Mediterranean Marine Science

Vol 24, No 3 (2023)

VOL 24, No 3 (2023)

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doi: [10.12681/mms.35564](https://doi.org/10.12681/mms.35564)

Short Communication

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net
www.hcmr.gr
DOI: http://doi.org/10.12681/mms.35564

The deep vault: a temporary refuge for temperate gorgonian forests facing marine heat waves

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Contributing Editor: Vasilis GEROVASILEIOU

Received: 04 October 2023; Accepted: 07 November 2023; Published online: 17 November 2023

Abstract

Climate change poses a significant threat to coastal areas, marked by the increasing intensity and frequency of marine heat waves observed in various ecosystems around the world. Over the last 25 years, a vast number of Mediterranean populations of the red gorgonian *Paramuricea clavata* have been impacted by marine heatwaves. The last mass mortality occurred during the summer of 2022 in the Western Mediterranean Sea, affecting mostly shallow populations (down to 30 m depth). Here we provide an assessment of the health status of mesophotic *P. clavata* populations down to 90 m depth to investigate a depth refuge hypothesis. Results show that the impact of marine heat waves decreases with depth, with a significant drop in mortality below 40 m depth. These observations support the hypothesis of a depth refuge from marine heat waves that may allow, at least temporarily, the maintenance of *P. clavata* in the Western Mediterranean Sea. The present study strongly advocates for further investigations and monitoring of the mesophotic zone to chart potential areas that could serve as deep refuge for gorgonians.

Keywords: Mass mortality events; sea-fan; Mediterranean Sea; mesophotic; deep refuge; extreme events; temperate corals; habitat-forming species; climate change; octocorals.

Introduction

Since 1990, marine heatwaves (MHWs) have increased in frequency, extent, and intensity worldwide, causing major changes in marine ecosystems (Dayan *et al*., 2023; Smith *et al*., 2023). Usually, when high and extreme temperatures are recorded, they are associated with intense mass mortalities of marine benthic organisms. A case in point is the red gorgonian *Paramuricea clavata* (Risso, 1827), one of the most affected species in the Mediterranean Sea during the summer period (July-August) (e.g., Rivetti *et al.,* 2014; Garrabou *et al*., 2022; Estaque *et al*., 2023). This gorgonian is a keystone engineering species, offering a forest-like habitat with a high three-dimensional complexity, especially when its populations reach high densities of large colonies (>20 cm high) (Rossi *et al*., 2017). Numerous vertebrates and invertebrates find shelter and food under their canopies (Ponti *et al*., 2018). Therefore, the fate of these forests is of great concern, as their degradation leads to strong impacts on the whole ecosystem with consequent loss of biodiversity and ecosystem services (Ponti *et al*., 2014; Paoli *et al*., 2017; Garrabou *et al*., 2021; Gómez-Gras *et al*., 2021; Rossi *et al*., 2022).

The first mass mortality events of *P. clavata* were reported in the 1980's and generally attributed to pollution, sometimes related to heavy rainfalls (see for instance Arnoux *et al*., 1992; Bavestrello *et al*., 1994). These relatively localized events affected both shallow and deep populations (down to 80 m). Since 1999, repeated mass mortality events have been recorded (2003, 2006, 2018, and 2022), mainly in shallow populations of the Western Mediterranean, affecting the coasts from Spain through France up to Italy, as well as the Adriatic Sea. The potential cause behind these drastic events has been attributed to temperature anomalies associated with MHWs (Cerrano *et al*., 2000; Perez *et al*., 2000; Garrabou *et al*., 2009, 2022; Grenier *et al*., 2023). Since then, researchers have been raising the alarm as current demographic trajectories of population decline could ultimately lead to the collapse of *P. clavata* populations, assuming that their resilience potential will decrease within the ongoing warming context (Garrabou *et al*., 2021). Nonetheless, some cases of population recovery have been recorded after two well documented mass mortality events in 1999 and 2003 (Cupido *et al*., 2009; Santangelo *et al*., 2015), with genetic studies highlighting the putative role of connectivity between shallow and deep populations as a driver of recovery success (Pilczynska *et al*., 2016; Padrón *et al*., 2018a).

In the summer of 2022, the Mediterranean was hit by one of the strongest MHWs ever recorded, affecting its western basin (Guinaldo *et al*., 2023), followed by an extensive red gorgonian mortality that began in August 2022 (Estaque *et al*., 2023). According to published observations, mortality rates were extreme down to 30 m (Estaque *et al*., 2023). Also other species of gorgonians, corals, algae, bryozoans, and sponges were severely affected, with bath sponges reported to be on the brink of local extirpation along the entire French Mediterranean coast (Grenier *et al*., 2023). Unlike *P. clavata*, whose habitat extends to depths of 200 m (Carpine & Grasshoff, 1975; Weinberg, 1976), the affected bath sponges on the French coast typically dwell in shallow water (10-20 m). The extirpation of this shallow water sponges populations matches *P. clavata* mortality events which have been reported almost excusively for shallow populations (15-25 m depth, rarely >30). The recent emergence of citizen science initiatives has led to increased early detections of these phenomena available and generated a wealth of data that were very difficult to obtain 20 years ago (Kelly *et al*., 2020; Vicioso *et al*., 2022). Nonetheless, these initiatives usually involve recreational SCUBA divers (Turicchia *et al.*, 2021; Figuerola-Ferrando *et al*., 2022), who rarely venture below 30 m. Hence, while monitoring efforts at depths below 30 m remain limited, the few existing observations suggest only a minor or no impact on *P. clavata* below 40 m (Arnoux *et al*., 1992; Linares *et al*., 2005; Pérez-Portela *et al*., 2016; Estaque *et al.*, 2023). Since the severity of these events seems to be closely linked to the duration of high temperatures exposure, and thus, to the depth of the thermocline (Pérez *et al*., 2006 and author's personal observations), more monitoring efforts should focus on deeper *P. clavata* populations to improve our understanding of the causal relationships between MHWs and species die-off, especially with regard to the potential of *P. clavata* to resist to MHWs effects at greatest depths. Indeed, the wide bathymetric distribution of *P. clavata* offers a glimmer of hope against the rather bleak backdrop of seemingly inevitable and dramatic future temperature increase.

