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MARINE KEYSTONE SPECIES ON THE BRINK OF EXTINCTION

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Brief abstract

For over two decades, marine heatwaves (MHWs) have triggered invertebrate disease outbreaks leading to mass bleaching and mortality events. A severe MHW hit the Mediterranean Sea in 2022, affecting key components of coastal marine ecosystems, among which bath sponges were the main victims. The Marseille region (NW Mediterranean) was one of the last refuges for these species, which have been harvested since Antiquity, but the 2022 MHW is here reported to have led this entire poriferan family to the extinction of all known dense populations.

Brief communication

From June to September 2022, the hottest summer on record according to Copernicus (<https://www.copernicus.eu/en/news/news/observer-wrap-europes-summer-2022-heatwave>), several consecutive heatwaves affected Europe¹. In France, it has been the third most intense event on record, the benchmark heatwave remaining that of August 2003, with extremely high temperatures that lasted for several days throughout the country (<https://meteofrance.fr/actualite/publications/2022-les-bilans-climatiques>). As in 2003, this new extreme event has particularly impacted Mediterranean countries and spread to the marine realm. The North Western part of the Mediterranean Sea has experienced the strongest anomaly, with Sea Surface Temperatures (SSTs) reaching 5°C higher than average (https://www.esa.int/Applications/Observing_the_Earth/Mediterranean_Sea_hit_by_marine_heatwave). Marine Heat Waves (MHWs) are generally not restricted to the ocean surface, and although there is a clear trend in their increasing frequency², they can have highly variable patterns, making it difficult to predict their occurrence and impact.

The intensity of the 2022 MHW experienced by the NW Mediterranean was unprecedented, with a warm water mass that plunged to over 20 m depth in some locations. The Marseille area experienced a record peak of 27.4°C in mid-August and a whole week displaying records over 26°C (Fig. 1A). The mean temperature during the two hottest months of the summer (July-August) was up to 2°C higher than in previous years, and even higher than the July-August mean temperature recorded during the reference summer of 2003 (Fig. 1A). Over 20 years of monitoring temperatures, only once was the temperature higher than this, reaching 27.7°C on August 9, 2018. However, it only remained above 26°C for 3 h that year, a very brief peak compared to 7 days in 2022. Past Mediterranean MHWs (e.g., 1999 and 2003) have been related to disease outbreaks and mass mortality of a wide range of benthic taxa, occasionally leading to species shifts^{3, 4, 5, 6}. Several species of sponges, gorgonians, bryozoans, tunicates, and mollusks, most of them keystone species that shape Mediterranean seascapes, were among the main victims of these MHWs. The recurrence of MHWs therefore appears to drive the current major biodiversity crisis in the Mediterranean Sea. Although very alarming, these past events reached the general public as related to disease outbreaks and mortality, not to the disappearance of species. Here we show that the 2022 NW Mediterranean MHW is, more directly in line with the 6th mass extinction expectations^{7, 8}.

Off the Marseille coast, the above-mentioned record temperatures coincided with the first observations of mass mortality in mid-August. From then on, the phenomenon rapidly spread down to 30 m depth, and new mortality cases were reported every day. This year, the main victims were again gorgonians and first and foremost, the purple sea-fan *Paramuricea clavata*. This species is a major contributor to shallow NW Mediterranean seascapes. In the Marseille region, one of the coldest parts of the NW Mediterranean⁶, this sea-fan was abundant at shallow depths. Today, thousands of naked axes of this forest-forming erect soft coral testify of its destruction between the surface and 25 m depth, reminiscent of an “underwater wildfire”. Fortunately, this charismatic species has a wide bathymetric distribution in the Mediterranean, and therefore, beyond a depth of 30 m and down to more than 100 m, it is still possible to find dense populations. The other Mediterranean gorgonian species (*Corallium rubrum*, *Eunicella singularis*, *E. cavolini*, and *E. verrucosa*) have also been impacted by the 2022 MHW, but only at shallow depths and in a much more limited way.

