24 years tracking mass mortality events and marine heatwaves: when observations overcome the worst scenarios

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Abstract

The Mediterranean Sea is considered a climate change hotspot exhibiting warming rates and marine heatwaves (MHWs) events higher than in the global ocean. Among others, these conditions have already resulted in the onset of widespread mass mortality events (MMEs) across the Basin during the last 24 years. Since the first observation of an unprecedented MME in 1999, several international collaborative initiatives devoted to track the impacts and quences of MHWs and promoting solutions to support the resilience of coastal habitats in the face of climate change have been developed. Herein, we review how the Mediterranean scientific community has been tackling the challenges associated with MMEs in the Mediterranean. Focusing on the experience of building the T-MEDNet, a collaborative observation network dedicated to track climate change impacts, we present the main research issues and outcomes, and provide insights into new scientific avenues. Up to now, through this collective effort, we have revealed that severe ecological impacts of MHWs are unfolding at an unexpectedly accelerated pace. This acceleration, along with the interacting effects of other climate change stressors, poses an unprecedented threat to the Mediterranean ecosystems' health and functioning. In this context, it is critical to reinforce and upscale ongoing collaborative efforts at different levels aiming to increase the resolution of empirical observation networks, experimental studies, and interdisciplinary research. Such concerted efforts are essential for enhancing our ability to thoroughly comprehend and effectively manage the consequences of climate change and associated extreme climatic events such as marine heatwaves.

Keywords: *ocean warming, mortality outbreaks, ocean observation, long-term ecological monitoring, evolution and ecology*

Introduction

The Mediterranean Sea is experiencing an increase in the frequency, extent, and intensity of marine heatwaves (hereafter MHWs) associated with anthropogenic climate change. One of the macroscopic measurable impacts of MHWs is the onset of mass mortality events (hereafter MMEs). While barely recognized by society at large, marine MMEs are one of the most predominant biological impacts of anthropogenic climate change and associated MHWs in the Mediterranean coastal ecosystems (Rivetti *et al*. 2014 ; Marbà *et al*. 2015 ; Cramer *et al*. 2018). Indeed, Mediterranean MHWs have triggered extensive climate-driven MMEs during the last decades and their occurrence and severity are expected to increase in the coming decades (Darmaraki *et al*. 2019 ; Garrabou *et al*. 2019).

Since the observation of the unprecedented mass mortality event in 1999, which affected both the French and Italian coasts of the northwestern Mediterranean, different research teams and programs have focused their efforts toward analyzing the different eco-evolutionary dimensions of MMEs. The ultimate goals of these efforts were to: i) enlarge our observation capacity at large-scale and long-term on MMEs; ii) provide a better understanding on the drivers triggering the MMEs; iii) analyze the consequences of MMEs at different biological organization levels; and iv) enhance our predictive capability on the future trajectories of coastal habitats in the face of anthropogenic climate change.

During the study of the 1999 MME, we realized the lack of high-resolution temperature series in the Mediterranean coastal habitats. To fill this knowledge gap, a monitoring strategy to track thermal conditions using underwater temperature data loggers was proposed and gradually deployed (Bensoussan *et al.* 2019). This was the origin of the collaborative T-MEDNet network devoted to track climate change effects in the Mediterranean coastal ecosystems (www.t-mednet.org). Over the past two decades, T-MEDNet has supported the implementation of cost-effective monitoring of seawater temperature conditions, as well as the ecological impacts of anthropogenic climate change in Mediterranean coastal ecosystems. This collaborative effort, in alliance with other pan-Mediterranean initiatives, such as the CIESM Tropical Signals program, resulted in the most comprehensive datasets of coastal temperature conditions and MMEs records across the Mediterranean Sea. This observational effort provided a robust basis to engage in fruitful research activities for the analysis of MMEs and MHWs.