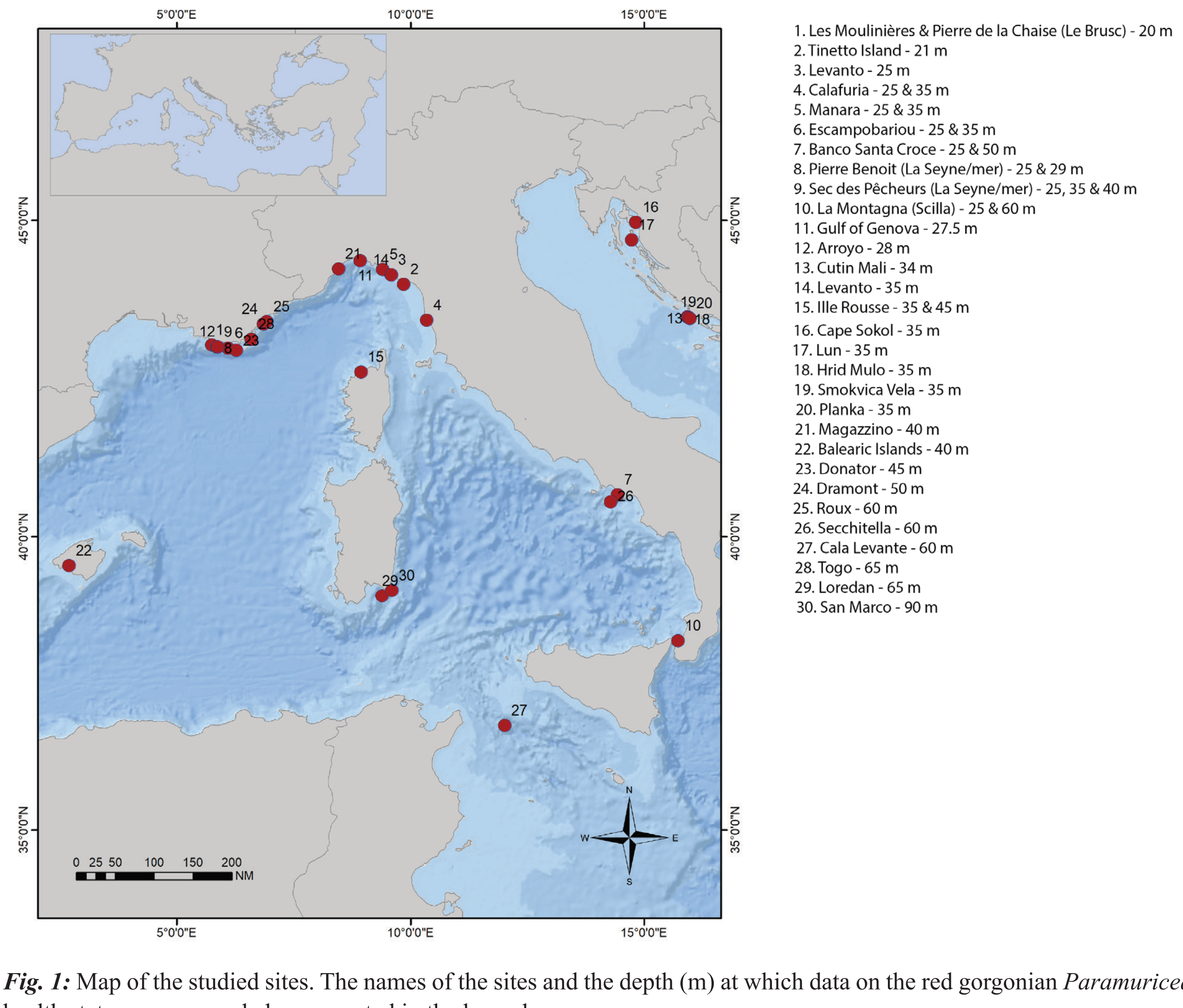

Fig. 1: Map of the studied sites. The names of the sites and the depth (m) at which data on the red gorgonian *Paramuricea clavata* health status were recorded are reported in the legend map.

Table 1. Data from the different populations examined in the present study.

