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Medium-term effects of die-off of rocky benthos in the Ligurian Sea. What can we learn from gorgonians?

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Mediterranean Sea ecosystems are experiencing a phase of major modifications owing to the fast increase in several disturbances such as pollution, eutrophication, habitat destruction, over-fishing, income of alien species, and climate change. One of the main problems in recent years is that global warming seems to intensify the effects of all the above-mentioned disturbances, dramatically reducing the biodiversity of the basin. The ever more frequent mass mortalities that are affecting shallow coastal environments are rapidly reducing the biomass of several filter feeders and both sponges and gorgonians are the most endangered taxa. In this paper we review the most recent episodes of mass mortality, mainly involving sea fans, and discuss the possible effects that the loss of these organisms can have on benthic assemblage structure. The data presented here are referred mainly to the study case of the MPA of Portofino (Ligurian Sea, Italy).

Keywords: mass mortality; growth form; Porifera; Cnidaria; Octocorals; global warming

1. Introduction

1.1. Mediterranean mass mortalities and their etiology

One of the most important phenomena involving Mediterranean shallow water benthic communities is that of mass mortalities which, in the last three decades, have involved coralline algae, sponges, corals, molluscs, echinoderms, and tunicates. These groups can often provide the vertical structure of many communities contributing to habitat heterogeneity and diversity [1]. These habitat modifiers undergo a multitude of interactions able to drive ecological and evolutionary processes. Their decrease or disappearance can negatively affect community stability especially when long-life span species are affected [2].

These mortalities are the consequence of diseases mainly attributed to several factors such as toxic microalgae, mucilages, pathogenic agents, thermal stress and oxygen depletion, generally related to climatic anomalies that led to a decrease in sea-water mixing and/or circulation and an increase in sea water temperature.

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1.1.1. Algal diseases

The blooms of the benthic dinoflagellate *Ostreopsis ovata* were implicated in 1998, 2001, 2002, and 2005 as causative agents of disease and mortality of sponges, the limpet *Patella coerulea*, the mussel *Mytilus galloprovincialis*, echinoderms (*Paracentrotus lividus* and *Coscinasterias tenuispina*) and tunicates [3].

Every summer since 2000, along the Ligurian coasts, coats of the filamentous cyanobacterium *Porphyrosiphon* sp. have developed in patches during periods of warm and calm water. In some cases, these coats can gradually cover the polyps of the zoanthid *Parazoanthus axinellae*, which develops dense mats of white hyphens of *Trichoderma viridens* and quickly degenerates. After three years, this disease led to a local decrease in the percentage of *P. axinellae* covering from 35% to 3% of the Portofino Promontory, promoting the growth of the encrusting demosponge *Crambe crambe* [4].

Mucilage events are recurrent in the Mediterranean Sea with important differences between the Adriatic and the Tyrrhenian Seas. In the Adriatic they often lead to anoxic episodes while in the Tyrrhenian Sea their effects are in relation to their taxonomic composition. The commonest species are algae of the group Chrysophyceae (*Nematochryopsis marina* and *Chrysonephos lewisii*) and a brown alga (*Acinetospora crinita*) [5,6]. One of these species, *C. lewisii*, has recently been introduced in the Mediterranean, rapidly occupying various areas of the Tyrrhenian and northern Adriatic Seas [7]. In general, the first two species are present until depths of 20 m, while *A. crinita* can live even at greater depths, causing serious damage to sessile benthic organisms in particular gorgonians [8].

1.1.2. Pathogens

Pathogenic agents have been hypothesised for Mediterranean bath-sponge disease since the 1980s, when rich bacterial populations were recorded associated to spongin fibres of dead specimens [9]. A similar disease was investigated during the death of the Great Barrier Reef sponge *Rhopaloeides odorabile*, where the evident degradation of the spongin fibres was caused by an α -proteobacteria [10]. This could also be an important result for the understanding of Mediterranean bath-sponge mortality.

The pathogenic bacterium *Vibrio shiloi* was involved in the case of the bleaching of the hard coral *Oculina patagonica* in the eastern Mediterranean Sea: the fireworm *Hermodice carunculata* is considered the winter reservoir and spring/summer vector of this pathogenic bacterium. The pathogen adheres to the coral mucus, penetrates into epithelial cells, multiplies into a viable but non-culturable form, and produces a toxin that inhibits photosynthesis of the zooxanthellae [11].

Recently also for gorgonians pathogens were detected but these cases are discussed below.

