



# Effects of the 2003 European heatwave on the benthic community of a severe transitional ecosystem (Comacchio Saltworks, Italy)

Cristina Munari\*

Department of Biology and Evolution, University of Ferrara, Via L. Borsari 46, I-44121 Ferrara, Italy

## ARTICLE INFO

### Keywords:

Climatic warming  
Heatwave  
Benthic community  
Indicators  
Transitional ecosystems

## ABSTRACT

The summer of 2003 was the warmest summer in Europe since the 16th century. Its consequences on the fauna of a transitional ecosystem were studied through biodiversity, functional and ecological indicators, from summer 2002 to winter 2005. The heatwave caused considerable changes in the benthic community structure and relative composition, persisting in 2005. Animal assemblages switched from mollusc- to annelida-dominated. Biodiversity and functional indicators captured changes in community structure and composition, proving to be powerful tools to detect responses related to global warming. Ecological indicators rendered a monotonic response oscillating between bad and poor ecological status across the study period. The resilience of mollusc biocoenosis resulted limited with respect to other taxa, posing concerns about their conservation if, as predicted, the frequency of summers as hot as that of 2003 will progressively increase to become the norm at the end of this century.

© 2011 Elsevier Ltd. All rights reserved.

## 1. Introduction

There is now no doubt about the effect of climatic change on ecosystems (Walther et al., 2002). The different scenarios outlined by the Intergovernmental Panel on Climate Change project an increase in global mean surface air temperature relative to 1990 of 1.4–5.8 °C by 2100 (IPCC, 2007), and a number of studies concerning the ecological consequences of climatic change has taken into account a gradual increase of temperatures. Besides the global warming, the frequency of extreme climatic events is also likely to increase (IPCC, 2007). As a matter of facts, the summer of 2003 was characterized by extremely high values of temperature at the daily, weekly and monthly scales. Monthly temperatures observed from June to August 2003 in central and southern Europe were beyond the historical distribution range (Schaer et al., 2004). Even at the seasonal scale, it was considered the warmest summer in Europe since the early-16th century (Luterbacher et al., 2004). The summer 2003 heatwave had major social and economical impacts: increased elderly mortality, increased wildfire activity, extensive loss of livestock, wilted crops, and loss of forest cover (UNEP, 2004). With the unprecedented nature of such events, science is faced with the challenge of predicting how ecological systems will respond. The effects of the heatwave of summer 2003 were detected on plankton (Maazouzi et al., 2008) and mollusc assemblages (Mouthon and Daufresne, 2006) of freshwater habitats,

and, in the marine realm, large-scale mass mortalities were observed in the northwestern Mediterranean (Garrabou et al., 2009). However, no study based on actual data has evaluated the ecological effects of the heatwave in transitional ecosystems (coastal lagoons, coastal ponds, etc.). Within the framework of the EU-funded LIFE00NAT/IT7215 project “*Restoration and habitat conservation in the Comacchio Saltworks*”, I studied the macrobenthic communities in the lagoons of the Comacchio Saltworks (Po River Delta, northeastern Italy), from 2002 to 2005. These data sets gave the opportunity to study the effects of the abnormally high temperatures of summer 2003 on the biocoenoses of these transitional waterbodies, a task which, to my knowledge, has been neglected so far.

The aquatic fauna inhabiting the lagoons of the Comacchio Saltworks are subjected to press disturbances, as nutrient loads, organic enrichment, and variations in salinity. In aquatic ecosystems, gradual changes in community structures may occur as the climate gradually changes (e.g., Bradley and Ormerod, 2001), but climate change may also reduce the resilience of current community states (van Nes and Scheffer, 2004), thus increasing the sensitivity of the communities to a given pulse disturbance. The objective of this study, therefore, was to test the hypothesis that severe climatic pulse events (in this case the heatwave of summer 2003) would affect the structure and composition of benthic assemblages in transitional ecosystems, shifting community state into another basin of attraction (*sensu* Gray, 1981). The null hypothesis was that benthic assemblages of these systems are resilient enough to recover quickly from such extreme disturbance events.

\* Tel.: +39 0532 455315; fax: +39 0532 455715.

E-mail address: [mnc@unife.it](mailto:mnc@unife.it)

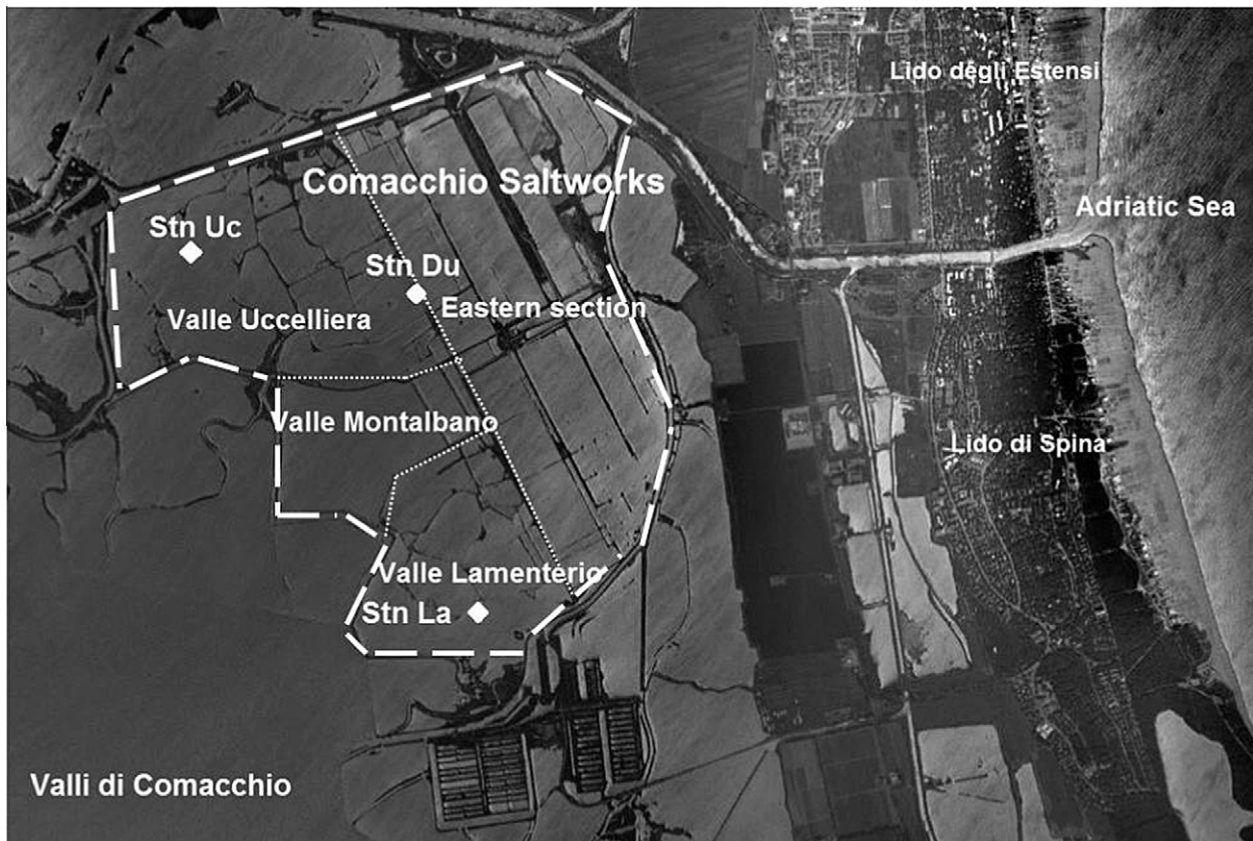


Fig. 1. Study area with sampling sites.