Data Source	Latitude (DD)	Longitude (DD)	Year	Area	Site	Site in Fig.2	Depth (m)	% affected
This study	43.07530556°N	5.74944444°E	2022	Cap Sicie (France)	Les Moulinières	1	20	90
This study	43.07444444°N	5.74944444°E	2022	Cap Sicie (France)	Pierre de la Chaise	1	20	86
T-MEDNet	44.02377778°N	9.85044444°E	2004	La Spezia (Italy)	Tinetto Island	2	21	78.0
T-MEDNet	44.02377778°N	9.85044444°E	2006	La Spezia (Italy)	Tinetto Island	2	21	84.0
This study	44.17072222°N	9.58541667°E	2022	Levanto (Italy)	Levanto	3	25	30.3
This study	43.46269444°N	10.34163889°E	2022	Livorno (Italy)	Calafuria shallow	4	25	54.1
This study	44.25002778°N	9.40486111°E	2022	Sestri Levante (Italy)	Manara	5	25	29.2
This study	43.02652778°N	6.09711111°E	2022	Giens (France)	Escampobariou	6	25	82.8
This study	40.68130556°N	14.43163889°E	2022	Gulf of Napoli (Italy)	Banco Santa Croce	7	25	28.0
This study	43.04725000°N	5.86736111°E	2022	Cap Sicie (France)	Pierre Benoit	8	25	85
This study	43.04725000°N	5.86736111°E	2022	Cap Sicie (France)	Pierre Benoit	8	25	95
This study	43.04311111°N	5.86336111°E	2022	Cap Sicie (France)	Sec des Pêcheurs	9	25	77
This study	38.26047222°N	15.71858333°E	2022	Sicily (Italy)	La Montagna (Scilla)	10	25	60
T-MEDNet	44.38900000°N	8.92669444°E	1993	Genova (Italy)	Gulf of Genova	11	27.5	80.0
This study	43.04755556°N	5.86930556°E	2022	Cap Sicie (France)	Arroyo	12	28	40.4
This study	43.04725000°N	5.86736111°E	2022	Cap Sicie (France)	Pierre Benoit	8	29	14
T-MEDNet	43.49330556°N	15.96916667°E	2009	Croatia	Cutin Mali	13	34	10
This study	44.17072222°N	9.58541667°E	2022	Levanto (Italy)	Levanto	14	35	13.2
This study	43.46269444°N	10.34163889°E	2022	Livorno (Italy)	Calafuria deep	4	35	17.4
This study	44.25002778°N	9.40486111°E	2022	Sestri Levante (Italy)	Manara	5	35	9.0
This study	43.02652778°N	6.09711111°E	2022	Giens (France)	Escampobariou	6	35	12.0
This study	42.65197222°N	8.94188889°E	2022	Corsica (France)	Ille Rousse	15	35	7.6
This study	43.04311111°N	5.86336111°E	2022	Cap_Sicie (France)	Sec des Pêcheurs	9	35	49
This study	43.04311111°N	5.86336111°E	2022	Cap_Sicie (France)	Sec des Pêcheurs	9	35	10
T-MEDNet	44.97025000°N	14.82122222°E	2009	Croatia	Cape Sokol	16	35	40.0
T-MEDNet	44.70416667°N	14.73388889°E	2009	Croatia	Lun	17	35	10
T-MEDNet	43.51330556°N	15.91861111°E	2009	Croatia	Hrid Mulo	18	35	10
T-MEDNet	43.51055556°N	15.94222222°E	2009	Croatia	Smokvica Vela	19	35	10
T-MEDNet	43.49330556°N	15.96916667°E	2009	Croatia	Planka	20	35	10
This study	44.26180556°N	8.46363889°E	2022	Vado Ligure (Italy)	Magazzino	21	40	7.9

Continued

Table 1 continued

Data Source	Latitude (DD)	Longitude (DD)	Year	Area	Site	Site in Fig.2	Depth (m)	% affected
This study	43.04311111°N	5.86336111°E	2022	Cap_Sicie (France)	Sec des Pêcheurs	9	40	10
T-MEDNet	39.52000000°N	2.70000000°E	2003	Spain	Balearic Islands	22	40	14.9
This study	42.99319444°N	6.27436111°E	2022	Porquerolles (France)	Donator	23	45	7.3
This study	42.65197222°N	8.94188889°E	2022	Corsica (France)	Ille Rousse	15	45	9.0
This study	43.40463889°N	6.85238889°E	2022	St Rapahael (France)	Dramont	24	50	1.9
This study	40.68130556°N	14.43163889°E	2022	Gulf of Napoli (Italy)	Banco Santa Croce	7	50	4.8
This study	43.43938889°N	6.92205556°E	2022	St Rapahael (France)	Roux	25	60	1.1
This study	40.56863889°N	14.28675000°E	2022	Gulf of Napoli (Italy)	Secchitella	26	60	3.8
This study	38.26047222°N	15.71858333°E	2022	Sicily (Italy)	La Montagna (Scilla)	10	60	8
T-MEDNet	36.82444444°N	12.01444444°E	2011	Sicily (Italy)	Cala Levante-Pantelleria	27	60	10
This study	43.16602778°N	6.59519444°E	2022	Cavalaire (France)	Togo	28	65	5.2
This study	39.13630556°N	9.39286111°E	2022	Sardinia (Italy)	Loredan	29	65	1.7
This study	39.10627778°N	9.59930556°E	2022	Sardinia (Italy)	San Marco	30	90	1.5

Bearing in mind that mass mortality events have been mainly associated with MHWs, and given the well-established decrease in temperature with depth, even within the context of a thermal anomaly regime (Juza *et al*., 2022; Dayan *et al*., 2023), deeper populations should be preserved (but see Neal *et al*., 2014; Venegas *et al*., 2019). Nevertheless, it is important to note that both the intensity and duration of MHWs-related thermal anomalies has increased and reached deeper waters over the past decade (Dayan *et al*., 2023).

