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Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave

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Abstract

Late in summer 2003, extensive mass mortality of at least 25 rocky benthic macro-invertebrate species (mainly gorgonians and sponges) was observed in the entire North-western (NW) Mediterranean region, affecting several thousand kilometers of coastline. We were able to characterize the mortality event by studying six areas covering the main regions of the NW Mediterranean basin. The degree of impact on each study area was quantified at 49 sites by estimating the proportion of colonies affected in populations of several gorgonian species compared with reference data obtained in years without mortality signs. According to these data, the western areas (Catalan coast and Balearic Islands) were the least affected, while the central areas (Provence coast and Corsica-Sardinia) showed a moderate impact. The northernmost and eastern areas (Gulf of Genoa and Gulf of Naples) displayed the highest impact, with almost 80% of gorgonian colonies affected. The heat wave of 2003 in Europe caused an anomalous warming of seawater, which reached the highest temperatures ever recorded in the studied regions, between 1 and 3 °C above the climatic values (mean and maximum). Because this exceptional warming was observed in the depth ranges most affected by the mortality, it seems likely that the 2003 anomalous temperature played a key role in the observed mortality event. A correlation analysis between temperature conditions and degree of impact seems to support this hypothesis. Under the present climate warming trend, new mass mortality events may occur in the near future, possibly driving a major biodiversity crisis in the Mediterranean Sea.

Keywords: disturbance, effects of climate change, marine biodiversity, mortality outbreak

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Introduction

Recent climatic trends have resulted in significant responses in marine ecosystems, such as pelagic produc-

tivity, shifts in species' geographical distributions, community composition changes, and modifications of migratory patterns (Rosenzweig *et al.*, 2007). The increase in mass mortality outbreaks in coastal ecosystems during the past few decades has also been linked to modifications in environmental conditions caused by global change (Harvell *et al.*, 1999; Harley *et al.*, 2006). In coastal ecosystems, coral reefs are suffering a dramatic increase in the frequency and intensity of mortality and

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disease, including several regional-scale mass mortality events in gorgonians (Nagelkerken *et al.*, 1997) and widespread coral bleaching episodes (Glynn, 1991; McWilliams *et al.*, 2005). In general, high-temperature conditions are documented to be concurrent with observations of mass mortalities (Harvell *et al.*, 1999; Lesser *et al.*, 2007). These events have occurred in the context of significant warming of the global average surface ($+0.76^{\circ}\text{C}$ for the 20th century; IPCC, 2007) and upper global ocean ($+0.3^{\circ}\text{C}$ from 1950 to 2000; Levitus *et al.*, 2000). Projections for the 21st century depict an increase in warming ($+1.8$ or $+3.5^{\circ}\text{C}$ depending on the emission scenario; IPCC, 2007) along with a very likely increase in the occurrence of heat waves (Déqué 2007; Diffenbaugh *et al.*, 2007). Under these conditions, incidences of mortality events may spread over larger geographic areas and a wider spectrum of organisms. This scenario could cause a marine biodiversity loss crisis. Analyzing the impact of these events at appropriate scales (spatial and temporal) and biological organization levels (species, populations, communities) is crucial to accurately anticipate future changes in marine ecosystems and propose adapted management and conservation plans.

In summer 2003, the European region suffered an exceptional heat wave (Luterbacher *et al.*, 2004; Schär *et al.*, 2004). This had dramatic social, economic, and environmental consequences, including an increase in heat-related human morbidity and mortality, forest fires, and widespread parasites (De Bono *et al.*, 2004). This event began in early June 2003 and lasted until mid-August, with air temperature records about $3\text{--}6^{\circ}\text{C}$ above the seasonal average in many parts of Europe (Schär *et al.*, 2004). This heat wave also affected the seawater temperature in the Northwestern (NW) Mediterranean region (Marullo & Guarracino, 2003; Sparnocchia *et al.*, 2006). In the marine realm, a large-scale mass mortality event was observed in different areas of the NW Mediterranean during this heat wave.

The NW Mediterranean has been affected by several severe mortality events of benthic invertebrate species during the last few decades (Coma & Ribes, 2003; Garrabou *et al.*, 2003). In 1999, an unprecedented large-scale mass mortality event was recorded, affecting about 30 benthic species over hundreds of kilometers of the NW Mediterranean coast (Cerrano *et al.*, 2000; Perez *et al.*, 2000). Anomalous high-temperature conditions during summer 1999 were identified as the main triggering factor of the mortality (Cerrano *et al.*, 2000; Perez *et al.*, 2000). Bearing in mind the warming trend observed in the Mediterranean (Bethoux *et al.*, 1990; Vargas-Yañez *et al.*, 2008) and the coincidence of the event with anomalous temperature conditions (Cerrano *et al.*, 2000; Romano *et al.*, 2000), it was hypothesized that new

mass mortality events could occur in the near future (Cerrano *et al.*, 2000; Coma *et al.*, 2000; Perez *et al.*, 2000). Unfortunately, this hypothesis was corroborated in 2003 when a further large-scale mass mortality event was observed in the NW Mediterranean region.

The main goal of this paper is to provide a comprehensive report on the impact of the 2003 mass mortality event in the NW Mediterranean area by providing data on the species affected, the intensity of the impact, the depth range affected, and the timing of the event for different NW Mediterranean areas. The affected communities have been studied during the last four decades by the staff of various research institutes. Therefore, even though we cannot provide quantitative data for all species, we contend that our observations on unusual mortality signs allow us to provide an unbiased assessment of the impact of the 2003 mass mortality event. Finally, data on temperature conditions during the summer of 2003 are also reported to analyze the potential role of anomalous temperature conditions in the occurrence of the event.