## 2. Materials and methods

### 2.1. Study site

The Comacchio Saltworks (550 ha; Fig. 1) is a man-made complex of scarcely vegetated shallow ponds by the Adriatic seashore, located in the northeastern part of the Valli di Comacchio (northeastern Italy). The Saltworks, whose present day form is owed to the Napoleonic Government in 1808, remained productive until 1985, when the Italian Ministry of Finance decided to cast off the production. Due to the presence of rare endemisms (e.g., the pickleweed *Salicornia veneta* Pignatti et Lausi) and protected (92/43/EEC and 79/409/EEC) habitats and species, actually the Comacchio Saltworks is a natural heritage (Ramsar Convention) comprised within the Po Delta Regional Park of Emilia Romagna. The Saltworks is basically divided into two parts: (i) a western section consisting of two main shallow lagoons (Valle Uccelliera, 80 ha, and Valle Lamentorio, 60 ha) acting as reservoirs, and (ii) an eastern section, characterized by smaller, regular ponds (preconcentrating, production and crystallizing ponds) used, until 1985, for salt production. The western section (which comprises a third, smaller basin, Valle Montalbano, not considered in this study because it was completely isolated and almost dry) is important for nesting and migrating birds, particularly Valle Lamentorio, which hosts one of the largest nesting flamingo (*Phoenicopterus ruber* Linnaeus, 1758) colonies of Europe. The aquatic environment of the western section is relatively variable and dictated by the condition of the incoming seawater (through the Foce, Bayon and Duomo canals), and the rates of precipitation and evaporation.

### 2.2. Biotic data

Sampling of benthic fauna occurred at two stations (stns Uc and Du) in Valle Uccelliera, and one (stn La) in Valle Lamentorio, in

August 2002, April, July and November 2003, July and November 2004 and January 2005. At Valle Uccelliera, stn Uc (44°39'37.01"N, 12°12'44.79"E; depth: 0.8 m) was in the central area of the lagoon, and was characterized by muddy sediments and the presence of a seagrass (*Ruppia cirrhosa* Petagna) bed; stn Du (44°39'28.93"N, 12°12'32.25"E; depth: 1.2 m) was in the easternmost part of the lagoon, close to the drain of the Duomo canal (and thus influenced by incoming waters from the canal), and was characterized by sandy bottoms and the presence of unclassified benthic filamentous seaweeds. Stn La (44°38'39.51"N, 12°12'48.53"E; depth 0.5 m) was in the southern area of Valle Lamentorio, and was characterized by bare, muddy sediments. Since both lagoons are characterized by very shallow areas and several emerging embankments, sampling stations were chosen for their accessibility (and, at Lamentorio, to avoid to disturb flamingoes). Benthic fauna was collected in triplicate with a Van Veen grab (area: 0.027 m<sup>2</sup>; volume: 4 l) and sieved through a 0.5 mm mesh. In the laboratory, macroinvertebrates were identified at the species level. Biomass of each taxon was determined through loss-on-ignition (48 h at 80 °C, 4 h at 450 °C).

Biodiversity indicators were: Hill's  $N_0$ , Shannon's  $H'$ , Pielou's  $J'$ , Margalef's  $d$  and Simpson's  $1 - \lambda'$ .

As functional indicators, exergy and specific exergy were considered. To estimate exergy, the method based upon the thermodynamic information due to DNA content was adopted (Jørgensen, 2006):  $Ex = \sum \beta_i C_i$ , where  $Ex$  is the exergy,  $C_i$  is the concentration in the system of component  $i$  (e.g., biomass of a taxonomic group), and  $\beta_i$  is a weighting factor expressing the quantity of information embedded in the biomass of the  $i$ -th component, choosing detritus as reference level (i.e.  $\beta_{Det} = 1$ ). Estimated  $\beta$  values are reported in Jørgensen (2006). Values of exergy were then calculated from the biomass of the different organisms (as g AFDW m<sup>-2</sup>) collected at each sampling date in each sampling station. Specific exergy

**Table 1**  
Biological traits considered and relative categories.

Biological traits	Traits categories	Labels
Feeding	Predator	P
	Herbivorous	H
	Deposit feeder	D
	Filter-feeder	F
Mobility	Sessile	SE
	Swim	SW
	Burrow	B
	Crawl	C
	Walk	W
Adult life habitat	Infafauna	I
	Epifauna	E
Body size (g AFDW)	Small (<0.001)	S
	Medium (0.01–0.05)	M
	Large (>0.05)	L
Life span (years)	Short (<1)	S
	Medium (1–5)	M
	Long (>5)	L
Reproductive technique	Asexual	A
	Sex: Gonocoric	G
	Sex: Hermaphroditism	H
Larvae	None (brooding)	N
	Benthic	B
	Planktonic-Lecitotrophic	L
Reproductive frequency	Planktonic-Planktotrophic	P
	Iteroparous	I
	Semelparous	S

(SpEx), the exergy per unit of biomass of each *i*-th taxonomic component, was calculated as:  $SpEx = Ex_i / Biom_i$  (Jørgensen, 2006).

Ecological indicators used were BITS (Mistri and Munari, 2008) and M-AMBI (Muxika et al., 2007). BITS was calculated using the freeware program available on [www.bits.unife.it](http://www.bits.unife.it). M-AMBI was calculated using the freeware program available on [www.azti.es](http://www.azti.es). For both indicators, reference conditions and values of ecological quality ratio (EQR) were those reported by the Italian legislation (Act 260/10) for the typology “M-AT-1, non-tidal coastal lagoon”. For BITS, reference conditions for status High was BITS = 2.8; EQR was High/Good = 0.87, Good/Moderate = 0.68, Moderate/Poor = 0.44, Poor/Bad = 0.25. For M-AMBI, reference conditions for status High were: AMBI = 1.85, Diversity = 3.3, Richness = 25; EQR was High/Good = 0.96, Good/Moderate = 0.71, Moderate/Poor = 0.57, Poor/Bad = 0.46.

Eight biological traits were chosen, related to aspects of life history and habits of the benthic fauna: feeding, mobility, adult life habitat, body size (measured as biomass), life span, reproductive technique, type of larva, reproductive frequency. Each trait was subdivided into a variable number of categories, for a total of 26 (Table 1).

### 2.3. Environmental data

Water and sediments were concurrently sampled with benthic fauna. Salinity was determined *in situ* with an ATAGO S/Mill-E refractometer, temperature and dissolved oxygen with an OxyGuard® Mk III probe. Water samples were refrigerated and immediately brought to a laboratory for analyses of nutrients (nitrogen and phosphorous) through standard methods (APAT, 2003). Sediments were collected with cores (4.5 cm i.d.), and, in the laboratory, organic matter content was determined through loss-on-ignition.

### 2.4. Statistical analyses

Environmental data were log-transformed and normalized, and then subjected to ordination by means of principal components

analysis (PCA). Macroinvertebrate community was investigated by means of ordination (MDS) based on the Bray–Curtis similarity index of untransformed abundance data. Differences between community structure in different periods were assessed by permutational non-parametric multivariate analysis of variance (PERMANOVA). For the one-way case, an exact *P*-value was provided using unrestricted permutation of raw data. In addition, *a posteriori* pairwise comparisons were performed. When low unique values in the permutation distribution were available, asymptotical Monte Carlo *P*-values ( $P_{MC}$ ) were used instead of permutational *P*-values ( $P_{PERM}$ ). Analyses were performed using PRIMER 6 and PERMANOVA+  $\beta$  2.0 (Anderson et al., 2008).