In this study, we quantify the health status of *P. clavata* populations down to 90 m depth in the Mediterranean Sea (Fig. 1) and investigate the depth refuge hypothesis, i.e., we assess the maximum depths to which this species was impacted by MHWs. Our study attempts to elucidate the potential role of the mesophotic zone as a refuge for this species severely impacted by the effects of climate change.

Materials and Methods

We conducted mortality surveys on 43 populations located outside marine protected areas (MPAs) along the Western Mediterranean Sea, focusing on depths ranging from 20 to 90 m (Table 1; Fig. 1). A total of 32 surveys were collected by SCUBA diving by the authors of the present study between October 2022 and March 2023, while the remaining 11 surveys were extracted from the MME-T-MEDNet database (Cerrano *et al*., 2000; Cupido *et al*., 2008; Garrabou *et al*., 2009, 2019).

A standardized protocol for underwater data collection was applied, based on a rapid assessment method to determine the health status of the colonies (Garrabou *et al*., 2019) (t-mednet.org/MME). Figure 2 shows colonies of *P. clavata* both affected by mortality event (shallow populations; Fig. 2A) and in good health status (deep populations; Fig. 2B) for comparison. Approximately 100 adult colonies (> 15 cm in height) were inspected at each location and scored as affected when more than 10% of the colony presented necrosis. In affected colonies, we distinguished between the occurrence of a denuded axis (AD), indicating a very recent impact, axis with epibiosis (AE), indicating that the necrosis could be due to a past mortality event, and the presence of both denuded axis and epibiosis (AED). Since the MME-T-MEDNet dataset on mortality percentages only refers to recent mortality, we considered as affected all those colonies presenting > 10% of the denuded axis (AD + AED).

Two exclusion criteria were applied to the MME-T-MEDNet dataset:

1) Protection effect: According to Zentner *et al*. (2023), MPA can mitigate the effects of climate change on *P. clavata* populations by reducing sources of mortality other than water temperature increase (e.g., SCUBA divers' frequentation). Therefore, only data from populations dwelling outside MPAs were included, to avoid confounding effects between depth and protection status.
2) Accuracy of depth recording: In the MME-T-MED-

Fig. 2: Deep refuge. A: a shallow population (< 40 m) with a high percentage of affected colonies (Photo credits: T. Estaque). B: a deep population (> 40 m) with no signs of mortality (Photo credits: A. Rosenfeld, UNESCO and 1 Ocean Foundation).

Net dataset, the population survey depth is not given precisely but as a depth range with an upper and a lower bound. As we intend to establish a relationship between depth and percentage of affected colonies, accurate depth information is crucial. Therefore, we selected only those populations where the depth range (uncertainty) was less than 10 m and used the mean between the upper and lower bounds.

The relationship between depth and percentage of affected colonies was investigated following a three-steps procedure. Firstly, we selected the model that best described the relationship between the two variables using an Akaike information criterion (AIC) approach (Akaike, 1978). Testing linear, power, and exponential models we retained the power model as it resulted in the lowest AIC value. Secondly, the strength of the non-linear relationship between the two variables was quantified by the Spearman correlation coefficient. Thirdly, the functional relationship between the variables was described using a non-linear least square (NLS) regression model (using the R software, function "stat_smooth"). A Student t-test was applied to assess the difference in mean Boxplot representing the percentage of affected colonies in shallow (< 40 m depth) and deep (> 40 m depth) P. clavata populations.-homogeneity of variance, a log transformation of the data was applied. The choice of the depth threshold of 40 m was based on previous studies suggesting the absence of MHWs-related impact below this depth (Arnoux *et al.*, 1992; Linares *et al.*, 2005; Pérez-Portela *et al.*, 2016; Estaque *et al.*, 2023).

Results

The percentage of affected colonies in the 43 populations of the present study varied from 95% at Cap Sicié (25 m depth; La Seyne sur mer, France) to 1.1% at Cap Roux (60 m depth; St. Raphael, France; Table 1; Fig. 2).

A significant negative correlation between the percentage of affected colonies and depth was found (rho = -0.89, $p < 0.001$).

The relationship between depth and percentage of affected colonies was best described by a decreasing power curve with exponent -3 (Fig. 3). The regression model showed that a significant and high proportion of mortality variability was explained by depth ($F_{(1\text{-}41)} = 147.25$, p-value < 0.001, $R^2 = 0.78$).

A difference in the mean values of the percentage of affected colonies was found between shallow (< 40 m depth; 42.1% ± 32.1 SD) and deep populations (> 40 m depth; 6.2 % ± 4.1 SD) (Fig. 4; t-test: t = -6.23 df = 41, p-value < 0.001).

Discussion

According to the "deep reef refugia" hypothesis (DRRH), marine populations inhabiting deeper zones should be less impacted by climate change-associated disturbances, particularly those stemming from rising seawater temperatures. The pivotal role of depth in mitigating this impact is widely accepted (Glynn, 1996; Bongaerts *et al*., 2010; Bridge *et al*., 2014; Bongaerts & Smith, 2019).

