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# Temporal trends of two iconic Mediterranean gorgonians (*Paramuricea clavata* and *Eunicella cavolini*) in the climate change context

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ABSTRACT

Gorgonians are iconic species of Mediterranean benthic communities. They are ecosystem engineers and their conservation is essential for the biodiversity of marine communities. Yet these long-lived species are particularly vulnerable to natural or anthropogenic disturbances. The objective of this study is to define the demographic characteristics and health status of the gorgonian forests for two species of gorgonians *Paramuricea clavata* (Risso, 1826) and *Eunicella cavolini* (Koch, 1887) over fifteen years. The potential impact of changing environmental conditions is assessed by studying, at different depths, trends in temperature and planktonic changes (phytoplankton biomass and zooplankton abundance) over the study period. Our results indicate that there is a change in population structure of the two gorgonian species with a significant decrease in recruitment in recent years. For *E. cavolini*, the necrosis significantly increased between 2004 and 2019 (from 9.66% to 25.63% of injured colonies and from 0.24% to 4.75% of dead colonies, respectively). For *P. clavata*, the population was particularly damaged in 2004 with 14.81% of dead colonies. While necrosis significantly decreased between 2004 and 2014, a significant increase is observed between 2014 and 2019 (from 1.92% to 4.44% of dead colonies). In addition, it appears that large size colonies are more affected by necrosis, and reciprocally. Our main hypothesis is that these changes could be related to the consequences of climate change. Seawater temperature recorded on the same site, over a period of 32 years, shows a significant increase of the number of marine heat waves (MHWs) per year, especially since 2008. In addition, the study of the temperature changes along depth showed fewer and shorter MHWs in deep waters. Disturbance levels observed in these two gorgonian species (shift in population structure, temporal development of necrosis) are discussed in relation to past and present human-induced threats. The quantitative information obtained in this study provides a data baseline precious for future long-term monitoring, appearing as particularly relevant in a context of climate change.

## 1. Introduction

Mediterranean coralligenous assemblage is defined as a complex biogenic structure mainly produced by the accumulation of encrusting algae developing on hard substrates under dim light conditions (Ballesteros, 2006). This mediterranean habitat extends mainly from 20 to 130 m depth (Bellan-Santini and Poizat, 1994; Bensettiti et al., 2004). According to the typology of Mediterranean benthic biocenoses of the Barcelona Convention, 5 facies are referenced for coralligenous assemblage: facies with *Eunicella cavolini*, facies with *Eunicella singularis*, facies with *Leptogorgia sarmentosa*, facies with *Paramuricea clavata* and facies with *Parazoanthus axinellae* (Michez et al., 2014). Gorgonian forests are one of the most emblematic marine communities of the Mediterranean Sea, associated with coral assemblages, they constitute the second spot of high biodiversity in the coastal zone after *Posidonia oceanica* meadows (Gibson et al., 2006). Furthermore, due to their structural complexity and their beauty, gorgonian forests are among the most attractive seascapes for scuba divers (Chimienti et al., 2017).

The red gorgonian *Paramuricea clavata* and the yellow gorgonian *Eunicella cavolini* are key species in the shallow Mediterranean benthic ecosystem. They contribute to creating complex habitats that can provide shelter for other organisms. They grow to form dense forests enhancing the morphological seascape complexity structuring the habitat and favouring the maintenance of species richness (Ponti et al.,

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2018; Ponti et al., 2016; Rossi et al., 2017). In addition, these gorgonian species act like engineering species by modifying locally the circulation of currents, the rate of sedimentation and the level of shade (Cerrano et al., 2010; Gili and Coma, 1998). These temperate species live between 4 m and 220 m for *E. cavolini* and between 15 and 105 m for *P. clavata* in locations characterized by strong currents (Di et al., 2018; Gori et al., 2011; Michez et al., 2014; Sini et al., 2015). Like many coral species, mediterranean gorgonians are long-lived species with low growth rate (~1.8 cm $y^{-1}$), late maturity (~13 years), low recruitment (mean of 1.9 ind.$m^{-2}$) and low post-settlement survival rates (Coma et al., 2001; Coma et al., 1998; Garrabou and Harmelin, 2002; Linares et al., 2007; Torrents et al., 2008). These characteristics make them particularly vulnerable to both global and local threats.