Differences among biodiversity, functional and ecological indicators (calculated on the mean abundance of three replicated samples) across the study period were investigated through one-way ANOVA and post-hoc comparisons (Tukey's HSD test). Relationship between indicators and environmental variables gathered in summers 2002, 2003 and 2004 were assessed through Spearman's rank correlation using the BIOENV procedure (Clarke and Gorley, 2006).

## 3. Results

In summer 2003, water temperature raised to over 30 °C (in summer 2002 and 2004 it was around 25 °C). This led to a drastic reduction in dissolved oxygen concentration, whose values felt to hypoxic conditions (1–2 mgL<sup>−1</sup>), and to an increase of ammonia concentration (31–72 µgL<sup>−1</sup>) in the water column. Probably due to high evaporation rates, also salinity increased greatly (47–56 psu, whereas in summer 2002 and 2004 it was comprised between 34 and 37 psu). Variations in nutrients (nitrates and phosphates) concentration seemed independent from the heatwave. Fig. 2 shows the values of environmental variables at the three sites. Fig. 3 displays the first two axes of the PCA ordination. PC1 accounted for 37.2, PC2 for 24.5 and PC3 for 19.3% of the total variability. On the first axis, the parameters which contributed most to ordination were temperature (coefficient of PC1 eigenvector: 0.577) and dissolved oxygen (−0.526). On the second axis these were salinity (0.259) and ammonia (−0.722). The third axis (not shown) was characterized by sedimentary organic matter (0.683) and nitrates (−0.708).

Sixteen taxa were gathered in the study period (Table 2), belonging to Annelida (6 taxa), Mollusca (5 species), Crustacea (4 species), and Insects (1 species). The MDS ordination is shown in Fig. 4. Sample points of summer 2003 are segregated apart at the extreme right handside of the plot, while those of stns Uc and La after the heatwave segregate together at the left handside of the plot. The community at stn Du seems to maintain some specificity. PERMANOVA evidenced significant differences ( $P_{PERM} = 0.0048$ ) in community structure and composition between the various periods. Pairwise tests showed that major differences occurred between summer 2002 and summer 2003 ( $P_{MC} = 0.0389$ ), and between summer 2002 and autumn 2003 ( $P_{MC} = 0.0666$ ). Before the heatwave, the contribution of taxa to benthic animal abundance had molluscs (e.g., Uc: 75%, Du: 53.9% of total abundance) and chironomids (e.g., La: 39.4%, of total abundance) as dominant groups. In summer 2003 an abrupt change was observed in community structure and composition. This change occurred with a drastic fall in abundance and diversity (Fig. 5). At all the three sites the mollusc biocoenosis was particularly sufferent, and all but one (*Ecrobia ventrosa* Montagu, 1803) taxa disappeared. The mean abundance of the surviving species fell considerably, being represented by only a few individuals, and showed no sign of recovery until 2004. From 2004 onwards, abundances raised to values similar of those before the heatwave, but the relative



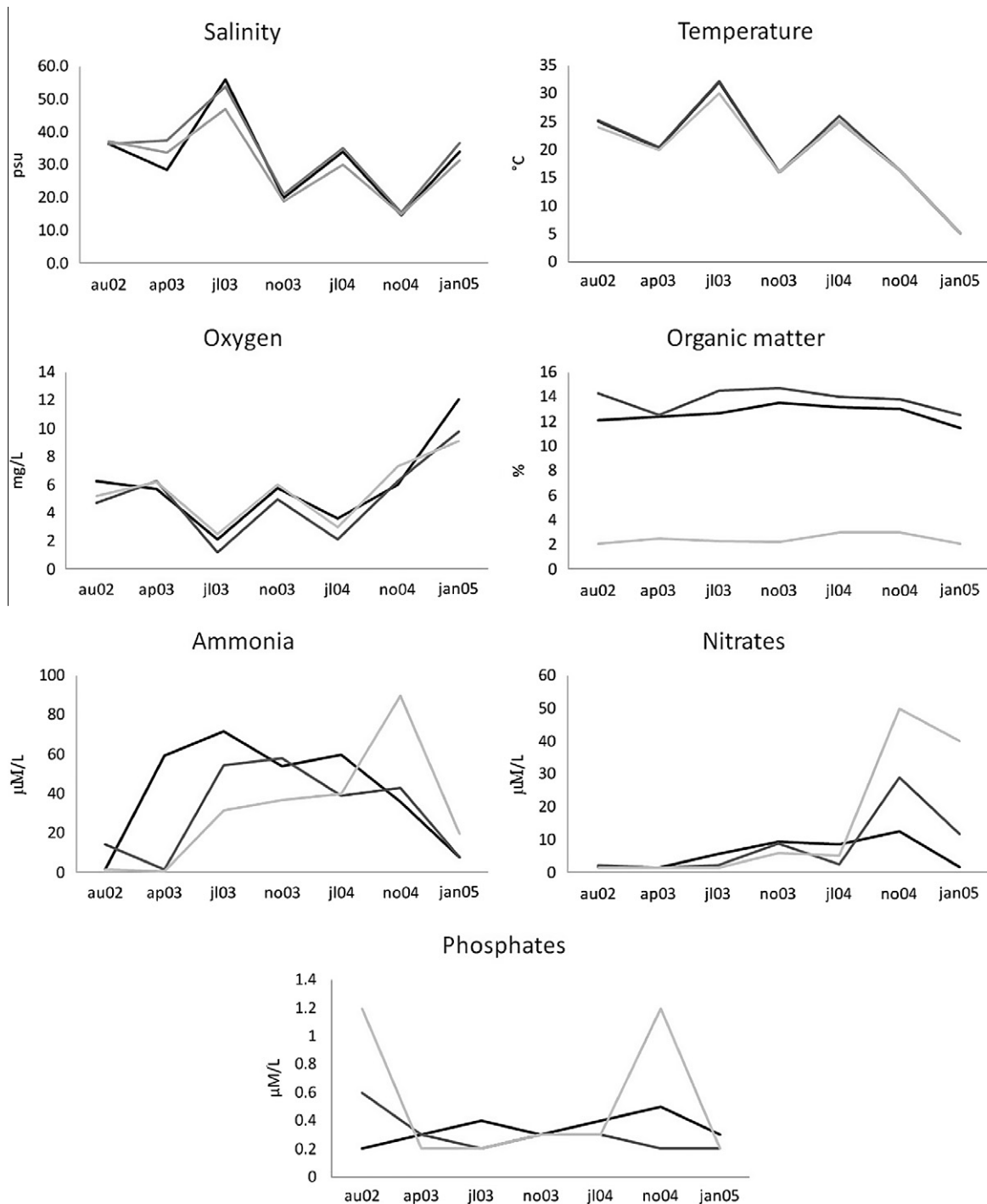


Fig. 2. Values of environmental variables during the study period (black line: stn Uc; dark grey: stn La; light grey: stn Du).

dominance of taxa changed. At Uc and La chironomids (67.3% and 55.2% of total abundance) and Annelida (30.9% and 40.6%) became numerically dominant, while at Du Annelida (66.3%) and the snail *E. ventrosa* (30.2%) were the most represented taxa.