Our findings suggest that the mesophotic zone below 40 m depth might serve as a refuge for the Mediterranean *P. clavata*, providing shelter from the effects of marine heatwaves (MHWs), at least until 2022. Although the dataset used in this study is the most comprehensive and covers the broadest bathymetric range to date, our knowledge of this species' spatial distribution and conservation status beyond 40 m remains scant because of the limited number of available observations below this depth (but see Linares *et al*., 2022 https://cormednet.medrecover.org/). This dearth of knowledge impedes the precise delineation of bathymetric boundaries for such mortalities, and hampers the establishment of consistent knowledge base to forecast the impact of MHWs on *P. clavata* populations. The present study simultaneously provides empirical evidence of a higher survival of this gorgonian at greater depth and strongly advocates for further investigations of the mesophotic zone to chart potential areas of deep refuge for *P. clavata*. In this context, the recent democratization of technological solutions to explore the marine environment (e.g., closed circuit scuba diving, cabled observatories, remotely operated vehicles) provides a tangible avenue for deploying novel monitoring programs.

It should be noted that the observed refuge effect is likely to change in the near future, due to the expected increase in MHWs frequency and severity (Dayan *et al*., 2023), which means that these events will extend their influence also in deeper, currently sheltered, areas. Historically, MHW events have demonstrated moderate impacts on gorgonian populations down to 65 m in Italy (Cerrano *et al*., 2000; Pérez *et al*., 2000). Furthermore, thermal tolerances described by previous investigations of shallow populations may not be directly transferable to their deeper counterparts (e.g., Crisci *et al*., 2017; Gómez-Gras *et al*., 2022). A decline in shallow populations could augment the level of isolation of deep populations, possibly resulting in higher sensitivity to thermal anomalies due to local adaptations to colder and more thermally stable conditions, thus elevating population vulnerability (Gómez-Gras *et al*., 2022). In the specific case of *P. clavata*, thermotolerance in shallow populations (< 40 m depth) does not appear to be influenced by depth, and substantial inter-individual variability in responses to

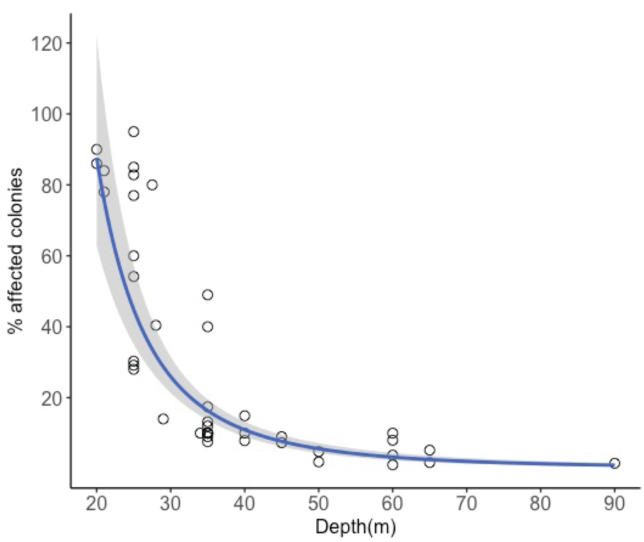

Fig. 3: Decreasing power curve describing the relationship between mortality (% of affected colonies) and depth. The grey area represents the 95% confidence interval.

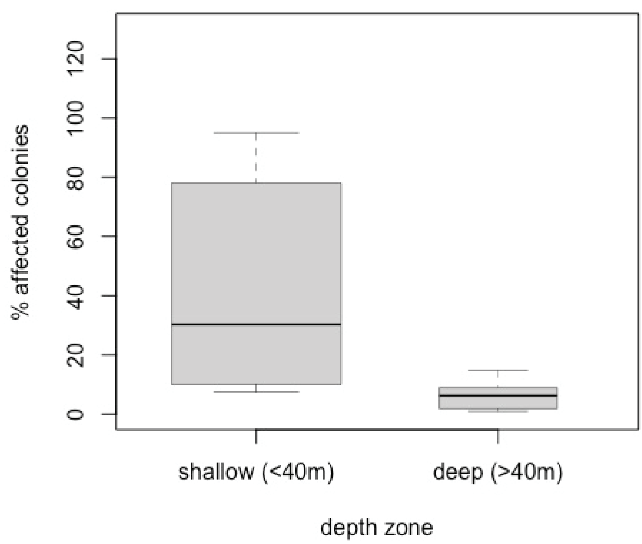

Fig. 4: Boxplot representing the percentage of affected colonies in shallow (< 40 m depth) and deep (> 40 m depth) *P. clavata* populations.

thermal stress implies the potential for local adaptation among isolated populations (Gómez-Gras *et al*., 2022). However, adaptation processes in deep populations have not been investigated so far. A crucial step towards understanding the potential resilience of species with broad bathymetric ranges involves assessing genetic connectivity between shallow and deep populations. Regrettably, such studies on connectivity across varying depths are scarce (Mokhtar-Jamaï *et al*., 2011; Pilczynska *et al*., 2016), and only one study exists that has focused on deep populations (Pérez-Portela *et al*., 2016). On the other hand, studies on vertical connectivity between *P. calvata* populations indicate limited gene flow, typically constrained to distances of approximately 100 m (Mokhtar-Jamaï *et al*., 2011). Nonetheless, a study documenting the potential recovery of an impacted *P. clavata* population in the Ligurian Sea, demonstrated gene flow spanning over 30 km (Padrón *et al*., 2018b).