Among the 136 species of anthozoans present in the Mediterranean Sea (gorgonians included), 13% are threatened with extinction (Otero et al., 2017). Under the regional Mediterranean Red List (version 3.1) provided by the International Union for Conservation of Nature (IUCN), *P. clavata* is listed as Vulnerable. *E. cavolini* is classified as Near Threatened, reflecting concern that they are close to qualifying for a threatened category and that they may do so in a near future (Otero et al., 2017). While direct contact (fin stroke or net pulling) can lead to localized damage of gorgonians (Bavestrello et al., 1997; Coma et al., 2004), biological invasions and mass mortality events (MME) linked to climate change may affect gorgonian populations at a larger scale (Cebrian et al., 2012; Cerrano et al., 2000; Garrabou et al., 2009, 2019).

Climate change induces a multitude of disturbances (*e.g.* increase in average temperature, rise in sea level, acidification of the oceans), including an increase in frequencies and intensities of extreme climatic events such as storms, floods and heat waves - a prolonged period when temperatures are abnormally higher than normal - (IPCC, 2013; Oliver et al., 2018; Perkins et al., 2012). Heat waves can affect both terrestrial and marine ecosystems (Gugliotti et al., 2019; Halpern et al., 2008; Jentsch et al., 2007; Smith, 2011). According to atmospheric conventions, a marine heat wave (MHW) is a "prolonged discrete anomalously warm water event that can be described by its duration, intensity, rate of evolution, and spatial extent" (Hobday et al., 2016) and has a strong effect on marine ecosystem structure and functioning (Caputi et al., 2016; Rose et al., 2012; Rubio-Portillo et al., 2016; Smale et al., 2019; Thomsen et al., 2019). As an example, in the Mediterranean Sea, in 2003, a MHW led to increased mortality of *Posidonia oceanica* shoot (Marbà and Duarte, 2010) and benthic invertebrates including gorgonians (Garrabou et al., 2009, 2019).

To date, most of the studies focusing on gorgonian populations have been carried out over short periods (few months), generally after mass mortality events (Cerrano et al., 2000; Garrabou et al., 2009; Gugliotti et al., 2019). Thus, if immediate effects of climatic events on these species are well known, like the increase in the frequency and intensity of disease and mortality and disease (Garrabou et al., 2009, 2019; Marbà et al., 2015; Rivetti et al., 2014; Rubio-Portillo et al., 2016), medium and long-term effects are less documented (Verdura et al., 2019). However, the Action Plan for the conservation of the corals and other calcareous bio-concretions in the Mediterranean Sea (formulated by UNEP-MAP-SPA / RAC (2017)) recommends long-term monitoring (*i.e.* decades) to have a better understanding of sessile benthic community trend. The Action Plan also highlights the need to incorporate in this monitoring the measurement of environmental parameters to better associate populational changes with the hydrographic conditions. Thus, regular monitoring of gorgonian populations appears as essential not only to assess their conservation status and detect impacts due to continuous and/or temporary changes but also to implement and evaluate the effectiveness of management plans. Moreover, due to their characteristics and their sensitivity to disturbances and increasing stresses, gorgonians have been proposed as indicators of the effects of climatic anomalies on the entire coralligenous community (Deter et al., 2012; Linares et al., 2008a). Finally, monitoring of coralligenous reefs is required for the implementation of European Marine Strategy Framework Directive (MSFD 2008/56/EC) and the Barcelona Convention Decision seeking to maintain the Good Environmental Status of assemblages.

To this purpose, this paper describes 3 years of monitoring over fifteen years (2004, 2014 and 2019) of demographic characteristics of two key gorgonian species *P. clavata* and *E. cavolini* regarding climate change. The aims of this study were: (i) to quantify the abundance and health status of gorgonians at different depths (ii) to appraise their population size structure and (iii) to gain insight into the possible factors affecting their health status with monitoring biotic (chl *a* and zooplankton) and abiotic (sea surface temperature and marine heat waves) parameters.

## 2. Materiel and methods

### 2.1. Sampling design

#### 2.1.1. Sampling site

The study was conducted in the Calvi Bay (Corsica, France). It is an oligotrophic area (Gazeau et al., 2016) which is considered as an unpolluted reference site for the northwestern Mediterranean Sea (Gobert and Richir, 2019). The Gulf of Calvi has an area of about 22 $km^2$, opens to the Ligurian Sea on the northeast with a border of about 6 km and connects to the deep sea by a canyon.