In Fig. 5 values of biodiversity, functional and ecological indicators are shown. Significant differences were recorded for  $N_0$  ( $P = 0.0004$ ),  $H'$  ( $P = 0.0005$ ),  $J'$  ( $P = 0.04$ ),  $d$  ( $P = 0.003$ ), and  $1 - \lambda'$  ( $P = 0.0017$ ) across the study period. The heatwave provoked most of biodiversity indicators ( $N_0$ ,  $H'$ ,  $d$  and  $1 - \lambda'$ ) to significantly (Tukey's HSD tests: all  $P < 0.001$ ) drop down to extremely low values with respect to summer 2002 and spring 2003. At the end of the

study period (winter 2005), not one had reached the values exhibited before the heatwave. Among functional indicators, exergy captured the effects of the heatwave on community structure ( $P = 0.033$ ), exhibiting dramatically low values in summer 2003. Specific exergy, although exhibiting no statistically significant differences across the study period ( $P = 0.44$ ), showed minimum values during and immediately after the heatwave, and then raised according to recolonization processes. Conversely, ecological indicators seemed less able to discriminate among ecological conditions before, during and after the heatwave. AMBI showed quite a puzzling response ( $P = 0.6$ ), which was corrected, in M-AMBI's

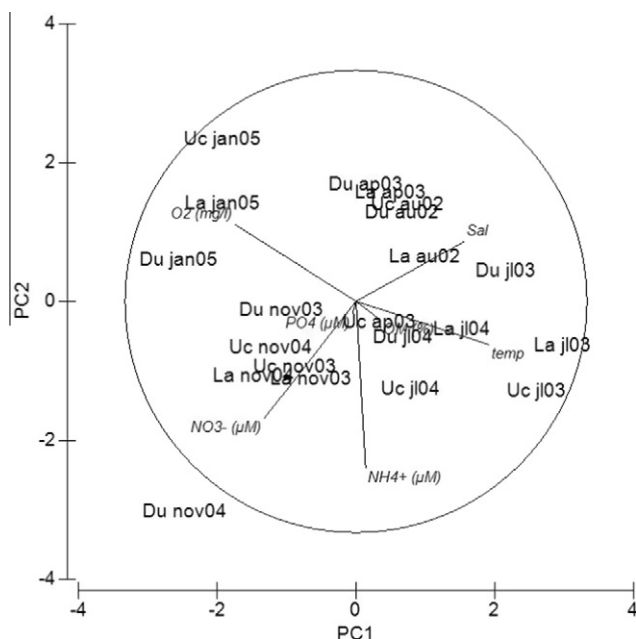


Fig. 3. PCA plot of environmental variables.

response ( $P = 0.0003$ ), by the effects of diversity (see Fig. 5, where  $H'$  and M-AMBI show exactly the same trend across the study period). BITS showed a decreasing and then an increasing trend, although not statistically significant ( $P = 0.76$ ). Despite this, the ecological quality status through BITS and M-AMBI resulted always comprised between bad and poor status.

Table 3 shows the combination of environmental parameters providing the highest Spearman's correlation with biodiversity, functional, and ecological indicators. Most indicators showed quite high correlation with temperature and dissolved oxygen (e.g.,  $N_0$ ,  $d$ ,  $Ex$ ,  $SpEx$ , M-AMBI).  $J'$ ,  $H'$  and  $1 - \lambda'$  resulted more influenced by oxygen, nitrogen (ammonia or nitrates) and salinity, while BITS exhibited a weaker correlation with sedimentary organic matter.

The traits analysis allowed to identify principal features of the benthos, before and after the heatwave. Fig. 6 shows the dominant biological characteristics of the benthic community before and after the heatwave: major changes (e.g., feeding technique, life span, body size, etc.) probably reflected the change in taxa dominance (Annelida vs Mollusca) that occurred after summer 2003. After the heatwave, deposit-feeders became even more dominant, at the expense of herbivorous and, especially, filter-feeders. Long and medium life span organisms almost disappeared, as well as large and medium-sized animals. A decrease in crawling and an increase in burrowing mobility type seemed also evident, as well as a decrease in epifaunal and an increase in infaunal life habitat.

Table 2

Average abundance ( $\pm$ SD) of taxa encountered in the study period (Au: August, Ap: April, Ju: July, etc.).