Materials and methods

Study areas

This study encompasses a large geographic scale, covering the main rocky coasts over several thousands of kilometers of coastline from $39^{\circ}50'\text{N}$ $0^{\circ}40'\text{E}$ in Spain to $40^{\circ}34'\text{N}$ $14^{\circ}20'\text{E}$ in Italy, including the main Mediterranean islands (Balearic, Corsica, and Sardinia; Fig. 1). In an attempt to provide data on the extent and impact of the 2003 mass mortality event at the regional scale, the NW Mediterranean region has been divided into six main study areas, each spanning hundreds of kilometers of coastline (Fig. 1). A total of 49 sites were surveyed throughout the study. For each area, between 4 and 14 sites were surveyed (Table 1).

For each area, we collated reports of the 2003 mass mortality events for the rocky coasts collected by various research teams from Spain, France, and Italy. These included reports of park officers of different marine protected areas and diving clubs operating in the study areas.

Impact assessment of the 2003 mortality event

Data on mortality impact were based on qualitative and quantitative surveys. In the qualitative surveys, lists of species showing clear-cut signs of recent necrosis, such as denuded skeletons in gorgonians, sponges, and scleractinian corals and empty valves attached to the substratum in bivalves, were acquired for each study site. All species included in the qualitative surveys were large, macrobenthic, easily identifiable species, and

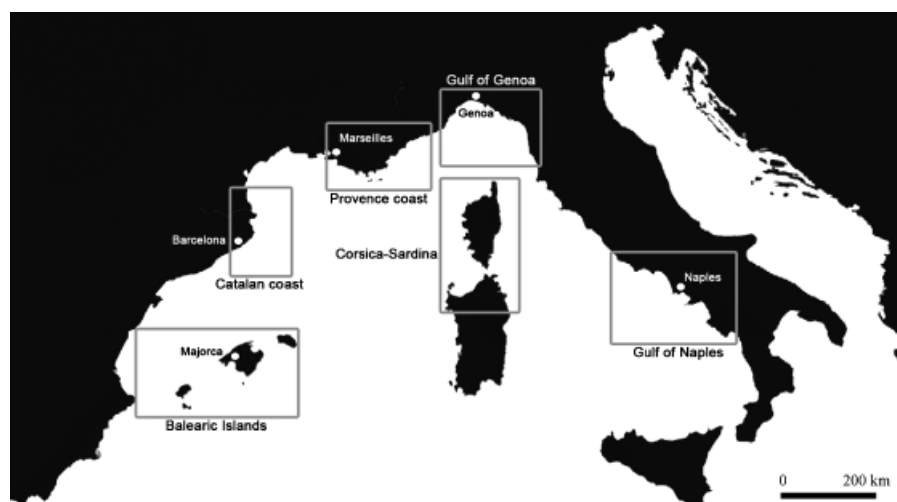


Fig. 1 Northwestern Mediterranean showing the limits of the six study areas where surveys of the 2003 mass mortality were conducted.

often abundant at the surveyed sites. The depth range affected by mortality and data on the timing of the event were provided for each site.

The quantitative surveys focused on gorgonian species because (a) they were abundant at all study areas and are considered engineering species in Mediterranean communities, (b) the effects of mortality are easy to quantify, and (c) gorgonian populations have been monitored at several study sites for up to 15 years, so they provide an excellent baseline that is not available for other affected species (Harmelin & Marinopoulos, 1994; Garrabou & Harmelin, 2002; Coma *et al.*, 2004; Linares *et al.*, 2008). Four gorgonian species were considered in assessing the quantitative impact of the 2003 mass mortality event: the red gorgonian *Paramuricea clavata*, the yellow gorgonian *Eunicella cavolinii*, the white gorgonian *Eunicella singularis*, and the red coral *Corallium rubrum*.

Surveys quantified the percentage of recent tissue necrosis (i.e., denuded axis or recent epibiosis) in about 100 colonies for each species present at each study site and depth range. We considered a colony to be affected by the mortality when it showed recent tissue necrosis over $\geq 10\%$ of its surface. For each survey, the percentage of affected colonies was calculated as an indicator of the mortality impact. This indicator was chosen instead of the mean extent of necrosis or the whole mortality rate for two main reasons. First, the mean extent of tissue necrosis could introduce a potential bias in a large-scale assessment, because it integrates the effects of past disturbances suffered by gorgonian populations (e.g., Harmelin & Marinopoulos, 1994; Coma *et al.*, 2004; see 'Discussion'). Second, previous studies showed that the immediate impact of the mass mortality events is much smaller in terms of total colony mortality than partial mortality (Cerrano *et al.*, 2005; Linares *et al.*, 2005).

Surveys were carried out at the end of 2003 (September to November) just after the observation of the mortality event. In 2003, a total of 93 surveys (more than 10 000 colonies observed) were carried out in the six study areas (Table 2a). A Kruskal–Wallis analysis was used to test for the differences in the impact among study areas (including all gorgonians species considered in each study area). Multiple comparisons were also performed to determine specific interarea differences. We used nonparametric analysis because the data followed neither normality nor homogeneity of variances after different transformations.

We ultimately compared the results of the 2003 surveys with surveys carried out in 2002, 2004, and 2005 (unaffected years), for which a total of 36 surveys (more than 6000 colonies observed) were performed on the Catalan coast, Provence coasts, and Corsica-Sardinia study areas (Table 2b). In this comparison, we only used surveys carried out on the red gorgonian *P. clavata*. For this species, the dataset was the largest available, allowing a reliable evaluation of the impact of the 2003 mortality event. Data from unaffected years was pooled and compared with the 2003 data using a Kolmogorov–Smirnov test. As previously, we used nonparametric analysis because the data followed neither normality nor homogeneity of variances after different transformations. The Kolmogorov–Smirnov test and the Kruskal–Wallis test were computed using the program STATISTICA (version 8.0, StatSoft, Inc., Tulsa, OK, USA).