Measurements of the size and necrosis of *E. cavolini* and *P. clavata* were carried out in the Gulf of Calvi, more particularly, on the Revellata cape site (42.585046 N, 8.7273076 E). It is located inside a classified Natura 2000 zone (FR9400574; FR9402018) and was considered as a reference zone with high species biodiversity. There are rich natural areas, characterized by the presence of coralligenous and infralittoral rocks with photophilic algae. *Eunicella cavolini* and *Paramuricea clavata* colonized the deeper slopes and overhangs, which made this zone rich and attractive to dive.

#### 2.1.2. Environmental data

Environmental parameters (temperature, chlorophyll *a* concentration and zooplankton abundance) were measured and sampled from the oceanographic station STARESO (Goffart et al., 2015; Fullgrabe et al., 2020), <500 m from the gorgonian sampling site (Revellata cape site).

Sea Surface Temperature (SST in °C) was continuously recorded at 3 m depth since 1987. In addition, since 2015, Sea Water Temperature (SWT) was measured continuously at 10 m, 20 m, 29 m and 36 m depth with data loggers (HOBO Pendant Temperature/Light Data Logger, model UA-002-64), with an acquisition time interval of 10 min.

Chlorophyll *a* concentration (noted chl *a*, in $\mu g.L^{-1}$) as proxy of phytoplankton biomass, and zooplankton abundance (ind.$m^{-3}$) were measured weekly since 2004 (Fullgrabe et al., 2020). Chl *a* samples were collected at 1 m depth in 1 L dark bottles, immediately filtered through a glass fiber filter (Whatman GF/F 25 mm), and stored at −20 °C until analysis. Chl *a* was then extracted from filters in 90% methanol from 2004 to 2016 and in 90% acetone from 2017 to 2019, disrupted using an IKA™ ultra-turrax™, and incubated at 4 °C overnight. Chl *a* concentrations were measured by HPLC-fluorescence detection from 2004 to 2016 (Goffart et al., 2015; Zapata et al., 2000) and by fluorimetry from 2017 to 2019 (Aminot and Kérouel, 2004).

Zooplankton were sampled and analyzed according to the methods described in Fullgrabe et al. (2020). Subsurface horizontal hauls were performed using a WP2 net of 200 μm mesh size with a 60 cm opening diameter. Concentrated samples were then preserved in 4% buffered formaldehyde solution and stored in 200 mL polyethylene terephthalate vials in the dark at room temperature until analysis. Zooplankton were identified and counted by digitizing the samples using a Zooscan with the open-source software Zoo/PhytoImage (Grosjean and Denis, 2014). Among the numerous taxa identified, three groups (eggs, nauplii and copepod) were selected because they are potential food sources for the studied species *E. cavolini* and *P. clavata* (Coma et al., 1994; Topçu et al.,

2019). Eggs, nauplii and copepod (from Fullgabre et al., 2020) are all named "zooplankton" in this study.

#### 2.1.3. Survey on gorgonians

The red gorgonian *P. clavata* and the yellow gorgonian *E. cavolini* dominate sessile benthic community of the studied area. These two species have been selected for long-term monitoring because they form typical Mediterranean facies of coralligenous reef (Michez et al., 2014; Sini et al., 2019; Sini et al., 2015), they are key species of this habitat (Crisci et al., 2011; Gili and Ballesteros, 1991; Michez et al., 2014; True, 1970) and they are good bioindicators for coralligenous assemblages monitoring (García-Gómez et al., 2020). Scientific literature already exists as they were among the most affected species during the Mass Mortality Events (MME) (Crisci et al., 2011; Garrabou et al., 2009, 2019). Furthermore, other macrobenthic species affected by MMEs showed inter-annual pattern of mortality similar to *E. cavolini* et *P. clavata*, so that the patterns observed for these species might be considered representative of the MMEs impacts for other organisms as well (Crisci et al., 2011; Garrabou et al., 2009; Perez et al., 2000).

This study is based exclusively on non-destructive methods, by means of visual inspections. *In situ* underwater gorgonian surveys were conducted within the upper distribution depth range of the species (< 40 m), according to four bathymetric layers (0-10 m, 10–20 m, 20–30 m and 30–40 m). Data for each species were collected in June in 2004, 2014 and 2019. The measurements were always made on the same vertical cliffs (8 in total) where all the colonies present were sampled in the same delimited zones. For technical reasons, data were not collected in 2019, in the 30–40 m bathymetric layer. In total, for the three years of sampling, the different measurements were done on 1537 individuals (1037 for *E. cavolini* and 500 for *P. clavata)*.