In this study, we provide a summary of the main outcomes obtained during the last two decades from different research projects on mass mortality events and marine heatwaves. We also discuss potential key observation activities and new scientific avenues. The main objective is to provide a panoramic understanding of the current state of knowledge concerning both MHWs and MMEs, thus supporting evidence-based decisions aimed at strengthening the resilience of Mediterranean coastal ecosystems in the face of anthropogenic climate change.

Methods

To characterize the spatial and temporal patterns of MMEs in the Mediterranean Sea, we compiled the most comprehensive dataset on these events from an extensive literature review analysis, besides the compilation of unpublished data from more than 30 research teams across eleven Mediterranean countries. The dataset contains a total of 1240 climate-driven mass mortality records. Mass mortality records were obtained from quantitative or semi-quantitative benthic surveys using different methods to assess the mortality impacts on local populations. A 'local' population is considered a group of colonies/individuals, (ranging from tens to hundreds of colonies/individuals depending on the species), dwelling in a specific geographic location defined by spatial coordinates and depth range. The surveys provided the percentage of colonies/individuals affected by mass mortality, *i.e.* indicating signs of necrosis over a relevant surface of the specimens (*e.g.,* hexa and octocorals, sponges, and bryozoans) or being dead (*e.g.,* mollusks). When the percentage of affected specimens was higher than 10%, the local population was considered to be affected by a MME. To facilitate a standardized monitoring approach for MMEs throughout the Mediterranean region, we developed a full toolkit including different training materials and database management within the T-MEDNet network (Garrabou *et al*. 2022a).

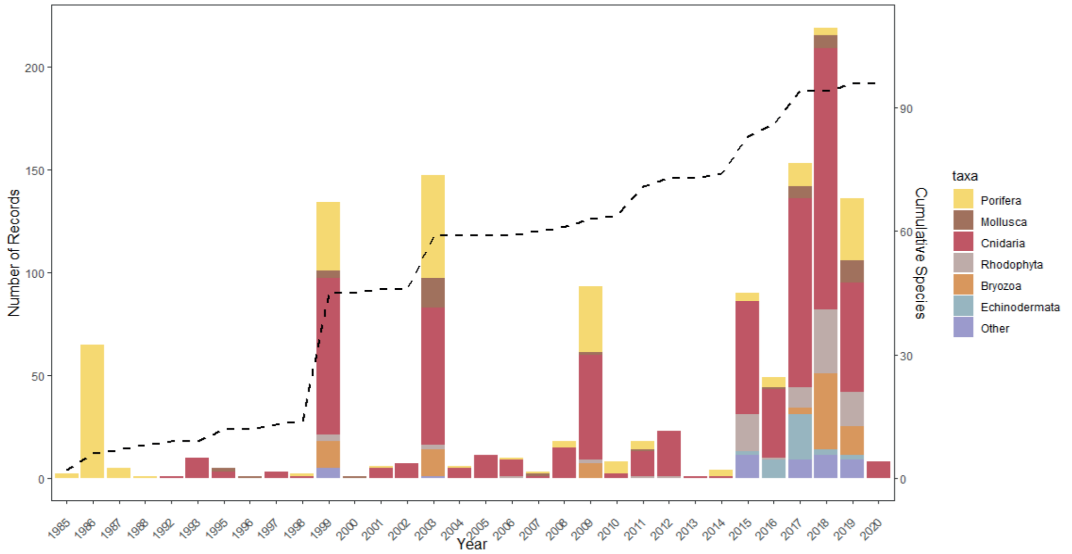
Besides providing an overview of the spatial-temporal patterns of MMEs at a Mediterranean level, we summarized the main research outcomes of the involved teams to provide up to date knowledge on their effects at different biological levels.