Temperature conditions during summer 2003

Temperature records from 1, 10, and 20 m depth were analyzed to determine the temperatures that occurred during the mass mortality of invertebrates at the end of summer 2003. A total of six temperature series were

Table 1 Impact characteristics and species affected during the 2003 mass mortality event in the six study areas

Impact characteristics	Study areas					
	1 – Balearic Islands	2 – Catalan coast	3 – Provence coast	4 – Gulf of Genoa	5 – Corsica and Sardinia	6 – Gulf of Naples
Number of surveyed sites per area	8	9	14	4	10	4
Maximum depth affected (m)	30–40	15–20	15–25	25–30	25–30	25–30
Total number of affected species	5	3	16	14	13	5
Affected species						
Gorgonians						
<i>Paramuricea clavata</i>	A	A	A	A	A	A
<i>Eunicella cavolinii</i>	NO	NO	A	A	A	A
<i>Eunicella sigularis</i>	A	A	A	A	NO	A
<i>Eunicella verrucosa</i>	NO	NO	NA	A	NO	NO
<i>Leptogorgia sarmentosa</i>	NO	NO	NA	A	NO	NO
<i>Corallium rubrum</i>	NA	A	A	A	A	NA
Scleractinians						
<i>Cladocora caespitosa</i>	A	NA	NA	A	NO	A
<i>Balanophyllia europaea</i>	NO	NO	NO	A	NO	A
Zoantharians						
<i>Parazoanthus axinellae</i>	NA	NA	NA	A	NA	NA
Sponges						
<i>Spongia officinalis</i>	NO	NA	A	A	A	NA
<i>Ircinia dendroides</i>	NO	NA	A	NO	NO	NO
<i>Ircinia variabilis</i>	A	NA	A	A	A	NO
<i>Ircinia oros</i>	NO	NA	NA	A	NA	NO
<i>Agelas oroides</i>	NO	NA	A	A	NA	NA
<i>Crambe crambe</i>	NA	NA	A	NA	A	NA
<i>Cacospongia</i> spp.	NO	NA	A	NO	A	NO
<i>Hippospongia communis</i>	NO	NA	A	NO	A	NO
<i>Petrosia ficiformis</i>	NO	NA	A	A	A	NA
Bryozoans						
<i>Myriapora truncata</i>	A	NA	NA	NA	NA	NA
<i>Sertella</i> spp.	NO	NA	NA	NA	A	NA
Bivalves						
<i>Spondylus gaederopus</i>	NA	NA	A	A	A	NA
<i>Lima</i> spp.	NA	NA	NO	NO	A	NA
<i>Arca</i> spp.	NA	NA	A	A	A	NA
<i>Ostrea edulis</i>	NO	NA	A	NO	NO	NA
<i>Lithophaga lithophaga</i>	NA	NA	A	NO	NO	NO

For each affected species, we provide information regarding the impact for each study area: A, affected; NA, not affected; NO, no observations available.

analyzed, some from national observatories and some collected by the research teams. These series provided temperature data for all of the study areas except for the Corsica-Sardinia area, for which temperature records were not available. The main features of the temperature series are shown in Table 3. The series of L'Estartit and Villefranche cover the last 30 years and are the longest temperature records for the NW Mediterranean. Not all depths were available for each site: only temperatures at 1 m were available at Columbretes (Balearic Island area), while the 10 m level is missing at L'Estartit (Catalan coast area). The six temperature records were collected using

various measurement strategies, although in general, temperature measurements were derived from routine measurements (daily, weekly, and biweekly) carried out near the coast. Average mean and maximum temperatures from 1 July to 30 September were calculated for each available year from the data series to examine the temperature anomaly of 2003 within each temperature record.

Temperature and mortality

A correlation analysis between the 2003 summer temperature conditions (TXS₂₀₀₃) and the percentage of

Table 2 (a) Mean, minimum, and maximum percentages of colonies with $\geq 10\%$ of colony surface showing recent necrosis (denuded axis or recent epibiosis) obtained from (1) *Paramuricea clavata*, (2) *Eunicella singularis*, (3) *Eunicella cavolinii*, and (4) *Corallium rubrum* gorgonian populations dwelling in different areas of the Northwestern (NW) Mediterranean. Surveys were carried out in late 2003 in the depth range affected by the 2003 mass mortality event. (b) Mean percentage of colonies with $\geq 10\%$ of colony surface showing recent necrosis (denuded axis or recent epibiosis) obtained from *Paramuricea clavata* populations dwelling in different areas of the NW Mediterranean in years not affected by mass mortality events

Study area	N surveys	N colonies	Depth range	% affected colonies		
				X ± SD	Minimum–maximum	
(a)						
(1) <i>Paramuricea clavata</i>						
Balearic Islands*	3	316	30–40	14.9 ± 23.4	0–41.8	
Catalan coast	15	1067	15–20	4.8 ± 6.3	0–21.2	
Provence coast	15	1680	5–25	28.5 ± 21.5	1.9–77.7	
Gulf of Genoa	4	300	25–30	82.5 ± 9.5	70–90	
Corsica-Sardinia	6	1417	15–25	54.4 ± 22.1	19.6–84.9	
Gulf of Naples	3	165	25–32	64.9 ± 15.0	12.5–100	
(2) <i>Eunicella singularis</i>						
Balearic Islands	5	896	15–20	9.5 ± 4.5	3.1–14.3	
Catalan coast	4	349	10–15	2.7 ± 2.4	0–5.7	
Provence coast	–	–	–	–	–	
Gulf of Genoa	2	100	25–30	85 ± 7.07	80–90	
Corsica-Sardinia	–	–	–	–	–	
Gulf of Naples	6	329	15–22	86.6 ± 12.3	11.1–100	
(3) <i>Eunicella cavolinii</i>						
Balearic Islands	–	–	–	–	–	
Catalan coast	–	–	–	–	–	
Provence coast	11	1147	15–25	14.5 ± 14.5	3.0–50.8	
Gulf of Genoa	1	100	10–30	90	–	
Corsica-Sardinia	7	848	15–20	17.1 ± 10.6	4.9–34.2	
Gulf of Naples	–	–	–	–	–	
(4) <i>Corallium rubrum</i>						
Balearic Islands	–	–	–	–	–	
Catalan coast	–	–	–	–	–	
Provence coast	8	1140	5–25	33.5 ± 28.0	5.7–91.4	
Gulf of Genoa	1	300	25–30	50	–	
Corsica-Sardinia	2	399	20–25	20.2 ± 17.9	7.6–32.9	
Gulf of Naples	–	–	–	–	–	
				% affected colonies		
Study area	N surveys	Survey years	N colonies	Depth range	X ± SD	Minimum–maximum
(b)						
<i>Paramuricea clavata</i>						
NE Spain coast	16	2002	1644	15–35	0	–
Provence coast	12	2004–2005	3142	15–35	1.9 ± 1.6	0–5.2
Corsica	8	2005	1577	18–25	0.5 ± 0.8	0–2.0
All areas	36		6363		0.8 ± 1.3	0–5.2