1.1.3. Thermal stress

More generally, thermal stress seems to be the most plausible explanation for the Mediterranean mass mortalities and some authors consider that exposure to high temperatures is also the main cause for tropical coral diseases, probably enhancing secondary opportunistic infections [12,13]. The effect of temperature on the metabolism has been thoroughly investigated at biochemical level on sponges: the immediate response of the temperate *Axinella polypoides* to a short-term heat stress exposure is an increase in amino acid incorporation, oxygen consumption and water filtration, although this effect is followed by a long-term depression [14,15]. It has also been experimentally demonstrated that in the Mediterranean stony coral *Cladocora caespitosa*, which lives close to its thermal limit during the summer period, a water temperature of 24 °C leads

to tissue necrosis in three weeks [16], suggesting that thermal stresses are due not only to the overcoming a temperature threshold but also to the time exposure at this thermal boundary, so that not only high temperature but also long-lasting thermal anomalies can lead to benthic diseases.

1.1.4. Oxygen depletion

High temperatures negatively affect the oxygen levels in seawater so that mainly sessile organisms always have to face at least two negative factors. For this reason, these disturbances are not predictable and generally run their course in a few days [17], limiting an exhaustive documentation. Mortalities related to anoxic events are well-documented in the northern Adriatic Sea and, even if they occur mostly in the late summer/autumn [18], the exact timing is related to local weather conditions [19]. The concomitance of shallow and calm waters clearly exacerbates the effects of oxygen depletion in the north Adriatic. Among the most frequently involved taxa it possible to include sponges, bivalves, gastropods, hermit crabs, brittle sea-stars, regular and irregular sea-urchins, sea cucumbers, and ascidians. A long-lasting decrease in water circulation in areas where benthic assemblages generally experience strong currents can also lead, on hard bottoms with a complex geomorphology, to patchy disease episodes and partially explains differential survival of specimens belonging to the same species [20].

2. Mass mortalities of Mediterranean gorgonians

Although several species and groups of sessile organisms have been hit by mass mortalities in the Mediterranean Sea, the phenomenon that has greatly altered the seascape of rocky bottoms is the frequent, sometimes dramatic, disease involving sea fans.

In the Mediterranean a first episode of gorgonian mass mortality was described in 1984 mainly regarding *Eunicella singularis* and *Corallium rubrum* [21]; later, in 1986, sponges were involved as well as gorgonians [9,22,23]. Subsequently, during 1993 *P. clavata* was affected both in the South of Italy in relation to a mucilage bloom [24] and in the North in relation to a sudden arrival of a cold and fresh water mass [25].

In the summer of 1999, the most widespread episode ever recorded in the Mediterranean affected millions of specimens of different benthic filter feeders, mainly sponges and gorgonians, in the north-west Mediterranean [26,27,29]. After this episode other intense mortalities were recorded during the summers of 2003, 2005 and 2006 [29,30] along the Italian coasts.

A study performed on diseased colonies attributed the 2003 event to the thermodependent pathogen *Vibrio coralliilyticus* [32].

Nevertheless thermal stress has generally been recognised as the main direct or indirect cause of these mortalities. *In situ* experiments conducted on explants of four species of sea fans tested during the summer crisis of 2003 demonstrated that thermal stress is able to produce a disease in all the tested species, albeit with varying intensity. The most sensitive species is *P. clavata* with an almost complete mortality of the transplants. On the contrary the species of the genus *Eunicella*, appear to be less sensitive to heat stress conditions with a survival rate ranging from 30 to 40% and a better ability to regenerate damaged tissues, particularly for *E. singularis* [32].

Although the acute episodes of gorgonian mortalities which recently occurred in the Mediterranean Sea have been well-described, few data about their medium-term effect on the population of the different species are available. Here we review and discuss some data regarding the modifications that are affecting gorgonian populations after the recent mortality events occurring along the Ligurian rocky coasts.

3. Intraspecific differences in sensitivity

A mass mortality episode not only drastically reduces the density of a benthic population but also strongly alters its structure if some categories of individuals show a differential sensitivity towards the disease. Data available for sea fan populations in the Ligurian Sea indicate that two main factors affect the sensitivity of sea fans to diseases: size (age) and sex of the colonies [33].