For the assessment of the main population characteristics, we followed the protocol proposed by Harmelin et al. (1999): colonies height (in cm), proportion of injured surface (in %), type of injury and the proportion of healthy colonies (in %) were chosen as the main population descriptors. The measurements were carried out on each colony and were distinguished according to the bathymetric layer described above. For each colony, "colony height" is the distance from the colony base to the tip of the furthest apical branch. The results were grouped in six size classes: [0–10 cm(, [10–20 cm(, [20–30 cm(, [30–40 cm(, [40–50 cm (and > 50 cm. The proportion of necrosis surface is estimated by evaluating the proportion of the total surface of the colony which appears denuded (no more coenchymal tissue) and/or recolonized by epibionts (Harmelin et al., 1999; Linares et al., 2005). Proportion of necrosis surface are classified according to seven levels: 0%, < 10%, [10–25%(, [25–50%(, [50–75%(, [75–99%] and 100% (dead colony). Types of necrosis are determined by the presence / absence of epibionts on necrotic parts. The greater the development of epibionts, the older the necrosis. The epibiont species observed allows us to estimate an approximate date for the necrosis. Three types of necrosis are identified, type A: a branch or piece of branch which is denuded but not recolonized, which indicates very recent necrosis (<1 month); type B: a necrotic part of the gorgonian where pioneer species of epibionts (filamentous algae, hydrozoans) are observed which indicates a relatively recent necrosis (1–12 month) and finally type C: important recolonization by epibionts of the necrotic parts, with species whose development time is longer such as bryozoans, sponges, algae, which reflects an old necrosis (> 12 months) (Harmelin et al., 1999; Linares et al., 2005). The proportion of healthy colonies is described according to proportion of necrosis surface: colonies are considered "healthy" for an injured surface lower than 10%, they are "affected" for an injured surface between 10 and 99%, and "dead" for a 100% (Garrabou et al., 2009; Linares et al., 2008a).

### 2.2. Data analysis

Data treatments, plots and statistical analyses were done using R version 3.5.3 (R Core Team, 2018).

#### 2.2.1. Marine heat waves

For all Sea Water Temperature (SWT) time series, Marine Heat Waves (MHW) were characterized with the R package heatwaveR. This package allows to calculate and display MHW according to the definition of Hobday et al. (2016) who defines a MHW as an anomalously warm event lasting at least five days, with temperatures warmer than the 90th percentile based on a baseline period. It also contains the functionality to calculate the categories of MHWs as outlined in (Hobday et al., 2018).

For each depth, three descriptors have been selected to characterize the MHW: the number of MHW per year, the average duration (in days) of the MHW per year and the mean intensity (in °C) of MHW. The intensity of MHW is defined as the temperature above the climatological mean, so the mean intensity during a MHW is the mean of daily intensities during the MHW (Hobday et al., 2016).

These three descriptors were separately analyzed using Generalized Linear Model (GLM) (function glm from the R package stats) with the two explanatory variables "Depth" and "Year". We used a Poisson distribution (log link function) to analyze the heat wave incidence numbers and a Gamma distribution (inverse link function) for the heat wave intensity. To analyze the heat wave duration, we used a quasi-Poisson distribution (log link function).

#### 2.2.2. Environmental variables decomposition

To determine the general trend of the SST, chl *a* concentration and zooplankton abundance over time, each time series was weekly regularized using the R function regul from the package pastecs, and decomposed into seasonal, trend and irregular components using a moving average (function decompose from the R package stats). The general trend of each time series was then extracted, and smoothed (function smooth from package castr) to only detect important variations over the years of the time series slopes, named breakpoints hereafter (function segmented from the package segmented).

To determine the relationship between the trends of the time series SST, chl *a* and zooplankton, pairwise Granger-causality tests were performed (function grangertest from the R package lmtest) in order to understand if the time series x is predictive of the future values of the time series y.

#### 2.2.3. Gorgonian data

Two different Cumulative Link Models (CLM) for ordinal data (function clm from ordinal R package) (Christensen, 2019) were used to statistically test the effect of "Depth", "Year" (three levels, 2004, 2014 and 2019) and gorgonian's height (as an ordinal factor with six size-classes 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm and > 50 cm) on degree of gorgonian's necrosis (as an ordinal factor with seven levels of necrosis: 0, <10%, 10–25%, 25–50%, 50–75%, >75%, 100%). The effect of "Depth" and "Year" have also been tested on gorgonian's height.