*In the Balearic Islands area, *P. clavata* was only affected in several sites from the Columbretes Marine Reserve (situated midway between Balearic Island and the continental coast of the Iberian Peninsula).

affected colonies (see above) explored the potential role of temperature in the mass mortality of invertebrates. The analysis was performed using only data from the Provence area, because in this area the 2003 surveys

cover affected and unaffected depth ranges (45 surveys observing more than 5000 colonies) and two temperature data series (Marseilles and Villefranche) were available (Table 3). We applied the nonparametric cor-

Table 3 Main features of temperature data series analyzed to determine the 2003 positive temperature anomaly in the North-western Mediterranean basin

Site	Study area	Period	Measurement depths (m)	Sampling frequency	Instrumentation	References
Columbretes	Balearic Islands	1991–2006	1	Daily	Mercury-in-glass thermometer	–
L'Estartit	Catalan coast	1975–2004	1, 20, 50, 80	Weekly	Reversing thermometers	Pascual <i>et al.</i> (1995)
Marseilles	Provence coast	1999–2004	1, 10, 15, 20, 25, 30, 35, 40, 45, 50	Biweekly–monthly	1994–2003: CTD ME ECO-57 2003–2004: SBE 911	Romano <i>et al.</i> (2000)
Villefranche	Provence coast	1975–2004	1, 5, 10, 15, 20, 25, 30, 35, 40, 50, 75	Weekly	1975–1995: Reversing thermometers 1995–2004: CTD SBE 911	Prieur (2002)
Genoa	Gulf of Genoa	1994–2004	1, 10, 20, 50, 80	Biweekly–monthly	ODAS buoy and Idronaut Ocean Seven probe	Siccardi <i>et al.</i> (1998), Schiaparelli <i>et al.</i> (2007)
Naples	Gulf of Naples	2001–2004	1, 10, 20, 30 up to 80	Weekly	CTD-Seabird 911 plus	Ribera d'Alcalà <i>et al.</i> (2004)

relation analysis (Spearman rank order, STATISTICA version 8.0, StatSoft, Inc.) because the percentage of affected colonies followed neither normality nor homogeneity of variances after different transformations.

Results

Temperature conditions during summer 2003

The six temperature series analyzed indicated positive temperature anomalies at 1 and 10 m depth in all study areas. The analysis of the longest data series available from the Catalan coast (L'Estartit, Spain, 1975–present), and Provence (Villefranche, France, 1975–present) showed that the 2003 summer was the warmest of the last 30 years. In general, at 1 and 10 m depth, the mean and maximum temperatures during the 2003 summer were greater than the mean values (Table 4). In the 2003 summer, temperature (TXS₂₀₀₃) varied between 23.8 and 27.5 °C, yielding differences between 0.7 and 2.8 °C in relation to average values (TXS). Regarding temperature maxima, Tmax₂₀₀₃ varied between 25.1 and 29.6 °C, representing 1.2 and 2.9 °C differences compared with the average maximum temperatures (Tmax) (Table 4). The Gulf of Genoa showed the highest deviations from the mean values (Table 4).

At 20 m depth, the 2003 mean summer temperatures (TXS₂₀₀₃) were similar or lower than the mean values (TXS). However, in most areas where mortality was observed beyond 20 m, temperature maxima (Tmax₂₀₀₃) were always more than 1 °C greater than the average maximum temperatures (Tmax), except in the Gulf of

Naples where the 2003 temperature maximum was about 0.5 °C lower than the average value (Table 4).

Qualitative surveys: species and depth range affected and timing of the mortality

Overall, 25 benthic species were affected in the NW Mediterranean region by the 2003 mass mortality event (Table 1). Most species showed signs of unusual total and/or partial mortality over large geographic areas (several hundreds of kilometers; Table 1 and Fig. 2). The affected species belonged to four phyla: Cnidaria, Porifera, Bryozoa, and Mollusca. All species are hard substrate dwellers and several are prominent components of the infralittoral and circalittoral communities (photophilic algae assemblages, precoralligenous, coralligenous, and semidark caves). The total number of affected species per study area varied from a minimum of three to five species in the southern areas to a maximum of 12–16 species in the northern ones. The depth range affected was limited to 15–30 m, except in the Balearic Islands area where effects could be detected up to 35–40 m. From the Catalan coast to the Gulf of Naples, the depth range affected increased west to east (Table 1).

In most areas, the first signs of mortality were observed at the end of August 2003. At that time, for the gorgonian *P. clavata*, colony parts showing necrosis displayed a change in color from red to gray, resulting from the decomposition of the organic parts of the cortex, leaving only sclerite aggregations. The remaining organic parts and sclerites then progressively detached from the colony's axis, resulting in the partial and total denudation of skeletons (Fig. 2a). As in pre-

Table 4 Temperature records (from 1 July to 30 September) at 1, 10, and 20 m depths obtained from each study area except for the Corsica-Sardinia area for the years indicated under 'Period'