Concerning size, after the 1999 mortality event, the gorgonian population structure showed a shift towards smaller sizes due to the fact that mainly large colonies were hit while small colonies were less affected and recovered faster [33]. This finding agrees with other evidence obtained for tropical octocorals, where small sea fans are more chemically defensive than large sea fans when attacked by pathogens. In particular, in the case of the Caribbean *Gorgonia ventalina*, anti-fungal activity decreases with increasing sea fan age [34]. For the Mediterranean episodes the greater resilience of small colonies has been related to a lower metabolism and a P/B ratio that decreases with age [8,35,36] and a reproductive effort that increases with colony size [37].

A study of the sex ratio performed on the population of *Paramuricea clavata* of the Portofino Promontory in 1997 showed a 1:1 value, whereas a significant male bias was observed in the same population (3.3:1) in 2002, three years after the destructive mass mortality of 1999 [33]. This bias is tentatively attributed to a higher reproductive effort of female colonies during the summer reproductive period, a season that in the Mediterranean Sea is characterised by energy shortage [38]. Moreover large eggs, occupying the gastral cavity of polyps, may limit or preclude feeding, leaving little or no space for captured food and digestive processes as documented for other octocoral species [39,40].

4. Effect on colony growth

During sea fan diseases most colonies are only partially affected, with portions of healthy coenenchyme and bare portions of the axial proteinaceous skeleton. In this condition colony recovery is related to the ability for fast growth of new coenenchyme on the naked portions of the skeleton.

Experimental data obtained from transplanted colonies evidenced differences between species regarding regeneration: *Paramuricea clavata* has a low regeneration capacity compared with *Eunicella* spp. and, among *Eunicella* species, *E. singularis*, symbiotic with zooxanthellae, has the highest resilience. These data derive from transplants that suffered a warming disease during the summer of 2003 [32] and the values are very low, ranging from an average daily recovery rate of 0.03 mm in *E. verrucosa* to 0.1 mm in *E. singularis*. These findings are one or two orders of magnitude lower than those derived from mechanical lesions (e.g. fishing lines, nets, etc) in healthy colonies (0.15–0.2 cm/day in *Paramuricea clavata*) [41] demonstrating that regeneration after thermal stress is strongly affected by the general suffering of the colony. Considering the general disease of the colonies affected by thermal stress and that the regeneration of injured modular organisms from wounds is size-dependent [42], the data probably do not adequately reflect the rate of regeneration which has been recorded for colonies injured by mechanical abrasions, where healthy tissue bordering the lesion is present [41].

In partially diseased colonies the laying of new coenenchyme is also impeded by epibionts quickly settling on the naked skeleton. *Eunicella singularis* is able to cover settled epibionts [43]. This ability is also known for other species and may lead to the formation of tumors [44]. Other species, like *Eunicella cavolinii*, are able both to eliminate the naked skeleton covered by epibionts and to cover the branch tips with new coenenchyme [22] resulting in a variation in branch

length and a reorganisation of colony shape. In the case of a diseased colony, autotomy is not a true reproductive strategy [45–47] but a way of reorganising the colony in relation to new environmental conditions. Fragmented branches may also have big portions of living coenenchyme but are generally not able to re-settle, as also happens for *Corallium rubrum* fragments [48].

5. Effect on colony shape

Colonial organisms are far more plastic than solitary forms. Gorgonians are passive filter feeders whose morphology is the optimal compromise between living colony tissues and water movement [50], based on the ratio between prey capture or energy intake and metabolic cost as a function of water flow [51,52]. Gorgonian shapes can vary in relation to the physical properties of the habitat and the changing environment of the colony itself [49,50].

The study of the recovery of the Portofino Promontory population of *P. clavata* showed that continuous episodes of tissue necrosis are able to decrease not only the average size of the colonies but also strongly affect the colony shape, which shifts from planar to bushy (Figure 1A). This is due to the growth of several new branches from the healthy base rather than to the regeneration of the main branch of the old colony. This way of recovery in colonies which are considered totally affected during mortality event is very unusual among Octocorals and resembles a sort of ‘vegetative suckering’ since it is certainly not due to newly-settled planulae close to the old colony (Figure 1A).

This fact is expected to have a significant impact on the gorgonian populations. In fact, experimental evidence shows that crowding among branches impedes growth, possibly through the capture of resources at the shaded branches (self-shading: [52]). Branching will become crowded and internal, with consequent inevitable shading, decreasing growth rate.