Model selection for CLMs and GLMs was done using automatic stepwise selection with the Akaike's Information Criteria (AIC). For model validation of CLMs and GLMs, we visually inspected residuals and tested the significance of predictors using type II deviance test, implemented in the Anova function of R package car (Fox and Weisberg, 2011). *Post hoc* comparisons were made using Estimated Marginal Means method (EMMeans). A probability level inferior to 0.05 was accepted as significant.

In addition, size structure of gorgonian populations was analyzed in terms of descriptive statistics using distribution parameters such as skewness and kurtosis. Skewness is a measure of the symmetry of a distribution using its mean, reflecting the proportion of small *versus* large colonies in a gorgonian population. If skewness is significant ($p < 0.05$) population size structure is asymmetrical. Positive skewness denotes the prevalence of small size colonies, while negative skewness

denotes the dominance of large size colonies in the population. Kurtosis is a measure of the peakedness of a distribution near its central mode. A significant kurtosis value ($p < 0.05$) indicates longer tails than would be expected for a normal distribution, and therefore a particular colony size prevails in the population. Skewness and kurtosis were calculated by means of the r-language functions agostino.test (Komsta and Novomestky, 2015) and anscombe.test (Anscombe and Glynn, 1983), which are available in the moments library of the R software platform.

## 3. Results

### 3.1. Marine heat waves

#### 3.1.1. Temporal trend of marine heat waves

The number of MHWs significantly increased (GLM-ANOVA, p value $\leq 0.0188$) during the 33-year long period (1987–2019) especially from 2008 onwards reaching a maximum of six MHW in 2017 (Fig. 1). Over the period 2005–2019 (15 years), 36 MHWs were measured with a total of 488 cumulative days, while 25 MHWs were estimated for the period 1987–2004 (18 years) and a total of 329 cumulative days. On the other hand, the average MHWs duration and intensity did not show a significant increase or decrease (Fig. 1).

#### 3.1.2. Influence of depth on MHW

During the 2015–2019 investigated period, depth influences significantly the variables "count" and "duration" (GLM-ANOVA, p value = 0.009 and p value = 0.008) (Fig. 2). As expected, there are fewer and shorter MHWs with depth. Indeed, the average number of MHWs was 4.40 ± 1.52 MHW at 3 m, two-fold lower at 20 m with 2.20 ± 1.79 MHWs and even lower at 36 m with 1.80 ± 0.84 MHWs. The same pattern is observed for the average duration with 14.45 ± 5.32 days at 3 m, 8.29 ± 2.08 days at 10 m and 7.40 ± 2.88 at 36 m depth (Table 1). Over these five years (2015–2019), all depths combined, no significant variation is noted in overall MHW occurrence (Table 2).

### 3.2. SST, chl a and zooplankton relationships

Between 2004 and 2010, SST significantly decreased by about 1 °C but shows a continuous increase from 2010 to 2019 (Fig. 3). These SST variations are significantly correlated with the chl *a* and zooplankton variations (Granger test, p values <0.05), which significantly decrease since 2012 for chl *a*, and since 2009 for zooplankton, excepted in 2012–2013 where a significant increase was observed for zooplankton, potentially because of a particularly cold winter not identified as a significant breakpoint in the SST trend. The Granger test did not identify a significant relationship between chl *a* and zooplankton trends.

### 3.3. Gorgonians

#### 3.3.1. Temporal trend on population structure in relation to depth

*E. cavolini* shows a similar number of colonies between 2004 and 2019 (n = 414 in 2004 and n = 428 in 2019) with a modification of the bathymetric distribution (Fig. 4). In 2004, no significant differences (EMMeans post-hoc comparison test, p value >0.05) are observed in population size structure between 0 and 10 m, 10–20 m and 20–30 m. However, the proportion of taller individuals (> 30 cm) of *E. cavolini* was significantly higher at 30–40 m than at 10–20 m (EMMeans post-hoc comparison test, p value <0.001; 8% and 1% respectively; Fig. 4), while none were observed at 0–10 m. In 2014, gorgonians were larger at 10–20 m and 20–30 m compared to the 0–10 m bathymetric layer (EMMeans post-hoc comparison test, p value = 0.0302 and p value = 0.0422, respectively). No colonies of *E. cavolini* has been censused between 30 and 40 m, contrary to 2004. In 2019, no colonies of *E. cavolini* has been censused between 0 and 10 m. Gorgonians were significantly taller at 20–30 m than at 10–20 m (EMMeans post-hoc comparison test, p value = 0.0391).