Site	Study area	Period	TXS	Tmax	TXS ₂₀₀₃	Tmax ₂₀₀₃
1 m						
Columbretes	1	1991–2006	25.9 ± 0.8	27.5 ± 0.9	26.7	29.6
L'Estartit	2	1975–2004	21.9 ± 0.7	24.0 ± 1.1	23.2	25.4
Marseilles	3	1999–2004	21.3 ± 1.5	24.4 ± 1.2	23.1	26.5
Villefranche	3	1975–2004	23.6 ± 0.8	24.6 ± 1.0	25.3	26.5
Genoa	4	1994–2004	23.6 ± 0.8	25.5 ± 1.3	26.4	27.8
Naples	6	2001–2004	25.6 ± 1.5	27.3 ± 0.9	26.3	28.6
10 m						
Marseilles	3	1999–2004	20.7 ± 1.7	23.9 ± 1.2	22.4	25.1
Villefranche	3	1975–2004	22.7 ± 0.8	23.8 ± 0.9	24.3	26.2
Genoa	4	1994–2004	22.8 ± 0.9	24.7 ± 1.8	25.2	27.6
Naples	6	2001–2004	24.6 ± 1.7	26.5 ± 1.3	25.3	28.3
20 m						
L'Estartit	2	1975–2004	20.2 ± 0.6	22.5 ± 1.0	20.8	23.3
Marseilles	3	1999–2004	19.5 ± 1.8	22.9 ± 1.9	19.9	21.8
Villefranche	3	1975–2004	21.1 ± 0.9	22.5 ± 0.9	21.3	23.8
Genoa	4	1994–2004	22.1 ± 1.7	22.4 ± 1.6	20.6	23.5
Naples	6	2001–2004	21.1 ± 2.3	23.9 ± 0.9	21.2	23.3

Two series (Marseilles and Villefranche) were analyzed for the Provence coast. Records were available at 1, 10, and 20 m depth at all sites, except Columbretes (only 1 m) (Balearic Islands study area) and L'Estartit (only 1 and 20 m) (Catalan coast area). TXS and Tmax refer to the average mean and maximum temperatures, respectively, obtained for the available period in each study area. TXS₂₀₀₃ and Tmax₂₀₀₃ refer to the average and maximum temperatures obtained for summer 2003.

vious events, this process could be sudden, with populations shifting from healthy to severely damaged over a few days. Once colonies lost their affected tissue, bare axial skeleton portions became colonized in the following weeks by macroscopic pioneer taxa such as hydroids, bryozoans, and serpulid polychaetes. At the end of September and early October, most gorgonian colonies showed some degree of recent epibiosis on their denuded axis, and thereafter, no further signs of mortality were observed, at least in these species. A similar pattern of tissue loss was found in the other affected gorgonian species (Fig. 2b and c). The scleractinian coral *Cladocora caespitosa* suffered extensive tissue loss directly through tissue necrosis or after suffering bleaching, resulting in the total or partial deaths of colonies (Fig. 2f). In sponges, specimens also showed total and/or partial death (Fig. 2d and e). The main affected sponge species were *Spongia officinalis*, *Petrosia ficiformis*, *Cacospongia* spp., and *Ircinia* spp. Skeletons in horny sponge species remained attached to the substratum as proof of recent mortality (Fig. 2e). Healed wounds were observed in late autumn 2003 in some specimens affected by partial mortality. In bivalve mollusk species, the presence of empty valves attached to the substratum indicated the abnormal recent deaths of individuals. High levels of recent injuries were also noted in some bryozoan species (*Myriapora truncata* and *Sertella* spp.).

Quantitative surveys

In 2003, gorgonian populations displayed a dramatic impact with an increase of about 5–82 fold of affected colonies compared with years without mortality for which values around 1% were found (Table 2b; Kolgomorov–Smirnov test, $P < 0.001$).

The degree of impact varied from about 5% in the least impacted area (Catalan coast) to 75–80% in the most impacted (Gulf of Genoa and Gulf of Naples) (Fig. 3). The Balearic Islands, Provence coast, and Corsica-Sardinia showed intermediate impact values of 15–35% (Fig. 3). These differences were statistically significant (Kruskal–Wallis test, $H = 57.39$, $df = 5$, $P < 0.001$), and overall, the multiple comparisons test supported the three degrees of impact observed. Interspecific differences in the degree of impact were also clear (Fig. 3). The red gorgonian, *P. clavata*, was among the most affected species in all areas, reaching up to an average of 80% of colonies affected in the Gulf of Genoa (Fig. 3 and Table 2a). The white and yellow gorgonian species, *E. singularis* and *E. cavolinii*, were also severely affected on the Italian coasts (Gulf of Genoa and Gulf of Naples), with values up to 80% (Fig. 3 and Table 2a). Meanwhile, in the other areas, both *Eunicella* species showed a low degree of impact (Fig. 3). For instance, only about 2% of *E. singularis* colonies were affected on the Catalan coast.