	Au2002	Ap2003	Ju2003	No2003	Ju2004	No2004	Ja2005
<i>Uccelliera stn Uc</i>							
<i>Ectobia ventrosa</i> (Montagu, 1803)	382.3 $\pm$ 336	493.3 $\pm$ 452	111 $\pm$ 37	382.3 $\pm$ 336	98.7 $\pm$ 21.4		74 $\pm$ 56.5
<i>Hydrobia acuta</i> (Draparnaud, 1805)	703 $\pm$ 481	160.3 $\pm$ 129					
<i>Cyclope neritea</i> (Linnaeus, 1758)	74 $\pm$ 74						12.3 $\pm$ 21.4
<i>Abra alba</i> (Wood, 1802)	727.7 $\pm$ 441	320.6 $\pm$ 140				86.3 $\pm$ 21.4	
<i>Polydora ciliata</i> (Johnston, 1838)				12.3 $\pm$ 21.4	3293 $\pm$ 1022	74 $\pm$ 97.9	3293 $\pm$ 2556
<i>Capitella capitata</i> (Fabricius, 1780)	172.7 $\pm$ 174	24.7 $\pm$ 21.4		24.7 $\pm$ 21.4	172.7 $\pm$ 174	197.3 $\pm$ 93.1	49.3 $\pm$ 85.4
<i>Streblospio shrubsolii</i> (Buchanan, 1890)				12.3 $\pm$ 21.4	24.7 $\pm$ 21.4		12.3 $\pm$ 21.4
<i>Alitta succinea</i> (Leuckart, 1847)	12.3 $\pm$ 21.4	49.3 $\pm$ 56			21.3 $\pm$ 21.4		
<i>Perinereis cultrifera</i> (Grube, 1840)		12.3 $\pm$ 21.4					
<i>Oligochaeta</i>		24.6 $\pm$ 42.7		24.7 $\pm$ 21.4			12.3 $\pm$ 21.4
<i>Idotea balthica</i> (Pallas, 1772)	12.3 $\pm$ 21.4						
<i>Gammarus aequicauda</i> (Martynov, 1931)							12.3 $\pm$ 21.4
<i>Monocorophium insidiosum</i> (Crawford, 1937)	86.3 $\pm$ 85						
<i>Palaemon elegans</i> (Rathke, 1837)	12.3 $\pm$ 21.4						
<i>Chironomus salinarius</i> (Kieffer, 1915)	641.3 $\pm$ 616	86.3 $\pm$ 21.4	12.3 $\pm$ 21.4	86.3 $\pm$ 149.5	2355 $\pm$ 1022	2343 $\pm$ 1399	10 643 $\pm$ 6402
<i>Uccelliera stn Du</i>							
<i>Ectobia ventrosa</i> (Montagu, 1803)	863.3 $\pm$ 1071	98.7 $\pm$ 21.4				111 $\pm$ 85.4	283.7 $\pm$ 56.5
<i>Hydrobia acuta</i> (Draparnaud, 1805)	1282.7 $\pm$ 1924	111 $\pm$ 85.4					197.3 $\pm$ 149.5
<i>Abra alba</i> (Wood, 1802)	12.3 $\pm$ 21.4						
<i>Polydora ciliata</i> (Johnston, 1838)		86.3 $\pm$ 149.5		86.3 $\pm$ 149.5	542.7 $\pm$ 444	419.3 $\pm$ 174	542.7 $\pm$ 444
<i>Capitella capitata</i> (Fabricius, 1780)	12.3 $\pm$ 21.4	86.3 $\pm$ 149.5	49.3 $\pm$ 42.7	86.3 $\pm$ 149.5			12.3 $\pm$ 21.4
<i>Alitta succinea</i> (Leuckart, 1847)		24.6 $\pm$ 42.7					
<i>Oligochaeta</i>	24.7 $\pm$ 42.7	12.3 $\pm$ 21.4	12.3 $\pm$ 21.4	24.7 $\pm$ 42.7			
<i>Idotea balthica</i> (Pallas, 1772)		12.3 $\pm$ 21.4				12.3 $\pm$ 21.4	
<i>Gammarus aequicauda</i> (Martynov, 1931)	12.3 $\pm$ 21.4				12.3 $\pm$ 21.4		12.3 $\pm$ 21.4
<i>Monocorophium insidiosum</i> (Crawford, 1937)	74 $\pm$ 42.7	74 $\pm$ 64		12.3 $\pm$ 21.4			
<i>Palaemon elegans</i> (Rathke, 1837)					12.3 $\pm$ 21.4		12.3 $\pm$ 21.4
<i>Chironomus salinarius</i> (Kieffer, 1915)	703 $\pm$ 484	86.3 $\pm$ 149.5	12.3 $\pm$ 21.4		12.3 $\pm$ 21.4		12.3 $\pm$ 21.4
<i>Lamenterio stn La</i>							
<i>Ectobia ventrosa</i> (Montagu, 1803)	283.6 $\pm$ 301	74 $\pm$ 74			382.3 $\pm$ 301	12.3 $\pm$ 21.4	74 $\pm$ 37
<i>Hydrobia acuta</i> (Draparnaud, 1805)	197.3 $\pm$ 85.4	24.7 $\pm$ 42.7					
<i>Abra alba</i> (Wood, 1802)		98.7 $\pm$ 93				86.3 $\pm$ 77	
<i>Cerastoderma glaucum</i> (Bruguière, 1789)		875.7 $\pm$ 140				12.3 $\pm$ 21.4	271.3 $\pm$ 186
<i>Polydora ciliata</i> (Johnston, 1838)	542.7 $\pm$ 444	419.3 $\pm$ 246.4	12.3 $\pm$ 21.4	703 $\pm$ 140	542.7 $\pm$ 444	2355.7 $\pm$ 21.4	16 921 $\pm$ 17 861
<i>Capitella capitata</i> (Fabricius, 1780)	49.3 $\pm$ 42.7	1036 $\pm$ 650	197.3 $\pm$ 186	24.7 $\pm$ 42.7	172 $\pm$ 186	12.3 $\pm$ 21.4	12.3 $\pm$ 21.4
<i>Streblospio shrubsolii</i> (Buchanan, 1890)							24.7 $\pm$ 21.4
<i>Alitta succinea</i> (Leuckart, 1847)		49.3 $\pm$ 56.5			49.3 $\pm$ 42.7		
<i>Oligochaeta</i>					12.3 $\pm$ 21.4		
<i>Monocorophium insidiosum</i> (Crawford, 1937)	49.3 $\pm$ 42.7				49.3 $\pm$ 42.7		
<i>Palaemon elegans</i> (Rathke, 1837)		12.3 $\pm$ 21.4					
<i>Chironomus salinarius</i> (Kieffer, 1915)	542.7 $\pm$ 204	2232 $\pm$ 1022	24.6 $\pm$ 42.7	2232 $\pm$ 1399	3293 $\pm$ 1022	5167 $\pm$ 2606	5735 $\pm$ 4751



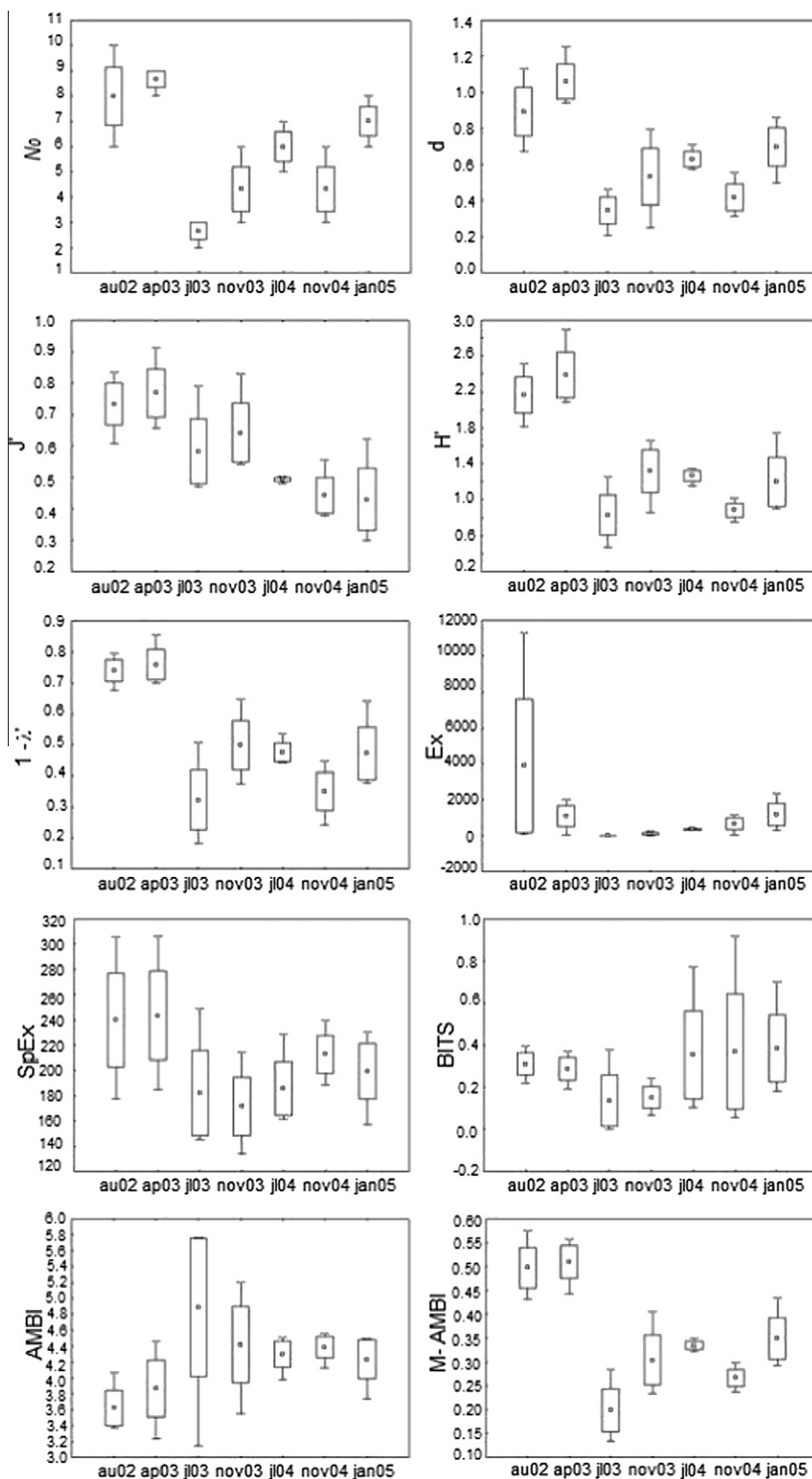


Fig. 5. Biodiversity, functional and ecological indicators (center point: average; box: standard error; whisker: full range of data).

mely rare. Although relatively common before the heatwave, the bivalve *Cerastoderma glaucum* (Bruguière, 1789) disappeared from Valle Lamentario, and seemed to recruit only at the end of 2004.