Results and discussion

Mediterranean mass mortality events - overview

The first large MMEs were reported in the mid '80s and affected few commercial sponge species in the southern and eastern Mediterranean regions (Fig. 1). The most dramatic events reported in terms of geographic extent and number of affected species occurred in 1999 and 2003 along the northwestern Mediterranean Sea (Cerrano *et al*. 2000; Perez *et al.* 2000; Garrabou *et al.* 2009). These two events affected more than 40 species from various taxa (*e.g.,* Porifera, Cnidaria, Bivalvia, Bryozoa, Ascidiacea) across thousands of kilometers of coastline. Following these main events, the mass mortality records indicate that MMEs had impacted smaller geographic areas and fewer species almost every year until the 2015-2019 period, when the Mediterranean Sea experienced exceptional thermal conditions resulting in the onset of five consecutive years of MMEs widespread across the Basin (Garrabou *et al*. 2022b). Finally, during the summer 2022, the Western Mediterranean experienced temperature breaking records associated to one of the most severe MHW (Juza *et al*. 2024), which resulted in one of the strongest ever observed MME in the northwestern Mediterranean Sea with up to 80% affected colonies across 26 locations (Estaque *et al*. 2023).

Overall, the number as well as the diversity of species affected by MMEs have been increasing over the last two decades. MMEs have affected a total of 96 species belonging to 10 different phyla (Fig. 1). Cnidaria, Porifera, and Bryozoa account for most of the impacted species, with octocorals (among cnidarians) being the most affected. Regarding the depth range, in general the MMEs affected the species dwelling from 0 to 40 m depth, with the intermediate depths (15-25m) being the most impacted. Finally, as mentioned above, over the last decades MMEs have become more frequent and have affected larger geographic areas (Fig. 1). According to the dataset collected the literature review, there is a lack of information from the southern and eastern Mediterranean coasts. Likewise, our review revealed the absence of consolidated MMEs monitoring efforts in the Mediterranean Sea (Garrabou *et al*., 2019, 2022b). The T-MEDNet network and other similar initiative should be promoted to fill these gaps and enhance our observation capabilities.



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N Species	2	6	3	1	1	1	3	1	1	2	39	1	4	4	34	4	4	5	3	6	25	7	14	10	1	4	23	15	31	26	34	2

Figure 1. Bars indicate the number of mass mortality records per main taxa reported during the period 1985 to 2020 (1985 was the first year for which information on MMEs was found). Dashed line shows the cumulative number of species affected by mass mortality during the 1985-2020 period. Data were collected from literature review and monitoring activities conducted by the T-MEDNet network. The table indicates the number of ecoregions (according to Garrabou *et al.* 2022b), number of taxa and number of species affected across years.

Regarding the life-history and functional traits, the species affected by MMEs correspond to long-lived species, with low growth rates and massive-arborescent growth forms, such as gorgonians and perennial seaweeds. In most cases, these species are considered foundation or habitat-forming species, playing a key structural and ecological role in the habitats in which they thrive. In the following sections a summary of the main findings on the consequences of MMEs at different biological levels is provided.

Consequences of MMEs at population level

According to our literature review, most studies on the consequences of MMEs in the Mediterranean at population level have focused on foundation species (*e.g.*, Turicchia *et al.* 2018 ; Garrabou *et al.* 2019 ; Chimienti *et al.* 2021 ; Verdura *et al.* 2021 ; Gómez-Gras *et al.* 2021a ; Ghanem *et al.* 2024). These studies were mostly based on demographic surveys quantifying the immediate impacts, which resulted in an increase of both total and partial mortality rates. They revealed that differential impacts at all biological levels (*i.e.,* among species, populations, individuals, and even within colonies) are one of the main characteristics of the MMEs (Cerrano *et al.* 2000 ; Garrabou *et al.* 2009, 2022b).