Given the rather somber forecast for shallow populations (Gómez-Gras *et al*., 2021), their survival in deep refuges depends on the degree of demographic connectivity between deep populations. In light of these considerations, the data presented here and the gaps in our understanding regarding the demography and physiology of deep populations underscore the compelling need to study mesophotic zones and elucidate connectivity among endangered populations through genetic connectivity and larval dispersal investigations (Sciascia *et al*., 2022). This emerging field in conservation ecology will need a more precise delineation of thermal seascapes across bathymetric gradients and their influence on species distributions. Only through this enhanced understanding, the projection models of MHWs (e.g., Martínez *et al*., 2023) can be effectively linked to the potential occurrence of disease outbreaks in deep populations, thereby enabling the forecast of the future trajectory of deep refuges.

Acknowledgements

The authors acknowledge Alexis Rosenfeld and UNESCO as well as Fondation 1 Ocean (fondation-1ocean.com) for the cooperation on this project. The authors also gratefully acknowledge Thierry Perez for the helpful proofreading of the manuscript. Part of the data has been extracted from MME-T-MEDNet database on mass mortality events in the Mediterranean t-mednet.org/MME. L. Bramanti was funded by "BNP PARIBAS climate change and biodiversity initiative" through the DEEPLIFE project; E. Manea was funded by the Marie Curie Actions through the project RESTORE (project number 101062275); B. Giordano was funded by the Doctorate School of the University of Cagliari; T. Estaque, J. Richaume and O. Bianchimani were funded by OFB (Office français de la Biodiversité); B. Mérigot and Q. Schull were supported by the LabEx CeMEB for the DEEP HEART project; J. Garrabou acknowledges the support of the Severo Ochoa Centre of Excellence, Grant/Award Number: CEX2019-000928-S, European Union Horizon 2020 research and innovation programme (Futuremares SEP-210597628) and TED2021-131622B-I00 CORFUN project. A special thanks to Roberto Rinaldi, Marco Panico, Aldo Ferrucci, Stefano Bianchelli, Cristina Condemi, Elena Persoglio, and the diving centers Pro Dive (prodive.it), Scilla Diving Center (Scilladiving.it), Dimensione Diving Lavagna (dimensionediving.com) and Epir Plongée (epirplongee.com) for the assistance in the deep dives and data collection.

Declaration of interests: The authors declare no competing interests.

References

Akaike, H., 1978. On the likelihood of a time series model. *Journal of the Royal Statistical Society*, 27 (3/4), 217-235.

Arnoux, A., Harmelin, J.-G., Monod, J.L., Romana, L.A., Zibrowius, H., 1992. Altérations des peuplements benthiques de roches profondes en Méditerranée nord-occidentale: quelque aspects biologiques et molysmologiques. *Comptes Rendus de l'Académie des Science. Série 3, Sciences de la vie*, 314 (5), 219-225.

Bavestrello, G., Cerrano, C., Zanzi, D., Cattaneo-Vietti, R., 1994. Damage by fishing activities to the Gorgonian coral *Paramuricea clavata* in the Ligurian Sea. *Aquatic Conservation-marine and Freshwater Ecosystems*, 7 (3), 253-262.

Bongaerts, P., Ridgway, T., Sampayo, E. M., Hoegh-Guldberg, O., 2010. Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. *Coral Reefs*, 29 (2), 309-327.

Bongaerts, P., Smith, T.B., 2019. Beyond the "Deep Reef Refuge" hypothesis: A conceptual framework to characterize persistence at depth. *Mesophotic Coral Ecosystems*, 881-895.

Bridge, T.C.L., Hoey, A.S., Campbell, S.J., Muttaqin, E., Rudi, E. *et al.*, 2014. Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery. *F1000Research*, 2, 187.

Carpine, C., Grasshoff, M., 1975. Les gorgonaires de la Mediterranee. *Bulletin de l'Institut océanographique de Monaco*, 71 (1430), 1-140.

Cerrano, C., Bavestrello, G., Bianchi, C.N., Cattaneo-vietti, R., Bava, S. *et al.,* 2000. A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (North-Western Mediterranean), summer 1999. *Ecology Letters*, 3 (4), 284-293.

Crisci, C., Ledoux, J.-B., Mokhtar-Jamaï, K., Bally, M., Bensoussan, N. *et al.,* 2017. Regional and local environmental conditions do not shape the response to warming of a marine habitat-forming species. *Scientific Reports*, 7 (1), 5069.

Cupido, R., Cocito, S., Sgorbini, S., Bordone, A., Santangelo, G., 2008. Response of a gorgonian (*Paramuricea clavata*) population to mortality events: recovery or loss? *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18 (6), 984-992.

Cupido, R., Cocito, S., Barsanti, M., Sgorbini, S., Peirano, A. *et al.*, 2009. Unexpected long-term population dynamics in a canopy-forming gorgonian coral following mass mortality. *Marine Ecology Progress Series*, 394, 195-200.