Concerning *P. clavata*, this species shows a decrease in the number of colonies between 2004 and 2019 (n = 351 in 2004, *n* = 104 in 2014 and n = 45 in 2019). In addition, no colonies were recorded between 0 and

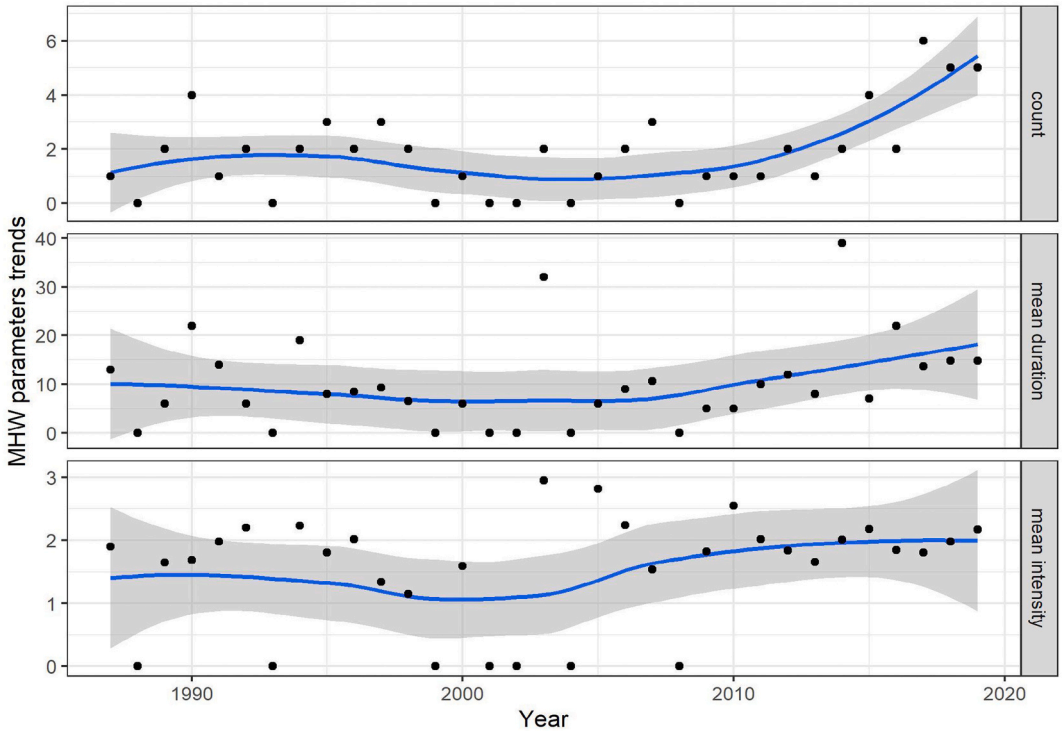


**Fig. 1.** MHWs temporal evolutions at 3 m depth, between 1987 and 2019. From top to bottom: MHWs number for each year (counts), mean MHWs duration for each year (in days), mean MHWs intensity per year (in C°). Blue line represents a LOcally Estimated Scatterplot Smoothing (LOESS) regression, shaded area is the zone that covers 95% confidence level of LOESS regression. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