At population levels, after the 1999 event, the percentage of dead colonies in red coral *Corallium rubrum* populations from the southeastern coast of France varied from less than 2% to more than 40% (Garrabou *et al.* 2001). After the 2003 MME, populations of *Paramuricea clavata* from the same area showed percentages of colonies affected by necrosis ranging from 2 to 80% (Garrabou *et al.* 2009). In general, studies monitoring population dynamics after MMEs showed null or quite limited recovery capacity (Cerrano *et al.* 2005 ; Santangelo *et al.* 2015 ; Gómez-Gras *et al.* 2021a). This lack or limited recovery is the result of the combination of slow population dynamics (slow growth and limited recruitment, Linares *et al.* 2007 ; Montero-

Serra *et al*. 2018), and low connectivity characterizing these species (Ledoux *et al*. 2010 ; Arizmendi-Mejía *et al*. 2015a), and the recurrent onset of MHWs during the last decades. These observations clearly point out to a collapse trajectory for most populations dwelling between surface and 30 m depth (Garrabou *et al*. 2021 ; Gómez-Gras *et al*. 2021a ; Bramanti *et al*. 2023). Bearing in mind the severity and the recurrent impacts, some populations can be considered already ecologically extinct, and, in the most dramatic cases, local extinctions have even been reported (e.g. Gómez-Gras *et al*. 2021a).

Community level consequences of MMEs

The ecological extinctions observed at the population level can lead to widespread structural and compositional changes at the community level, and to subsequent changes in ecosystem functioning, especially when lost species are functionally unique (Loya *et al*. 2001 ; Bellwood *et al*. 2004 ; Bianchi *et al*. 2014 ; Harvey *et al*. 2022). This is the case for octocorals and other habitat-forming species, which are among the most affected by MMEs (Garrabou *et al*. 2022b). These species dominate many diverse and abundant rocky habitats, such as coralligenous assemblages. They are considered to be functionally unique in the Mediterranean Sea because they provide a high structural complexity that is needed for many other associated species to thrive (Ponti *et al*. 2014, 2016, 2018 ; Verdura *et al*. 2019 ; Gómez-Gras *et al*. 2021b).

As extreme climatic events unfold, the populations of these species are likely to experience further declines in their distribution range across various spatial dimensions, encompassing vertical (from surface to deep ranges) and horizontal (from north to south and west to east) distribution at local, regional, or even at pan-Mediterranean scale. These declines will have significant consequences for the functioning of Mediterranean benthic ecosystems (Gómez-Gras *et al*. 2021b) and, subsequently, for the provision of associated services to human societies (Smith *et al*. 2021).

Exploring future trajectories of Mediterranean habitats under MHWs

During the last decades, research efforts were focused on the factors and processes that shape inter- and intra-specific differential responses (sensitivity) to heat stress associated to MHWs. The outcomes of these efforts are fundamental to develop climate resilience conservation and restoration tools and to better predict the vulnerability of benthic species to the expected increase in the MHWs regime.

Several studies contributed to fill the gap of knowledge on basic information, such as the identification of thermotolerance thresholds in affected species, mainly octocorals, bryozoans, and fucalean seaweeds (*e.g.,* Pagés-Escolà *et al*. 2018 ; Gómez-Gras *et al*. 2019 ; Verdura *et al.* 2021). Likewise, for some species, experimental studies allowed to identify the main factors modulating the differential responses within and between populations, such as sex, maturity, symbiosis, physiological condition, microbiome and diseases (Bally & Garrabou, 2007 ; Linares *et al*. 2008 ; Cebrian *et al*. 2011; Ledoux *et al*. 2015 ; Arizmendi-Mejía *et al*. 2015b ; Crisci *et al*. 2017 ; Gómez-Gras *et al*. 2022 ; Bonacolta *et al*. 2023, Rilov 2024). Besides, combining these studies with population genetics and transcriptomics allowed to explore the eco-evolutionary dynamics in some of the affected species. Overall these studies confirmed the sensitivity to warm temperatures, with important inter-individual and inter-population thermotolerance variations, across the tested populations and species. Yet, as our understanding of the underlying evolutionary processes remains scarce, whether or not one can expect these species to adapt to the current and expected warming conditions remains an open question. For instance, in the red gorgonian *Paramuricea clavata*, the differential response observed among populations in one experiment in controlled conditions involving eight populations from the French and Catalan coasts (Crisci *et al*. 2017) was related to genetic drift. In another study which focused on eleven populations from the northwestern Mediterranean Sea and the Adriatic Sea, some populations did show adaptive potential and /or adaptive phenotypic plasticity to future warming (Gómez-Gras *et al*. 2022).

