem to affect the estuarine species differently. The response of *C. carinata* to stressors was distinct from that of other key species, for example the gastropod *Hydrobia ulvae*. This mud snail succeeds perfectly in the *Z. noltii* bed and its density and biomass decreased substantially during the decline of the seagrass (Cardoso et al., 2008b). In this same system, *H. ulvae* was greatly affected by the 2000/2001 floods that removed part of the population, in contrast with what happened to the isopod population. Heat waves and droughts also affected the gastropod population, although indirectly through the decline of its habitat, the seagrass bed, with strong implications for this mud snail population (Cardoso et al., 2008b).

Conclusions

The effect of a given disturbance on a population depends greatly on its abundance and structure, which in turn will depend on the characteristics of the location that it inhabits. The density of *C. carinata* increased after the restoration programme, even in the *Z. noltii* bed and intermediate area, where it was previously scarce. This recovery was hampered by successive extreme climate events, especially droughts and heat waves, which led to extremely low densities in these areas. At the sand flat, macroalgal blooms were temporarily beneficial, reflected in increased growth rate, because of greater availability of resources; these benefits were not long-lasting, however, and led to population declines associated with repercussions on reproductive success. Floods and droughts influenced the dispersion of individuals, reflected in the overall population in terms of density and production, and reduced the growth rate of the individuals. This population suffered the strongest decline during the 2003 heat wave, which affected abundance, production, and reproduction. Its recovery was mostly because of the dispersion of newly recruited specimens from upstream areas of the estuary. Overall, an abundant and well age-structured population seems to be more resilient to disturbances, as seen in the sand flat, which followed a characteristic pattern of density, age structure, and reproduction through time; even when confronted with a density crash it was able to recover successfully in subsequent years. In contrast, populations with few individuals and with difficulties becoming established in a given environment will see their survival endangered. Adding stressors to a naturally disturbed population will destabilise it even more, seriously compromising its existence. Bearing in mind that climate change will continue to be a real issue affecting ecosystems worldwide, its repercussions will affect such populations, which will have difficulties surviving and be on the edge of collapse, with strong implications for the whole ecosystem.

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