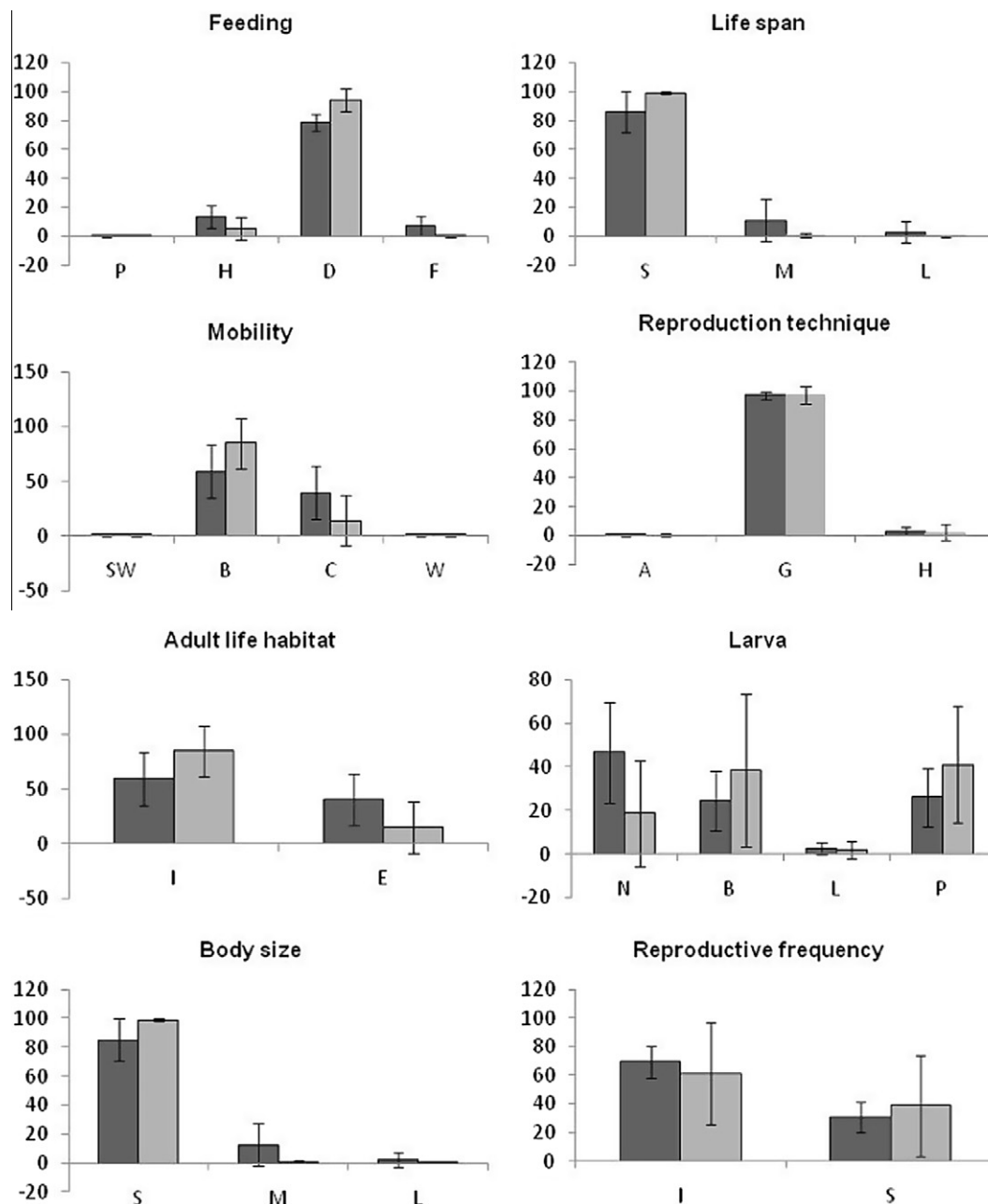
Biodiversity indicators have been largely utilized for assessment efforts, despite some contrasting conclusions (e.g., Spatharis et al., 2011). The present study case evidenced their ability in capturing

**Table 3**

BIOENV analysis: best correlated (Spearman's  $\rho$ ) environmental variables with considered indicators.

Indicator	Spearman's $\rho$	Best correlated variables
$N_0$	0.722	Temperature, oxygen
$d$	0.733	Temperature, oxygen, ammonia
$J'$	0.371	Oxygen, ammonia, nitrates
$H'$	0.780	Oxygen, ammonia
$1 - \lambda'$	0.779	Salinity, oxygen, ammonia
$Ex$	0.393	Temperature, oxygen
$SpEx$	0.253	Temperature, oxygen, ammonia
$BITS$	0.141	Organic matter
$AMBI$	0.413	Temperature
$M-AMBI$	0.721	Temperature, oxygen, ammonia

pulse disturbance effects on the benthic community structure. The higher severity observed in benthic response to disturbance at Valle Uccelliera is in accordance with the fact that communities of more stable environments are less adapted to fluctuations, whereas the relatively lower severity response observed at Lamenterio may be explained because the benthic community was already stressed by the somehow harsher environmental conditions caused, probably, by the absence of submerged vegetation, higher organic matter, lower dissolved oxygen. In the comparison of summers 2002, 2003 and 2004 biotic and environmental data, temperature and dissolved oxygen concentration resulted highly correlated with benthic community structure summarized by biodiversity indicators. It is known (Vaquer-Sunyer and Duarte, 2011) that warming negatively impact the survival of benthic organisms under low oxygen



**Fig. 6.** Frequency of categories for each biological trait, before (dark grey) and after (light grey) the heatwave of summer 2003 (labels on abscissa as in Table 1; bars: standard deviation).



conditions by reducing survival times. Temperature increases and oxygen depletion act synergically: warming accelerate oxygen depletion, but the negative effects of oxygen depletion are aggravated by the effect of warming in rising the oxygen requirements of organisms (Vaquer-Sunyer and Duarte, 2011).

According to the Italian National Act 260/10, the evaluation of the ecological quality status was done through the application of two ecological indicators, BITS and M-AMBI. The comparison between their results, in a context of general concordance of the patterns, evidenced the inefficiency of both indicators to capture an effect on the benthic community due to the pulse event of summer 2003. During the entire study period, the ecological quality oscillated between poor and bad status. In transitional ecosystems the benthic fauna is mainly composed by species tolerant of the naturally disturbed conditions, so the dominance of tolerant species does not always guarantee a correct assessment of poor or bad status of a site, as it happens in the coastal marine environment. Such natural disturbance selects the lagoon fauna, generally resulting in low number of species and taxonomic diversity (Dauvin, 2007). The combined effect of an impoverished species pools and a partial understanding of the species sensitivity/tolerance, makes the assessment of ecological status a very hard task in such environments. The concept of ecological status was developed, through the 2000/60/EC, for natural water bodies, in which it is a measured deviation from a reference condition. The 2000/60/EC also considers “Heavily Modified Water Bodies” (HMWB), water bodies resulting from physical alterations by human activity, which substantially change their hydrogeomorphological characters. The lagoons of the Comacchio Saltworks likely fall in this category, and instead of achieving, by 2015, a good ecological status, they should more correctly achieve at least a good ecological potential, following the definitions provided by Borja and Elliott (2007). Unfortunately, Italy (as well as many other Member States) has not yet tackled the definition of HMWBs and their ecological potential.