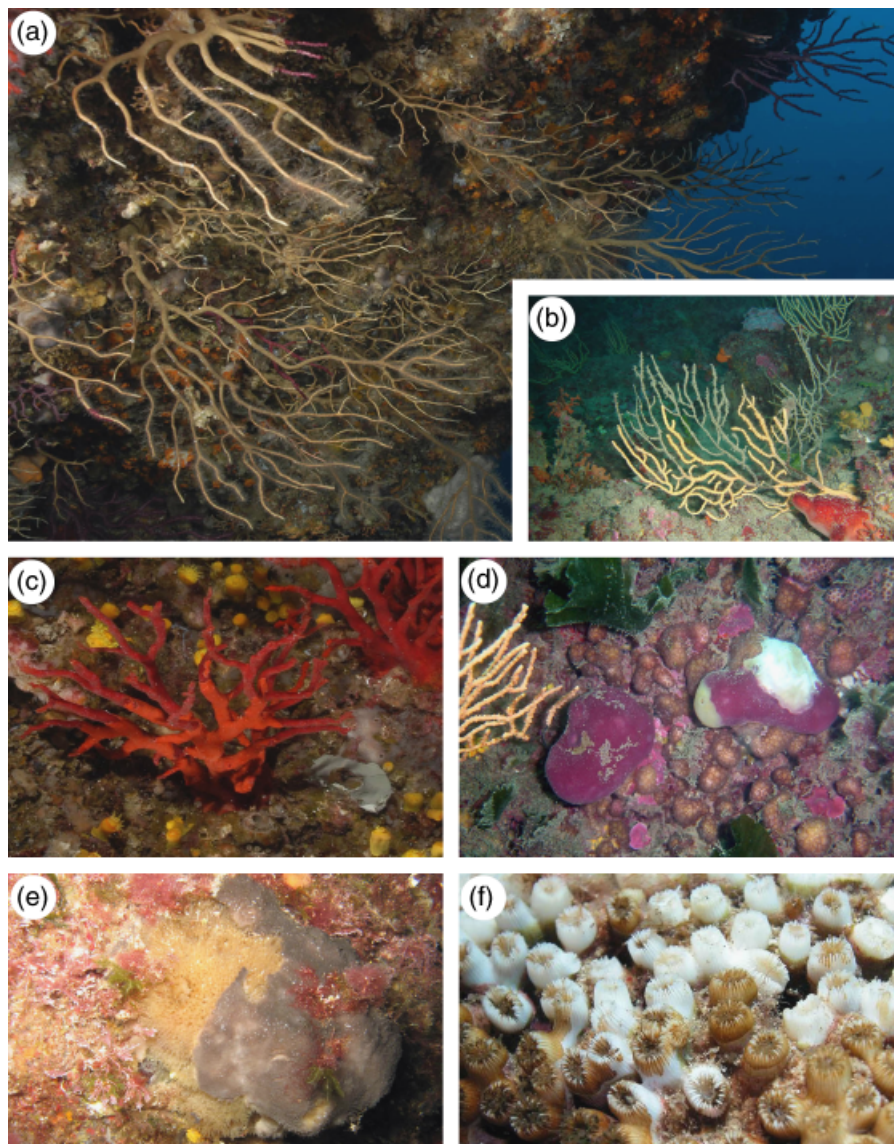


Fig. 2 Species affected by the 2003 mass mortality event. (a) *Paramuricea clavata* colonies showing almost complete loss of tissue (denuded axis, light brown areas), with only the tips of branches still alive (red parts) (19 m depth in the Réserve Naturelle de Scandola, Corsica-Sardinia). (b) *Eunicella cavolinii* showing recent signs of partial mortality (pale parts of the axis) at 25 m depth in the Portofino Promontory (Gulf of Genoa). (c) A red coral *Corallium rubrum* colony with signs of partial mortality (dark red areas) contrasting with live tissue (pale red areas) (Réserve Naturelle de Scandola, Corsica-Sardinia). (d) *Petrosia ficiformis* at 8 m depth showing partial mortality (white parts) (Gulf of Genoa). (e) *Spongia officinalis* displaying partial mortality (brown parts) (Réserve Naturelle de Scandola, Corsica-Sardinia). (f) *Cladocora caespitosa*: detail of polyps suffering tissue necrosis (Columbretes Islands Marine Reserve, Balearic Islands).

Finally, the red coral, *C. rubrum*, showed a variable response depending on the study area (Fig. 3 and Table 2a).

According to the number of affected species and the degree of impact in gorgonian populations, the lowest impact was found in the western areas, while the eastern ones showed the highest impact (Table 1 and Fig. 3).

Temperature and mortality

The Spearman rank order correlation analysis between the TXS₂₀₀₃ and the percentage of affected colonies showed a significant association (Fig. 4; $r = 0.51$, $P < 0.05$). The higher the temperature was, the higher was the impact on the populations (Fig. 4). The lowest values corresponded to surveys at depths unaffected by the mortality.

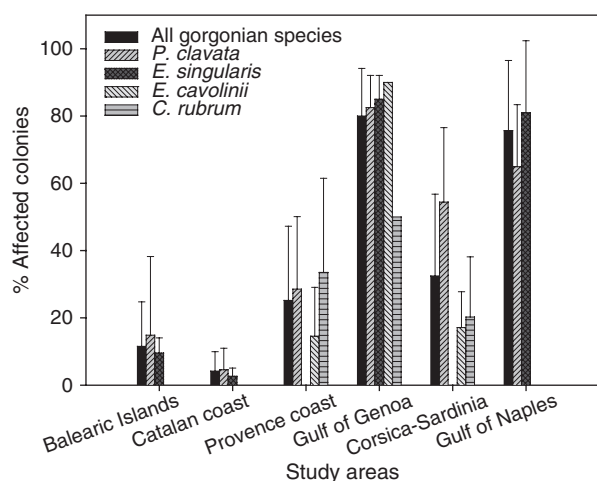


Fig. 3 Mean values of the percentage of colonies affected by the 2003 mass mortality event found in each study area considering data for all species surveyed and for each species (*Paramuricea clavata*, *Eunicella singularis*, *Eunicella cavolinii*, and *Corallium rubrum*).

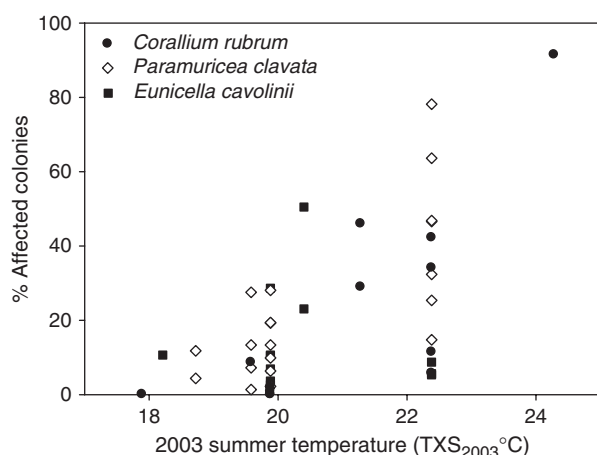


Fig. 4 Relationship between 2003 summer temperature conditions TXS₂₀₀₃ (mean 1 July to 30 September) and percentage of affected colonies in the Provence area observed in late 2003. Temperature data from Marseilles and Villefranche from 10, 15, 20, 25, and 30 m depth. Each data point represents data from one survey and the TXS₂₀₀₃ corresponding to the sampling depth.