The case of bath sponges (Porifera, family Spongiidae) is much more critical. These marine animals have been harvested since antiquity for the fineness, softness, and absorbent quality of their skeleton. This fishery remains nowadays a particularly lively cultural heritage in

several Mediterranean countries. It has been recently hypothesized that past MHWs, between the 1980s and today, played a key role in the disappearance of several sponge beds across the Mediterranean Sea, particularly in the Eastern basin⁹. The NW basin was one of the last parts of the Mediterranean Sea harboring dense populations of bath sponges, barely exploited, although in rather shallow waters. Evaluating the mortality of these marine animals can only be achieved by sponge experts, because many species of similar size and color can be confused underwater. Moreover, only experts can assess the vitality of individuals. The outcome of the 2022 MHW is unfortunately clear. All Spongiidae species known along the French coast (*e.g.* *Spongia officinalis*, *S. lamella*, *Hippospongia communis*) appear to have been wiped out between the surface and 25 m depth. Dense populations could only be found at these depths before the MHW. Densest populations of *S. officinalis* (Fig. 1B, C, D) used to occur at 10 m depth in the vicinity of Marseille, some of these populations having been monitored for over 25 years. Mortality rates are a bleak 100 % mortality; there are no survivors down to 25 m depth. After a total of 30 dives in 20 different locations along the French Mediterranean coast, only very few live individuals (1-4 per location) could be found between 25 m and 30 m, but no true population survived.

Sponges provide many important ecosystem services, such as shelter for various juvenile and adult animals. As filter-feeders, they recycle particulate and dissolved organic matter in the water column, thus affecting entire food-webs¹⁰. They are also well-known producers of bioactive compounds with potent pharmacological activities¹¹. For instance, bath sponges' chemistry is currently assessed for their neuropharmacological properties (*e.g.*, neuroprotective potential against Alzheimer's disease). In this context, bath sponge taxonomy and a part of the systematics are currently under revision, with species complexes to be deciphered and new species to be described (Grenier et al., 11th World Sponge Conference, Leiden, The Netherlands, 2022): a sponge biodiversity under risk of extinction before formal description.

Figure legend

Figure 1: Graphic illustration of the 2022 MHW and its impact on bath sponge populations. A) July-to-August seawater temperature recorded at 18 m depth at the "3PP" station, La Ciotat, near Marseille, South of France (43.163°N; 5.599°E) using *in situ* autonomous sensors during the 2022 MHW (red), in the two previous years (grey dotted lines), and during the reference 2003 MHW (orange dotted line). Only one record per day was used to draw the graph; mean values for the July-August period are reported as horizontal lines for each

reported year. An arrow points to the timing of the first reports of sponge mortality in mid-August; B) two living sponge species, *Ircinia oros* and the bath sponge *Spongia officinalis* (arrows), the latter with necrotic spots on its surface (September 7, 2022), scale bar 5 cm; C) The same two sponges after five days (September 12, 2022), *S. officinalis* is dying, covered by a white bacterial veil, scale bar 5 cm; D) A once rich and healthy population of *S. officinalis* at 10 m depth, September 21, 2022; Arrows point to *S. officinalis* dead skeletons left attached to the rocky wall, scale bar 20 cm.

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Online Methods section

Seawater temperature was recorded at 18 m depth at the “3PP” station, La Ciotat, near Marseille, South of France (43.163°N; 5.599°E) using *in situ* autonomous sensors during the 2022 MHW, a survey which started 20 years ago. Recorders were Seamon mini (Hugrún, Iceland) in 2003, one temperature measurement being obtained every 3 hours, and HOBO TidbiT V2 (Onset Comp., USA) for the other presented years, one temperature measurement obtained per hour. For a better readability, only one temperature record per day, the first of each day over July and August, was used to draw Figure 1A.

The impact of the 2022 MHW was evaluated by SCUBA diving, from the surface down to 50 m, in sites distributed 40 km East (Pointe Fauconnière), and 40 km West (Cap Couronne) of Marseille City (France). Each diving site corresponds to regular field stations that our team visited 20 times between January and late June 2022. Some of these sites have been monitored for 25 years, and in some cases sponge individuals were tagged for *in-situ* experiments. Monitoring was conducted by deploying a 1 m² quadrat along 50 m long transects. The densest bath sponge populations used to harbor more than 10 individuals per m², with a minimal size of 5 cm³ (0.2 g DW) to a maximal size of 10,500 cm³ (150 g DW). After the first reports of mortality in mid-August, 20 dives were conducted between the 29th of August and 28th of October 2022. Different stages of disease were observed, from the early occurrence of white bacterial veil at the sponge surface, necrosis, to the appearance of naked spongin skeletons. The repetition of dives could unfortunately confirm that the earliest signs of sponge disease always led to death in less than 3 days. During these dives, about 150 dead specimens were collected in order to check their taxonomic identity by observing their specific network of spongin fibers. As no individual appeared to have survived, we then focused on searching for the very few survivors in deeper waters.

