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Marine heatwaves on the rise: One of the strongest ever observed mass mortality event in temperate gorgonians

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Graphical abstract

Gorgonian population after the 2022 mass mortality event (MME) in the Calanques National Park. The year 2022 was marked by a historic gorgonian MME. This study describes the consequences for the red gorgonian (*Paramuricea clavata*) and red coral (*Corallium rubrum*) populations in the Calanques National Park (Marseille, France).

Climate change is currently impacting and threatening the entire biosphere, especially coastal marine ecosystems (Harley et al., 2006). In particular, climate change has been identified as a major driver of loss in coastal marine biodiversity and ecosystem functioning linked to the increase in the frequency and the intensity of marine heatwaves (MHWs) - anomalously prolonged periods of warm ocean temperatures or extremely warm temperature during short periods - (Smith et al., 2023). The Mediterranean Sea has particularly experienced widespread mass mortality events (MMEs) driven by MHWs across the basin over the last two decades (Garrabou et al., 2022). During summer 2022, the NW Mediterranean was affected by one of the strongest MME ever recorded in the region affecting several species including gorgonians, sponges, bryozoans, bivalve molluscs and calcareous algae. As in previous mass mortality events, mortality in these species resulted in the development of tissue necrosis affecting part of or the entirety of colonies (Fig. 1A). In the Calanques National Park, France, two of its most emblematic species, the red gorgonian (*Paramuricea clavata*) and the red coral (*Corallium rubrum*), were dramatically affected.

Thermal conditions in rocky coastal habitat in which the affected species thrive are subjected to widely varying conditions. Shallow populations (< 30 m) live under large seasonal and high-frequency temperature fluctuations, while deeper populations experience cooler and more stable conditions (Bensoussan et al., 2010). Shallow populations live very close to their upper thermotolerance limits (Gómez-Gras et al., 2022; Torrents et al., 2008), and are thus greatly threatened by MHWs (Garrabou et al., 2022). In the NW Mediterranean, these high-impact thermal anomalies are either characterized by short periods (2-5 days) with a mean temperature reaching 27°C and often associated with large diurnal variations, or characterized by long durations (up to 1 month) at warm and stable temperature (23-24°C) (Crisci et al., 2011). During the summer of 2022, while record-breaking heatwaves hit Europe, the Western Mediterranean Sea experienced record high MHWs (Guinaldo et al., 2023). The sea surface temperature (SST) reached extreme hot values, up to 30°C in its northern part, while summer mean temperature anomalies as high as 4.6°C could be evidenced from satellite data (https://www.mercator-ocean.eu/actualites/marine-heatwaves-mediterranean-summer-2022/). In the Calanques National Park, SST peaked over 28°C and our analysis reveals record high warm season MHW thermal stress reaching both

its highest duration (45 days), and its maximum and cumulative intensity (Tab. S4). Importantly, the hot waters extended well below the surface (*e.g.* > 27°C at 20 m) leading to record breaking subsurface MHW maximum intensity down to 25 m depth (+8.4°C at 25 m, Tab. S4). Overall, from July to the end of September, the 25°C threshold was passed for 32 days at 5 m depth and for 3 days at 30 m depth (Fig. 1B). These values correspond to the worst acute heat-stress of the past two decades (up to 24 years) and were 84% and 540% higher than previous *in situ* temperature records at 10 m and 25 m depth respectively.

These extreme thermal conditions resulted in a mass mortality event affecting at least 15 species belonging to 5 phyla. In this study, we assess the impacts on the two prominent habitat forming species across 50 km of coastline and from surface to 30 m depth, resulting in one the most comprehensive dataset recorded for a study area in the Mediterranean (Fig. 1A, S2, Garrabou et al. 2022). In contrast with previous MMEs recorded in the area (1999, 2003, 2006, 2018) the impact of the 2022 mortality was much more severe and affected deeper ranges (up to 30 m). In fact, these 25-30 m depth ranges were exposed for the very first time to temperatures above 25°C, considered as a potentially lethal acute heat stress threshold (Crisci et al. 2011). Bearing in mind that the study area has been monitored regularly during the last two decades, the observed mortality was unambiguously associated to the year 2022 MHWs. To assess the mass mortality impacts, we used a broadly used method based on the quantification of proportion of affected colonies (Garrabou et al. 2009, 2022) (for further information see Suplementary Materials). For the red gorgonian, *P. clavata*, 148 populations (including 26 sites and different depth ranges, Fig. S2) were surveyed for mortality impact from the surface down to 40 m, encompassing observations of 8998 colonies. In shallow waters (0-10 m and 10-20 m depth ranges), populations displayed on average > 80% of affected colonies, while in deeper waters (20-30 m depth range) the impact was only slightly lower, affecting > 65% of colonies (Fig. 1C, S1). This degree of impact was 142% higher than the impact recorded during the 2003 MMEs. These three depth ranges presented the highest proportions of affected colonies across depth strata (Kruskal-Wallis test, $Chi^2 = 24.58$, d.f. = 3, $p = 1.89e^{-5}$, followed by a Siegel and Castellan post-hoc test; Fig. 1C, and S1). Finally, populations dwelling at 30-40 m showed low levels of impact, with less than 10% of colonies being affected (Fig. 1C, S1). For the red coral, *C. rubrum*, a total of 17 populations (10 sites and different depth ranges) dwelling between 10 m and 30 m depth were surveyed, encompassing 1848 colonies. For 0-10 m and 10-20 m depth ranges, about 45% of the colonies were affected (Fig. S1), while in 20-30 m depth range, 35% of *C. rubrum* colonies showed recent necrosis. As for *P. clavata*, this degree of impact in *C. rubrum* was again higher than the one recorded during the 2003 MME. Populations deeper than 25 m depth did not display signs of mortality. Finally, during field surveys we conducted observations on the other species affected (*e.g.* sponges, bryozoans). While we were not able to quantify the severity of impacts, most species displayed clear signs of recent mortality impacts. Other factors such as diseases, mechanical disturbances and pollutants have been associated with the mortality impacts in gorgonian and other species. However, bearing in mind the 2022 MHWs and the associated temperature conditions, we contend that this was the primary factor triggering the observed mass mortality.