Discussion

Bearing in mind the number of affected species, the degree of impact, and the geographic extent, the 2003 mass mortality can be considered the largest mortality event ever to have occurred in the NW Mediterranean during the last few decades. Except for the 1999 event, all previous events affected a small number of species generally in a small spatial extent (hundreds of meters to a few kilometers of coastline). In 1999, a diversity of species similar to that of 2003 (30 species in 1999; Perez

et al., 2000) were affected but over a smaller geographic area. Besides the areas affected in 1999 (Cerrano *et al.*, 2000; Perez *et al.*, 2000; Coma *et al.*, 2006), the 2003 event also affected the Catalan coast, Corsica-Sardinia, and the Gulf of Naples. Both events occurred at the end of the summer (Cerrano *et al.*, 2000; Perez *et al.*, 2000). Finally, the 2003 mass mortality event was restricted to shallower waters than in the previous 1999 event, when the maximum depth reached 40 m in most parts of the affected areas (Table 1; Cerrano *et al.*, 2000; Perez *et al.*, 2000; Coma *et al.*, 2006). The geographic extent and the number of species affected by the 1999 and 2003 events in the NW Mediterranean region are comparable with some regional-scale bleaching events documented in the Caribbean and other tropical areas (McWilliams *et al.*, 2005).

Most of the species affected by the 2003 mortality event already suffered damages in previous events. At least four of the affected gorgonian species (*P. clavata*, *E. singularis*, *E. cavolinii*, and *C. rubrum*) had already suffered extensive damage in some areas of the Mediterranean during the last 20 years (Cerrano *et al.*, 2000, 2005; Perez *et al.*, 2000; Garrabou *et al.*, 2001; Linares *et al.*, 2005; Coma *et al.*, 2006; Gambi *et al.*, 2006; Sbrescia *et al.*, 2008). Among other anthozoan affected species, the scleractinian *C. caespitosa* had previously suffered severe bleaching during 1997–1999 (Perez *et al.*, 2000; Rodolfo-Metalpa *et al.*, 2000). Likewise, commercial sponges (*Spongia* spp., *Hippospongia communis*, *Ircinia* spp.) had been previously affected by a wide mortality outbreak in 1986 and 1999 as well as in other minor events (Vacelet, 1994; Cerrano *et al.*, 2000; Perez *et al.*, 2000). Among bryozoan species, *M. truncata* was affected during the 1999 event (Perez *et al.*, 2000). Meanwhile, the number of bivalve species affected increased dramatically from two to six during the 1999 and 2003 events, respectively. *Lima* spp. was the only species that displayed signs of mortality during these two major events. Furthermore, in the 1980s, *Lima* spp. and other species (*Spondylus gaederopus* and oysters) suffered extensive mortality in the Provence area (Meinesz & Mercier, 1983). The three Tunicata (solitary ascidian species) *Microcosmus* spp., *Halocynthia papillosa* and *Pyura dura* (Perez *et al.*, 2000), and the coralline red algae *Lithophyllum stictaeforme* (Cerrano *et al.*, 2000), which suffered extensive damage in 1999, showed no signs of mortality in 2003. In summary, anthozoans, sponges, and bivalves were among the most affected groups in the 2003 mass mortality event as in other mortality events observed in the Mediterranean during the last decades.

In this study, we provided for the very first time a comprehensive report on the impact of a mortality event that occurred in the NW Mediterranean. Compar-

ison with previous studies is not straightforward because different methods were used to assess the impact of events. Bearing in mind that current changes in the ecosystems concern large scales, we urgently need to develop standardized protocols able to efficiently evaluate the effects of disturbances over large geographic extents. Here, the use of the percentage of affected gorgonian colonies provided an excellent descriptor to quantify the impact of the mass mortality event at the regional scale. Evaluation of the status of populations through the use of this kind of indicator should be performed annually to obtain appropriate baseline data and expanded to groups other than gorgonians when possible. Only through the deployment of this strategy can we accurately evaluate the impacts of disturbances associated with global climate change and provide crucial data to analyze the potential factors associated with these dramatic events.

Potential causes of the 2003 mortality event

The analysis of surface sea temperature (SST) (data from 1985 to 2003) confirmed exceptional warming throughout the whole NW Mediterranean region (Marullo & Guarracino, 2003). However, the temperature anomaly was limited to shallow layers (<20 m depth) due to the calm weather conditions between June and August (Sparnocchia *et al.*, 2006). This could explain the differences in the temperature anomaly observed between 20 m and the other two shallower depths (Table 4).

In general, the depth range where signs of mortality were observed corresponded to the depths where extreme temperatures were recorded (Tables 1 and 4). Because the signs of mortality occurred just after the unusually warm period, the 2003 anomalous temperature likely played a key role in this widespread mortality event. The result of the correlation analysis seems to support this hypothesis (Fig. 4). In contrast to 2003, temperatures recorded during summer 1999 were not exceptional. However, in late summer 1999, the water column showed a very high stability with values around 24 °C, resulting in an anomalous warming of 2–3 °C in the water layer overlying the thermocline accompanied by its deepening (up to 30–40 m) (Romano *et al.*, 2000). This exceptional stratification may explain the differential depth range affected in both mortality events.

Exposure to anomalous high temperatures may produce several effects. Exposure to lethal temperatures acts directly on organisms causing metabolic dysfunctions (Torrents *et al.*, 2008). Exposure to sublethal temperatures can also act directly causing physiological stress that may result in an energy shortage due to increased respiration rate (Coma *et al.*, 2002) and/or

decrease the efficacy of defense (Cossins & Bowler, 1987; Coma & Ribes, 2003) and indirectly trigger the development of pathogens (Toren *et al.*, 1998; Banin *et al.*, 2001, 2003). In fact, the bacteria *Vibrio coralliilyticus* has been recently identified as a causative thermodependent pathogen from diseased *P. clavata* colonies sampled in 2003 (Bally & Garrabou, 2007). However, microorganisms found on colonies during the 1999 gorgonian mortality event appeared to be opportunistic rather than disease-causing (Cerrano *et al.*, 2000; Martin *et al.*, 2002).