Dayan, H., McAdam, R., Juza, M., Masina, S., Speich, S., 2023. Marine heat waves in the Mediterranean Sea: an assessment from the surface to the subsurface to meet national needs. *Frontiers in Marine Science*, 10, 1045138.

Estaque, T., Richaume, J., Bianchimani, O., Schull, Q., Mérigot, B. *et al.,* 2023. Marine heatwaves on the rise: one of the strongest ever observed mass mortality event in temperate gorgonians. *Global Change Biology*, 29, 6159-6162.

Figuerola-Ferrando, L., Linares C., Zentner Y., López-Sendino P., Garrabou, J., 2022. A rapid assessment method for citizen-scientists to monitor the conservation status of Mediterranean coralligenous assemblages. p. 47-52. In: *Proceedings of the 4th Mediterranean Symposium on the conservation of Coralligenous & other Calcareous Bio-Concretions (Genova, Italy, 20-21 September 2022)*. Bouafif, C., Ouerghi, A. (Eds). SPA/RAC publications, Tunis.

Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P. *et al.*, 2009. Mass mortality in Northwestern Mediterranean rocky benthic communities: Effects of the 2003 heat wave. *Global Change Biology*, 15 (5), 1090-1103.

Garrabou, J., Gómez-Gras, D., Ledoux, J.-B., Linares, C., Bensoussan, N. *et al.*, 2019. Collaborative database to track mass mortality events in the Mediterranean Sea. *Frontiers in Marine Science*, 6, 707.

Garrabou, J., Ledoux, J.-B., Bensoussan, N., Gómez-Gras, D., Linares, C., 2021. Sliding Toward the collapse of Mediterranean coastal marine rocky ecosystems. *Ecosystem Collapse and Climate Change*, 241, 291-324.

Garrabou, J., Gómez-Gras, D., Medrano, A., Cerrano, C., Ponti, M. *et al.,* 2022. Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. *Global Change Biology*, 28 (19), 5708-5725.

Glynn, P.W., 1996. Coral reef bleaching: facts, hypotheses and implications. *Global Change Biology*, 2 (6), 495-509.

Gómez-Gras, D., Linares, C., Dornelas, M., Madin, J.S., Brambilla, V. *et al.*, 2021. Climate change transforms the functional identity of Mediterranean coralligenous assemblages. *Ecology Letters*, 24 (5), 1038-1051.

Gómez-Gras, D., Bensoussan, N., Ledoux, J.B., López-Sendino, P., Cerrano, C.F. *et al.,* 2022. Exploring the response of a key Mediterranean gorgonian to heat stress across biological and spatial scales. *Scientific Reports*, 12 (1), 21064.

Grenier, M., Idan, T., Chevaldonné, P., Pérez, T., 2023. Mediterranean marine keystone species on the brink of extinction. *Global Change Biology*, 29 (7), 1681-1683.

Guinaldo, T., Voldoire, A., Waldman, R., Saux Picart, S., Roquet, H., 2023. Response of the sea surface temperature to heatwaves during the France 2022 meteorological summer. *Ocean Science*, 19 (3), 629-647.

Juza, M., Fernández-Mora, À., Tintoré, J., 2022. Sub-regional marine heat waves in the Mediterranean Sea from observations: long-term surface changes, sub-surface and coastal responses. *Frontiers in Marine Science*, 9, 785771.

Kelly, R., Fleming, A., Pecl, G.T., von Gönner, J., Bonn, A., 2020. Citizen science and marine conservation: a global review. *Philosophical Transactions of the Royal Society B*, 375 (1814), 20190461.

Linares, C., Coma, R., Diaz, D., Zabala, M., Hereu, B. *et al.*, 2005. Immediate and delayed effects of a mass mortality event on gorgonian population dynamics and benthic community structure in the NW Mediterranean Sea. *Marine Ecology Progress Series*, 305, 127-137.

Linares, C., Figuerola-Ferrando, L., Gómez-Gras, D., Pagés-Escolà, M., Olvera, A. *et al.*, 2022. CorMedNet: building a database on the distribution, demography and conservation status of sessile species for Mediterranean coralligenous assemblages. p. 80-85. In: *Proceedings of the 4th Mediterranean Symposium on the conservation of Coralligenous & other Calcareous Bio-Concretions (Genova, Italy, 20-21 September 2022)*. Bouafif, C., Ouerghi, A. (Eds). SPA/RAC publications, Tunis.

Martínez, J., Leonelli, F.E., García-Ladona, E., Garrabou, J., Kersting, D. *et al*., 2023. Evolution of marine heatwaves in warming seas: The Mediterranean Sea case study. *Frontiers in Marine Science*, 10, 1193164.

Mokhtar-Jamaï, K., Pascual, M., Ledoux, J.-B., Coma, R. *et al*., 2011. From global to local genetic structuring in the red gorgonian *Paramuricea clavata*: The interplay between oceanographic conditions and limited larval dispersal. *Molecular Ecology*, 20 (16), 3291-3305.

Neal, B.P., Condit, C., Liu, G., Dos Santos, S., Kahru, M. *et al.*, 2014. When depth is no refuge: cumulative thermal stress increases with depth in Bocas del Toro, Panama. *Coral Reefs*, 33 (1), 193-205.