6. Effect on population structure

Studies conducted before and after the mortality event of 1999 [33] indicated that on the cliff of the Portofino Promontory the colony density fell from 20 to 5 colonies/m². After the first reproductive period following the mortality event, the colony density returned to values similar to those recorded before the die-off episode (25 col/m²). In the following years the colony density maintained similar values, after a slight decrease in autumn–winter 2001. However, after the mortality event (October 1999), the population size structure showed a shift towards smaller sizes. Before the mortality event, the percentage frequencies of the size classes (considering an interval of 5 cm) between 0 and 20 cm in height in the population were similar (each being about 20%), while after the die-off the smallest size class (0–5 cm) became the most abundant (more than 60%) due to the disproportionate loss of the larger size classes [33].

Considering that gorgonians are important engineering species, it is evident that a decrease in the average size of the population negatively affects habitat heterogeneity [27,33] (Figure 1 B–E). Several authors suggest a positive link between heterogeneity of the habitat and biodiversity (e.g. [53]) whereby repetitive mortalities in the same populations may lead to a general loss of tridimensionality of the biocoenosis with a consequent decrease in the complexity of the communities. The removal of species able to shape the architecture of habitats and thus increase their complexity or influence the biogeochemistry of bottom sediments could have significant effects on local biodiversity and important water–sediment processes [54]. Moreover, also a reduction of larval settlement can be documented as a consequence of loss of engineering or canopy forming species [27].