Besides anomalous temperature conditions, several putative agents have been identified or evoked as the cause of mortality outbreaks in the Mediterranean, including pathogens for sponges and sea urchins (Vacelet *et al.*, 1994; Boudouresque & Verlaque, 2001), drops in salinity for gorgonian species (Bavestrello *et al.*, 1994), and the development of filamentous algae (Mistri & Ceccherelli, 1996; Schiaparelli *et al.*, 2007). However, high temperatures were a common environmental condition in most events. Finally, global warming has been associated with the increase in different mortality outbreaks in marine species such as seagrasses, fishes, corals, and sea urchins worldwide (Harvell *et al.*, 1999; Atrill *et al.*, 2004; Lesser *et al.*, 2007).

Differential mortality at the intraspecific and interspecific levels, across spatial scales from meters to hundreds of kilometers, was a common phenomenon for the 2003 mass mortality event (Figs 3 and 4). Similar observations were made for previous events in the Mediterranean (Cerrano *et al.*, 2000; Perez *et al.*, 2000) and worldwide, such as extensive bleaching of coral species in different parts of the world (Hughes *et al.*, 2003; McWilliams *et al.*, 2005). These observations provide clear and empirical evidence for the absence of a single mass mortality threshold for species and populations, which may be modulated by both physical and biological factors. For instance, in the Gulf of Naples, differential mortality could be attributed to the high variability in the local hydrographic conditions (Ribera d'Alcalà *et al.*, 2004), as proven in the case of bleaching events (Nakamura & van Woesik, 2001), while among biological factors, adaptation mechanisms could play a key role in the response of populations to temperature stress (Torrents *et al.*, 2008). Despite the complexity underlying the biological response, two major trends can be anticipated regarding the potential impact of warming in the NW Mediterranean region. First, bearing in mind the hydrodynamic conditions in the region, shallow populations (0–50 m) will be most exposed to future mortality events. Second, populations of affected species dwelling in northern areas may be more vulnerable than southern ones, because they are probably adapted to colder temperature conditions and are found in shallower waters

(Zabala & Ballesteros, 1989; Linares *et al.*, 2008). Overall, research on the environmental, physiological, or genetic determinants of this differential response should be considered a major challenge for the coming years. Revealing these factors will help determine how species will cope with future environmental changes and how humans can undertake actions to promote the resilience of affected communities (Hughes *et al.*, 2003).

Consequences of mass mortality events

Most of the affected species are characterized by high longevity and slow population dynamics with low growth, recruitment, and mortality rates (Pansini & Pronzato, 1990; Garrabou & Harmelin, 2002; Coma *et al.*, 2004; Linares *et al.*, 2008). Thus, a dramatic increase in mortality rates (total and partial), as well as short times between mortality events, may produce severe consequences for the viability of most affected populations (Linares *et al.*, 2007). Data on the impact and recovery in gorgonian and sponge populations from the 1999 mass mortality events showed a dramatic decrease in the biomass of populations and a very slow recovery during the 4 years following the impact (Cerrano *et al.*, 2005; Linares *et al.*, 2005; Coma *et al.*, 2006; J. Garrabou *et al.*, unpublished data). Similar patterns were found for populations surveyed after the 2003 event (Cigliano & Gambi, 2007; J. Garrabou *et al.*, unpublished data), except in populations from the Catalan coast, which showed only a low impact. In this area, recovery was complete in the year following the event (R. Coma, unpublished data).

Because several species have suffered damage across a large geographic extent, concerns regarding their recruitment or spill-off from other areas, and therefore their persistence, are justified and large-scale conservation plans are urgently needed. Finally, it must be taken into account that (1) species considered in this study are large, prominent, and easily identifiable, but that small, cryptic, or poorly known species are also affected by such large-scale events (Chevaldonné & Lejeune, 2003; Scinto *et al.*, 2007); and (2) species such as large sponges, erect bryozoans, and gorgonians provide biogenic structure, so other species not directly affected by the mass mortality but structurally dependent on affected larger taxa could also indirectly suffer the impact through modification of habitat conditions (e.g., flow regime, food availability, shelter) (Soulé *et al.*, 2003; Ribes & Coma, 2005).

Summary and predictions

Projections available for the Mediterranean basin region for the 21st century indicate warmer and drier condi-

tions with a dramatic increase in the frequency and persistence of extreme events such as heat waves (Stott *et al.*, 2004; Déqué 2007; Diffenbaugh *et al.*, 2007; IPCC, 2007). For instance, the number of heat wave days may be multiplied by 10 by the end of the current century (Déqué 2007). Although the relationship between weather and oceanographic conditions is not straightforward, long-term studies on seawater temperature conditions already show a clear-cut warming trend of coastal waters worldwide (Southward *et al.*, 1995, 2005; Levitus *et al.*, 2000; Vargas-Yáñez *et al.*, 2008; J.C. Romano *et al.*, unpublished data). In addition, a recent study on oceanographic conditions of the Mediterranean Sea during the 21st century supports a clear-cut picture of warming, with a nearly spatially homogenous increase in SST of +3.1 °C in 2099 (Somot *et al.*, 2006). These results agree reasonably well with the warming trends calculated from coastal time series over the past three decades (Vargas-Yáñez *et al.*, 2008; J.C. Romano *et al.*, unpublished data).

In this context, the repetition of large-scale mortality events can be expected during the next decades. Consequences of these events could severely expose populations of affected species to local ecological extinction processes, threatening the conservation of the rich Mediterranean biodiversity (Bianchi & Morri, 2000; Ballesteros, 2006; Bianchi, 2007). This climate change is the latest form of human disturbance affecting the Mediterranean coastal communities at the regional scale through mortality outbreaks and shifts in species distributions (Francour *et al.*, 1994; Bianchi & Morri, 2000). The expansion and intensification of climate change effects together with the effects of other strong disturbances (pollution, mechanical habitat destruction, invasive species, and overfishing) may act together, driving the Mediterranean to a major biodiversity crisis during the 21st century (Bianchi & Morri, 2000; Jackson *et al.*, 2001; Sala, 2004).

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