Ecological indicators are usually based on an ecosystem component (e.g., macrobenthos), but, despite providing useful informations on the ecological status of the environment through the response of that ecosystem component to disturbance, they do not reflect ecosystem complexity. Conversely, goal functions express emergent properties of an ecosystem arising from self-organization processes in the run of its development: exergy is defined as the distance between present state of the system and the state of it in thermodynamic equilibrium with the environment (Jørgensen, 1997), while specific exergy reflects the degree of ecosystem development, demonstrating the level of evolutionary development of organisms the ecosystem consists of (Jørgensen, 1997). Recently, many authors recommended the use of goal functions in environmental monitoring as holistic and quantitative parameters reflecting the ecosystem state and its anthropogenic changes (Silow and In-Hye, 2004; Austoni et al., 2007; Pranovi et al., 2007). Results from this study strongly rehenforce those recommendations. During the heatwave, exergy dropped to extremely low values at all sampling sites, fully reflecting the dramatic scenarios experienced by benthic communities in summer 2003. Exergy then raised to higher figures (similar to those before the heatwave) accordingly to the recolonization processes occurring after the heatwave. Specific exergy, particularly, evidenced the shift in community dominance from mollusc-dominated ones before the heatwave, to annelid-dominated ones after the heatwave. At stn Du, after the summer 2003 decline, specific exergy raised to almost the same values of 2002, despite some zigzagging pattern, reflecting the increase in the structural complexity of the macrobenthic community. Conversely, at stn Uc, specific exergy was almost constantly decreasing after the heatwave, well capturing the community shift from

a basin of attraction characterized by molluscs to another one characterized by annelids, and, indirectly, also reflecting the habitat impoverishment caused by the reduction of the seagrass bed. At stn La, an abrupt increase in both goal functions was observed in autumn 2004: in communities dominated by *r* strategists (e.g., *Capitella capitata* Fabricius, 1780,  $\beta = 133$ ; *Chironomus salinaris*,  $\beta = 167$ ), exergy and specific exergy may shift quite drastically as a function of stochasticity of recruitment dynamics, especially when the “quantity of information” (*sensu* Jørgensen, 2006) of recruiting species is higher (in this case *Cerastoderma glaucum*,  $\beta = 310$ ).

Ecosystem processes strongly depend on functional diversity, defined as the value and range of functional traits of the organisms present in a given ecosystem (Diaz and Cabido, 2001). Several different species perform similar roles (i.e. exhibit similar traits) within communities, and reductions (or elimination) of a particular species performing a particular role may be compensated by an increase in other similar species (Frost et al., 1995). In this study, reductions in the frequency of many traits were observed (i.e. feeding, life span, mobility, adult life habitat, type of larva and body size), but compensation did not occurred. Two biological traits have repeatedly been used to describe the response of the transitional waters benthic community to different environmental conditions: feeding and body size distribution. Other biological traits, such as mobility, type of larva and reproduction strategy, have received less attention; however, they represent important functions of the community such as substrate utilization, ability of dispersion and energy allocation (Marchini et al., 2008). From summer 2003 onwards, the benthic fauna was dominated by infaunal, small-sized, short-lived deposit feeders. The heatwave of summer 2003 led to a loss of the larger, long-lived species, such as filter feeding bivalves or carnivorous polychaetes, in favour of more opportunistic, short-living taxa, mainly small-sized, deposit-feeding worms. Feeding interactions have been promoted as the most important factor structuring invertebrate communities (Pearson and Rosenberg, 1987), and organisms' feeding mechanisms can dictate their response to disturbance and/or impacts. Traits analysis showed that feeding mechanisms were important in determining differences between the communities before and after the heatwave. The changes in feeding frequencies observed after the heatwave, not compensated through the increase in other similar species, may also have implications for ecosystem processes: i.e. the very low occurrence of herbivorous and filter-feeder taxa might decouple benthic-pelagic dynamics (as happened in the neighbouring Valli di Comacchio; Munari et al., 2005). Results from this study also strengthen the recent proposal of body size as an effective indicator for assessing changes in transitional water communities (Basset et al., 2004), since the pulse disturbance almost eliminated medium and larger-sized organisms.

Finally, although this study showed an immediate effect of the heatwave of summer 2003, together with subsequent successional changes in the benthic community, caution is needed before drawing definitive conclusions, probably because insufficient pre-heatwave data were available. It can be that the pre-heatwave potential variability of benthic communities of Comacchio Saltworks was not fully ascertained. Studies attempting to assess the effects of pulse disturbance, when little pre-perturbation data are available, should be better performed with more complex sampling strategies (e.g., a before-after, control-impact approach). In reality such an ideal sampling strategy may not always be practical or possible, especially when a disturbance event impacts large areas (or even an entire continent, like the heatwave of summer 2003), and the chance of finding undisturbed control sites (quite close to the impacted ones in order to avoid spatial artifacts into the analysis) are extremely rare. A major caveat we have to accept is that, in certain circumstances (like continental-scale heatwaves), the ideal

sampling strategy may literally be impossible because of the very nature of the disturbance.

## 5. Conclusions

The heatwave of summer 2003 caused considerable changes in the benthic community structure and relative composition in the lagoons of Comacchio Saltworks. Results from this study highlight that benthic communities of severe transitional systems may switch rapidly to alternative attractors in response to a relatively small change in external conditions. Biodiversity and functional indicators captured changes in community structure and composition, proving to be powerful tools to detect responses related to global warming. Conversely, ecological indicators rendered a monotonic response oscillating between bad and poor ecological status across the study period. The changes in trait frequencies observed after the heatwave may have implications for ecosystem processes. Resilience depends on disturbance nature and intensity, and except in the case of a lasting change in the habitat (e.g., the reduction of seagrass at Valle Uccelliera), in transitional systems it is reported to be generally high (e.g., Mistri, 2002). The resilience of mollusc biocoenosis to the heatwave of summer 2003 was essentially limited to a partial recolonization by a gastropod species. This may suggest that the recovery of mollusc populations will probably need more years than those encompassed by this study (and that the recovery of small-sized gastropods is faster than that of bivalves). Simulations predict that the frequency of summers as hot as that of 2003 will progressively increase to become the norm in the second half of the 21st century (Schaer et al., 2004). If true, the majority of mollusc species inhabiting severe transitional systems (like Comacchio Saltworks), whose shallow waters are directly exposed to climatic warming, are probably threatened much more than other taxa inhabiting those ecosystem.

## Acknowledgments

This work was supported through the project LIFE00NAT/IT7215. I wish to thank F. Ghion (ARPA Ferrara) for water analyses, and M. Mistri (University of Ferrara) for constructive criticism. I am indebted to an anonymous Reviewer whose comments and suggestions greatly improved the quality of this manuscript.