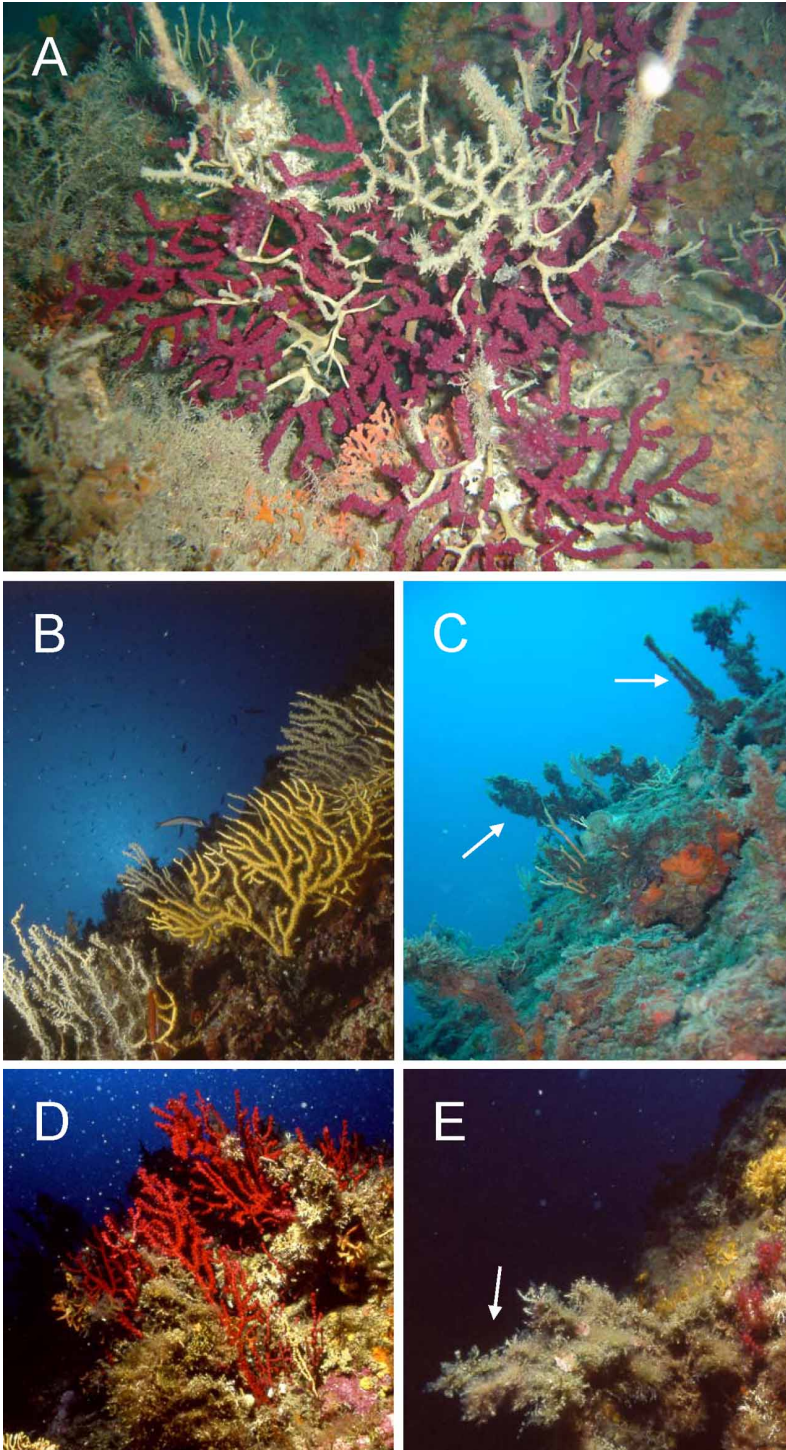


Figure 1. Gorgonians from the MPA of Portofino. (A) unusual bushy shape of a *P. clavata* colony repeatedly affected by disease episodes. (B) An *Eunicella cavolinii* population a few days after the 1999 mortality event; (C) The same population two years later, arrows indicate the main axis of dead colonies; (D) A *Paramuricea clavata* population two months after the 2003 mortality; (E) The same population three years later, the arrow indicates a dead colony. On the right there are two small *P. clavata* recruits.

7. Recovery perspectives

The geomorphology (semi-closed sea) and the geographic position (in a temperate area) of the Mediterranean Sea are so peculiar that the basin can be considered as a sort of natural laboratory where it is possible to study the effect of global warming. In recent years, Mediterranean Sea communities have modified their pattern of species composition [55]. Among the benthic invertebrates, those species which were considered common less than ten years ago (such as bath-sponges) are now considerably reduced or locally extinct and some thermophilic species, like the big, shallow water hydrozoans *Pennaria disticha*, have started to appear regularly (unpublished data).

Nevertheless, at seascape level, the most evident impact is due to the mass mortalities of benthic Cnidaria which, because of their shape, size, and colour characterise the relatively deep Mediterranean seascapes. In shallow waters the continuous decrease in colonies on the Portofino Promontory benthic assemblages concerns sea fans and particularly the purple gorgonian *Paramuricea clavata*. This great reduction in filter feeders, particularly sea fans, could have an unexpected influence on the entire coastal habitat. Filter feeders in fact can extract huge amounts of seston (mainly microplankton and detrital POC) [38,56] from column water and their disappearance or reduction could alter the usual benthic trophic web. The unexploited food which becomes available for other suspension feeders and organisms that in the last few years seem to be ever more frequent, such as gelatinous plankton in general [57], may represent a possible consequence of these recent trophic disequilibria.

At present on the Portofino Promontory there is a clear distinction between the deep and the superficial populations of *P. clavata*. While the former (below 40 m depth) are made up of a size class frequency distribution typical of the population of species (with big colonies more frequent than recruits) and have a normal 1:1 sex ratio, the latter (above 40 m depth) are mainly or exclusively made up of small, infertile colonies and the rare mature colonies are strongly biased towards male gender. This bulk of evidence strongly supports the idea that the high recruitment, normally observed also in the shallow water population (about 7–8 col/m², 1–5 cm of height), is mainly due to larvae produced by the deepest colonies. This larval upwelling could be crucial for the ecological resilience of superficial populations and for this reason the connectivity between shallow and deep populations needs to be investigated and deep water rocky bottoms must be carefully studied and considered in coastal management projects. Populations living on cliffs 25–35 m deep have scarce possibility to recover [58] compared with cliffs that can receive a larval supply from deeper colonies. Projects for the restocking of gorgonians are feasible [59–61] but mortalities can limit their effectiveness. There has been significant interest in the role of larval supply and bottom-up *versus* top-down processes in structuring marine communities, but studies have focused mainly on suspension feeding invertebrates living in temperate rocky intertidal and subtidal habitats [62–64]. Research should now also be extended to circalittoral assemblages.

Twenty years of observations carried out in the Marine Protected Area of Portofino (Ligurian Sea) have clearly demonstrated that the major changes in the benthic communities related to global warming are not due to slow and progressive modifications but to wide and intense mass mortalities.

These episodes have greatly modified the structure of hard bottom benthic communities. In the sea, anomalous warming has effects on the distribution, the physiology, and the phenology of several species, even producing some particular adaptations. When physiology is affected, the most evident effect is mortality, even if the impact on the colonies can have different intensity, being total or partial. When recovery is compromised it can also expose the ecosystem to invasive species, and thereby reduce, or at least challenge, the resilience of the ecosystem [65].

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