Recovery of gorgonian populations from the 2022 MME is going to be extremely difficult or impossible. The unprecedented severity of impact combined with the slow population dynamics (low growth and recruitment), low connectivity and impairment of reproduction output in the remaining surviving colonies point to a collapse trajectory for most populations dwelling between 0-30 m depth (Garrabou et al. 2021). Besides, in the context of ongoing warming, we can expect new MHWs events will affect the impacted depth ranges, probably resetting the incipient recovery of populations. The main consequence of the 2022 MME will be a dramatic shift in the upper depth distribution of

the affected species from 10 m down to more than 30 m depth. Given the ecological importance of red gorgonian and red coral as habitat forming species, their collapse will drive an important loss of habitat complexity which in turn has important ecosystem-level consequences and will result in the loss of the services they provide (Garrabou et al., 2021; Gómez-Gras et al., 2021).

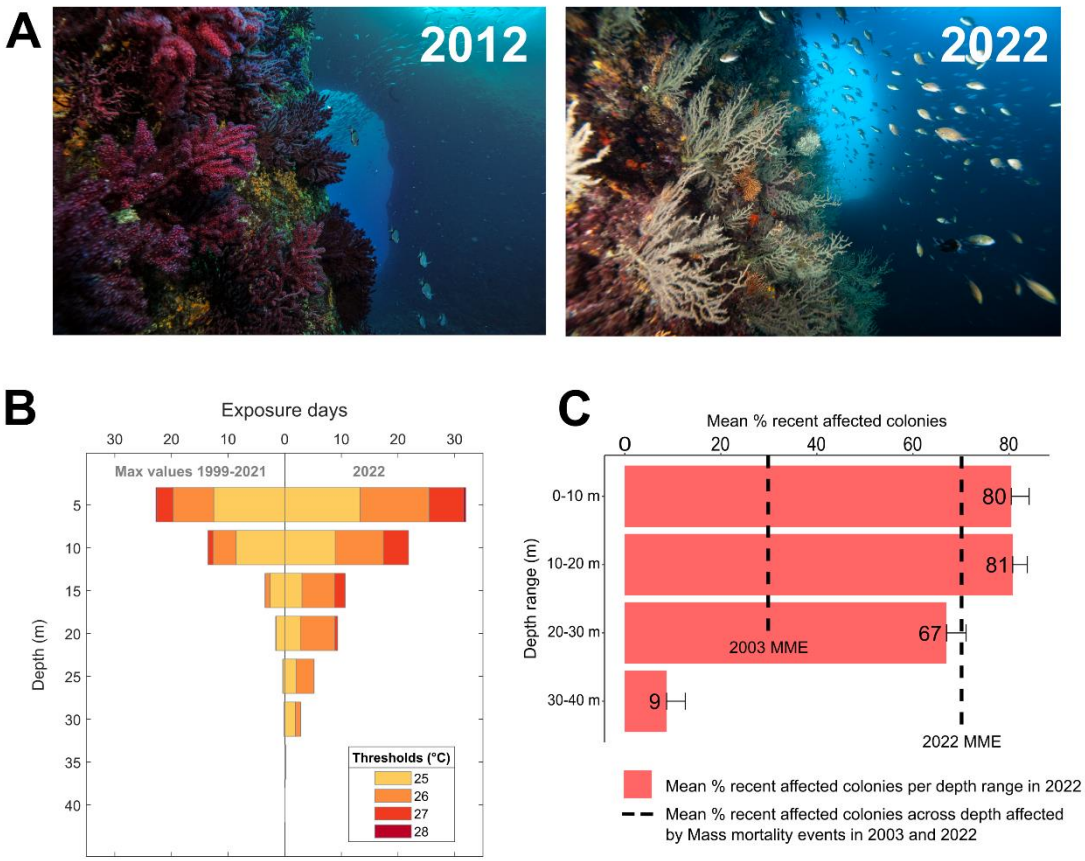

Figure 1: (A) Before and after impact of mass mortality on red gorgonian *Paramuricea clavata* during the marine heatwave of summer 2022 in the Calanques National Park (Marseille, France): before (left 2012) gorgonians displaying red-purple color and after (right 2022) the dead skeletons of gorgonians showing brownish color; (B) Warm season (July, August, September) acute heat stress days by depth (5 m - 40 m) for different thresholds from 25°C to 28°C at Riou south station (43.1727°N, 5.3902°E) within the Calanques National Park (Marseille, France) in 2022 in comparison with historical recorded temperature during last two decades (data provided by the regional temperature observation network T-MEDNet, www.t-mednet.org, site Riou Sud, Dorian Guillemain, OSU Institut Pytheas UMS 3470); (C) mean percentage of *P. clavata* colonies affected by recent necrosis surveyed in 2022 at 4 depth-range (0 to 40 m) encompassing 148 populations covering 26 sites, the dotted lines show the average proportion of colonies affected across all depth ranges in 2003 (historical MME, affected populations up to 25 m depth) and 2022.

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