Padrón, M., Costantini, F., Bramanti, L., Guizien, K., Abbiati, M., 2018a. Genetic connectivity supports recovery of gorgonian populations affected by climate change. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28 (4), 776-787.

Padrón, M., Costantini, F., Baksay, S., Bramanti, L., Guizien, K., 2018b. Passive larval transport explains recent gene flow in a Mediterranean gorgonian. *Coral Reefs*, 37 (2), 495-506.

Paoli, C., Montefalcone, M., Morri, C., Vassallo, P., Bianchi, C.N., 2017. Ecosystem Functions and Services of the Marine Animal Forests. In: *Marine Animal Forests*. Rossi, S., Bramanti, L., Gori, A., Orejas Saco del Valle, C. (Eds). Springer International Publishing, Switzerland.

Perez, T., Garrabou, J., Sartoretto, S., Harmelin, J.-G., Francour, P. *et al.*, 2000. Mortalité massive d'invertébrés marins: un événement sans précédent en Méditerranée nord-occidentale. *Comptes Rendus de l'Académie des Science*, 323 (10), 853-865.

Perez, T., Lejeusne, C., Aurelle, D., Bensoussan, N., Boury-esnault, N. *et al*., 2006. Évaluation des modifications de la biodiversité marine sous l'influence du changement global en Méditerranée nord-occidentale. In : *Colloque de restitution IFB – GICC, Réponses adaptatives au changement global : résultats et prospective, 18-20 septembre 2006*.

Pérez-Portela, R., Cerro-Gálvez, E., Taboada, S., Tidu, C., Campillo-Campbell, C. *et al.*, 2016. Lonely populations in the deep: genetic structure of red gorgonians at the heads of submarine canyons in the north-western Mediterranean Sea. *Coral Reefs*, 35 (3), 1013-1026.

Pilczynska, J., Cocito, S., Boavida, J., Serrão, E., Queiroga, H., 2016. Genetic diversity and local connectivity in the Mediterranean red gorgonian coral after mass mortality events. *PLoS ONE*, 11 (3), e0150590.

Ponti, M., Perlini, R.A., Ventra, V., Grech, D., Abbiati, M. *et al.*, 2014. Ecological shifts in Mediterranean coralligenous assemblages related to gorgonian forest loss. *PLoS ONE*, 9 (7), e102782.

Ponti, M., Turicchia, E., Ferro, F., Cerrano, C., Abbiati, M., 2018. The understorey of gorgonian forests in mesophotic temperate reefs. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28 (5), 1153-1166.

Rivetti, I., Fraschetti, S., Lionello, P., Zambianchi, E., Boero, F., 2014. Global warming and mass mortalities of benthic invertebrates in the Mediterranean Sea. *PLoS ONE*, 9 (12), e115655.

Rossi, S., Bramanti, L., Gori, A., Orejas, C. 2017. An Overview of the Animal Forests of the World. In: *Marine Animal Forests*. Rossi, S., Bramanti, L., Gori, A., Orejas Saco del Valle, C. (Eds). Springer International Publishing, Switzerland.

Rossi, S., Bramanti, L., Horta, P., Allcock, L., Carreiro-Silva, M. *et al*., 2022. Protecting global marine animal forests. *Science*, 376 (6596), 929-929.

Santangelo, G., Cupido, R., Cocito, S., Bramanti, L., Priori, C. *et al*., 2015. Effects of increased mortality on gorgonian corals (Cnidaria, Octocorallia): different demographic features may lead affected populations to unexpected recovery and new equilibrium points. *Hydrobiologia*, 759 (1), 171-187.

Sciascia, R., Guizien, K., Magaldi, M.G., 2022. Larval dispersal simulations and connectivity predictions for Mediterranean gorgonian species: sensitivity to flow representation and biological traits. *ICES Journal of Marine Science*, 79 (7), 2043-2054.

Smith, K.E., Burrows, M.T., Hobday, A.J., King, N.G., Moore P.J. *et al*., 2023. Biological impacts of marine heatwaves. *Annual Review of Marine Science*, 15 (1), 119-145.

Turicchia, E., Ponti, M., Rossi, G., Milanese, M., Di Camillo, C.G. *et al.*, 2021. The reef check mediterranean underwater coastal environment monitoring protocol. *Frontiers in Marine Science*, 8, 620368.

Venegas, R.M., Oliver, T., Liu, G., Heron, S.F., Clark, S.J. *et al*., 2019. The rarity of depth refugia from coral bleaching heat stress in the western and central pacific islands. *Scientific Reports*, 9 (1), 19710.

Vicioso, M., López-Sendino, P., Espeja, S., Garcia, M., Agell, G. *et al*., 2021. Observadores del mar: transformative marine citizen science. p. 242-244. In: *The ocean we want: inclusive and transformative ocean science*. Pelegrí J.L., Gili J.M., Martínez de Albéniz M.V. (Eds.). Institut de Ciències del Mar, CSIC, Barcelona.

Weinberg, S., 1976. Revision of the common Octocorallia of the Mediterranean circalittoral. I. Gorgonacea. *Beaufortia*, 24 (313), 63-104.

Zentner, Y., Rovira, G., Margarit, N., Ortega, J., Casals, D. *et al*., 2023. Marine protected areas in a changing ocean: adaptive management can mitigate the synergistic effects of local and climate change impacts. *Biological Conservation*, 282, 110048.