Despite such efforts, most studies concerned a very limited number of populations over a limited geographic area. Only few studies have considered populations over a wide distributional species range (*e.g.,* Gomez-Gras *et al*. 2022). There is an urgent need to span our experimental efforts to cover a larger number of species and to test larger numbers of populations coming from the whole distribution range. This is the required step to enhance our capacity to inform on the transformation of the structure and functioning of coastal Mediterranean habitats face due to the observed and predicted increase of MHWs regime.

Relationship between MMEs and MHWs

Unraveling the intricate interplay between the biological responses of marine biodiversity and the diverse gradients of heat exposure stands as a rarely explored challenge (Cheung *et al*. 2021 ; Hughes *et al*. 2021). Indeed, the high variability of responses observed among different species and populations across spatial and temporal scales, as well as the lack of empirical datasets on these extreme (rare) events, undermine our ability to understand this relationship.

In spite of this, several studies have confirmed the relation between MHWs and MMEs using both MHWs derived from satellite sea surface and *in situ* temperature data in the Mediterranean (*e.g.,* Verdura *et al*. 2021; Garrabou *et al*. 2022b). However, as mentioned above, these studies have also shown a high variability in the level of mortality impact for a similar heat exposure. The main component explaining this variability could be linked to: i) properties of the MHWs such as timing, duration, maximum, and cumulative intensity (Hodbday *et al*. 2016; Elzahaby *et al*. 2021); ii) species physiology and taxonomy (*i.e.,* differences among species and populations, including their specific thermal niche, thermotolerance, and physiological status) (see for example Arizmendi-Mejía *et al*. 2015b; Crisci *et al*. 2017; Gómez-Gras *et al*. 2019); and iii) the ecological memory on the recurrence of MHWs or other adaptative or acclimatization processes over the same geographic areas, which may alter the response of populations re-exposed to MHWs (Kersting and Linares, 2019 ; Turner *et al*. 2020 ; Hughes *et al*. 2021).

To bolster our predictive capacity concerning the ecological impacts of MHWs, needed measures encompass: i) persistent advocacy for recording long-term series of *in situ* temperature and for monitoring mass mortality series across the Mediterranean, so as to facilitate the construction of an extended historical record essential for precise MHWs identification and the potential onset of MMEs (Garrabou *et al*. 2022b ; Juza *et al.* 2024); ii) advancing our comprehension of the physical mechanisms propelling MHWs, both on the surface and at depth (Elzahaby *et al*. 2021); iii) the formulation of more comprehensive heat stress indicators adeptly considering both exposure duration and intensity (Cheung *et al.* 2021; Hughes *et al.* 2021, Lacer, 2024, Liguori 2024, Schlegel 2024, Simon 2024) and iv) engaging interdisciplinary research focused in understanding the factors and mechanisms responsible for the observed contrasted responses of species and populations across multiple spatial and temporal scales.

Conclusion

The increase in frequency, intensity, and spatial scales of MHWs is driving major ecological changes in marine ecosystems worldwide (Smith *et al*. 2021). Our results clearly indicate that the Mediterranean Sea is experiencing an acceleration of anthropogenic climate change impacts and reveal worrisome signals that large-scale MMEs and MHWs are no longer the exception but might become the new "normal".

As the global ocean, in general, and the Mediterranean Sea, in particular, are entering in unchartered territories, it is critical to reinforce and upscale ongoing collaborative efforts to increase the resolution of empirical observation networks, experimental settings, and interdisciplinary research. Such concerted efforts are essential for enhancing our ability to thoroughly comprehend and effectively manage the consequences of climate change.

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