## References

- Amaral, M.J., Costa, M.H., 1999. Macrobenthic communities of salt pans from the Sado Estuary (Portugal). *Acta Oecologica* 20, 327–332.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to software and Statistical Methods. PRIMER-E Ltd Plymouth, UK, pp. 214.
- APAT, 2003. Metodi analitici per le acque. APAT-ISPRA-CNR, Manuali e Linee Guida, 29/2003, p. 1153.
- Austoni, M., Giordani, G., Viaroli, P., Zaldivar, J.M., 2007. Application to specific exergy to macrophytes as an integrated index of environmental quality for coastal lagoons. *Ecological Indicators* 7, 229–238.
- Barnes, RSK., 2005. Interspecific competition and rarity in mudsnails: feeding interactions between and within *Hydrobia acuta neglecta* and sympatric *Hydrobia* species. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15, 485–493.
- Basset, A., Sangiorgio, F., Pinna, M., 2004. Monitoring with benthic macroinvertebrates: advantages and disadvantages of body size descriptors. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14, S43–S58.
- Borja, A., Elliott, M., 2007. What does “good ecological potential” mean, within the European Water Framework Directive? *Marine Pollution Bulletin* 54, 1559–1564.
- Bradley, D.C., Ormerod, S.J., 2001. Community persistence among stream invertebrates tracks the North Atlantic Oscillation. *Journal of Animal Ecology* 70, 987–996.
- Castel, J., Labourg, P.J., Escaravage, V., Thimel, A., 1990. Distribution quantitative du meio- et macrobenthos dans des lagunes mixohalines: influence du confinement sur le partage des ressources. *Oceanologica Acta* 13, 349–359.
- Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual Tutorial. PRIMER-E Ltd., Plymouth, UK, 190 pp.
- Dauvin, J.C., 2007. Paradox of estuarine quality: Benthic indicators and indices, consensus or debate for the future. *Marine Pollution Bulletin* 55, 271–281.
- Diaz, S., Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16, 646–655.
- Directive of the European Parliament and of the Council 2000/60/EC establishing a framework for community action in the field of Water Policy. Available at: [http://europa.eu/eur-lex/pri/en/oj/dat/2000/l\\_327/l\\_32720001222en00010072.pdf](http://europa.eu/eur-lex/pri/en/oj/dat/2000/l_327/l_32720001222en00010072.pdf).
- Frost, T.M., Carpenter, S.R., Ives, A.R., Kratz, T.K., 1995. Species compensation and complementarity in ecosystem function. In: Jones, C., Lawton, J. (Eds.), *Linking Species and Ecosystems*. Chapman and Hall, New York, pp. 24–239.
- Garrabou, J., Coma, R., Bensoussan, N., et al., 2009. Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Global Change Biology* 15, 1090–1103.
- Gray, J.S., 1981. *The Ecology of Marine Sediments*. Cambridge University Press, Cambridge, 85 pp.
- IPCC, 2007. Climate change 2007: the physical science basis. Contribution of Working Group I. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), *Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp. 996.
- Jørgensen, S.E., 1997. *Integration of Ecosystem Theories: a Pattern*, second ed. Kluwer Academic Publishers, Dordrecht, Boston, London.
- Jørgensen, S.E., 2006. Application of holistic thermodynamic indicators. *Ecological Indicators* 6, 24–29.
- Luterbacher, J., Dietrich, D., Xoplaki, E., et al., 2004. European seasonal and annual temperature variability, trends and extremes since 1500. *Science* 303, 1499–1503.
- Maazouzi, C., Masson, G., Izquierdo, M.S., Pihan, J.C., 2008. Midsummer heat wave effects on lacustrine plankton: variation of assemblage structure and fatty acid composition. *Journal of Thermal Biology* 33, 287–296.
- Marchini, A., Munari, C., Mistri, M., 2008. Functions and ecological status of eight Italian lagoons examined using biological traits analysis (BTA). *Marine Pollution Bulletin* 56, 1076–1085.
- Mistri, M., 2002. Persistence of benthic communities: a case study from the Valli di Comacchio, a Northern Adriatic lagoonal ecosystem (Italy). *ICES Journal of Marine Sciences* 59, 314–322.
- Mistri, M., Munari, C., 2008. BITS: a SMART indicator for soft-bottom, non-tidal lagoons. *Marine Pollution Bulletin* 56, 587–599.
- Mouthon, J., Daufresne, M., 2006. Effects of the 2003 heatwave and climatic warming on mollusc communities of the Saône: a large lowland river and of its two main tributaries (France). *Global Change Biology* 12, 441–449.
- Munari, C., Mistri, M., 2008. Biodiversity of soft-sediment benthic communities from Italian transitional waters. *Journal of Biogeography* 35, 1622–1637.
- Munari, C., Balasso, E., Rossi, R., Mistri, M., 2006. A comparison of the effect of different types of clam rakes on non-target, subtidal benthic fauna. *Italian Journal of Zoology* 73, 75–82.
- Munari, C., Rossi, R., Mistri, M., 2005. Temporal trends in macrobenthic community structure and redundancy in a shallow coastal lagoon (Valli di Comacchio, northern Adriatic Sea). *Hydrobiologia* 550, 95–104.
- Muxika, I., Borja, A., Bald, J., 2007. Using historical data, expert judgement and multivariate analysis in assessing reference conditions and benthic ecological status, according to the European Water Framework Directive. *Marine Pollution Bulletin* 55, 16–29.
- Pearson, T.H., Rosenberg, R., 1978. Feast and famine: structuring factors in marine benthic communities. In: Gee, J., Giller, P. (Eds.), *Organization of Communities Past and Present*. Blackwell Scientific Publications, Oxford, pp. 373–398.
- Pranovi, F., Da Ponte, F., Torricelli, P., 2007. Application of biotic indices and relationship with structural and functional features of macrobenthic community in the lagoon of Venice, an example over a long time series of data. *Marine Pollution Bulletin* 54, 1607–1618.
- Santamaria, L., Hootsmans, M.J.M., 1998. The effect of temperature on the photosynthesis, growth and reproduction of a Mediterranean submerged macrophyte, *Ruppia drepanensis*. *Aquatic Botany* 60, 169–188.
- Schaer, C., Vidale, P.L., Luethi, D., et al., 2004. The role of increasing temperature variability in European summer heatwaves. *Nature* 427, 332–336.
- Short, F.T., Neckles, H.A., 1999. The effects of global climate change on seagrasses. *Aquatic Botany* 65, 169–196.
- Silow, E.A., In-Hye, O., 2004. Aquatic ecosystem assessment using exergy. *Ecological Indicators* 4, 189–198.
- Spatharis, S., Roelke, D.L., Dimitrakopoulos, P.G., Kokkoris, G.D., 2011. Analyzing the (mis)behavior of Shannon index in eutrophication studies using field and simulated phytoplankton assemblages. *Ecological Indicators* 11, 697–703.
- Stott, P.A., Stone, D.A., Allen, M.R., 2004. Human contribution to the European heatwave of 2003. *Nature* 432, 610–614.
- UNEP, 2004. The European Summer Heat Wave of 2003, UNEP Brief. United Nations Environmental Programme, Nairobi, Kenya.
- van Nes, E.H., Scheffer, M., 2004. Large species shifts triggered by small forces. *American Naturalist* 164, 255–266.
- Vaquer-Sunyer, R., Duarte, C.M., 2011. Temperature effects on oxygen thresholds for hypoxia in marine benthic organisms. *Global Change Biology* 17, 1788–1797.
- Vieira, N., Amat, F., 1997. The invertebrate benthic community of two solar salt ponds in Aveiro, Portugal. *International Journal of Salt Lake Research* 5, 281–286.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebe, T.J., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.