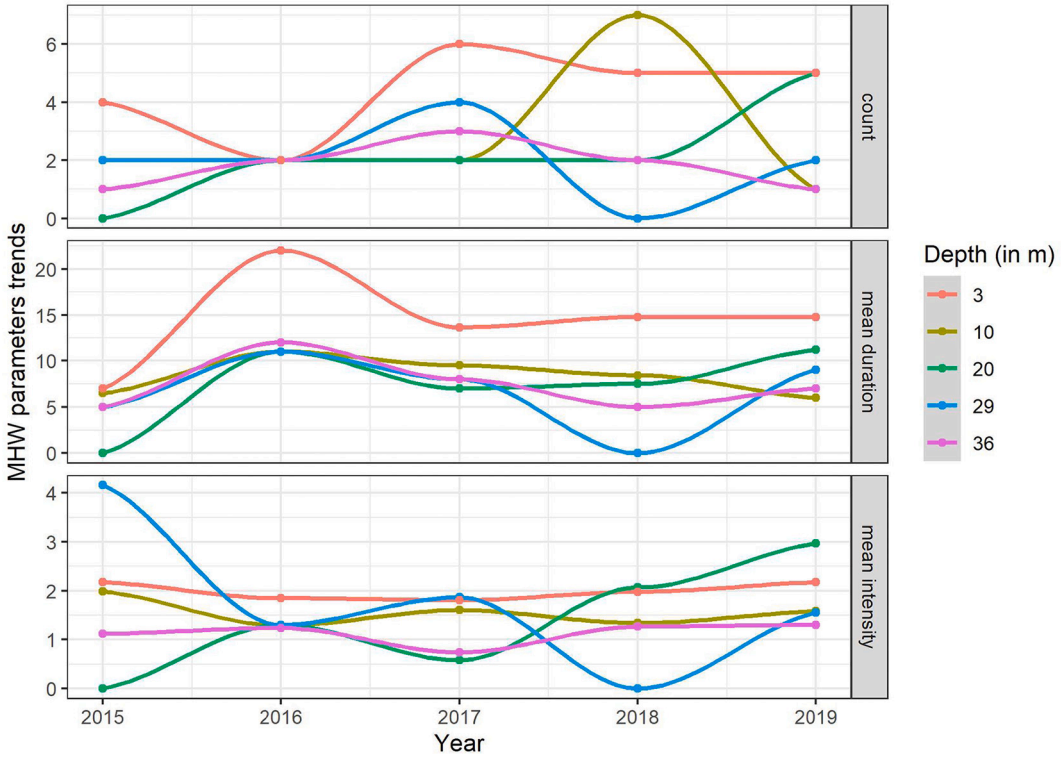


**Fig. 2.** MHWs temporal evolutions, between 2015 and 2019, at 3 (red), 10 (yellow), 20 (green), 29 (blue) and 36 (purple) m. From top to bottom: MHWs number for each year (counts), average MHWs duration for each year (in days), and average MHWs intensity for each year (in °C). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**
Means of the MHW descriptors by depth, all years combined for the period 2015–2019. For each parameter, a red intensity gradient is applied (dark red to light red: high parameter value to low parameter value). Duration is in days and intensity in °C.

| | Subsurface | 10 m | 20 m | 29 m | 36 m |
|---|---|---|---|---|---|
| Count | 4.40 | 2.80 | 2.20 | 2.00 | 1.80 |
| Duration | 14.45 | 8.29 | 7.34 | 6.60 | 7.40 |
| Intensity | 2.00 | 1.56 | 1.38 | 1.78 | 1.13 |

**Table 2**
Means of MHW descriptors by year between 2015 and 2019, all depths combined. For each parameter, a red intensity gradient is applied (dark red to light red: high parameter value to low parameter value). Duration is in days and intensity in °C.

| | 2015 | 2016 | 2017 | 2018 | 2019 |
|---|---|---|---|---|---|
| Count | 2.00 | 2.00 | 3.40 | 3.20 | 2.80 |
| Duration | 4.63 | 13.40 | 9.23 | 7.15 | 9.60 |
| Intensity | 2.08 | 1.40 | 1.32 | 1.33 | 1.91 |

10 m, in accordance with the typical lower bathymetric distribution observed for this species. However, individuals between 10 and 20 m observed in 2004 were not found in 2014 and in 2019. Overall, the population structure of *P. clavata* changes with depth with larger individuals mainly observed in deeper waters (Fig. 5). In 2004, the 10–20 m bathymetric layer was characterized by small individuals with 64% of the colonies being in the 0–10 cm size class, and 36% in the 10–20 cm size class. Very large individuals (> 40 cm) were mainly observed at 30–40 m and represent 18% of the population at this depth range.

Over the time, *E. cavolini* and *P. clavata* population structures have shifted with a dominance of medium-sized individuals in 2014 and 2019, compared to small-sized individuals in 2004 (p value <0.0001; Table 3). Indeed, in 2004, 57% and 44% of *E. cavolini* and *P. clavata* colonies were characterized by small individuals (0–10 cm) compared to 24% and 7% in 2014, and to 27% and 2% in 2019, respectively.

Skewness coefficients in *E. cavolini* indicate that all size distributions

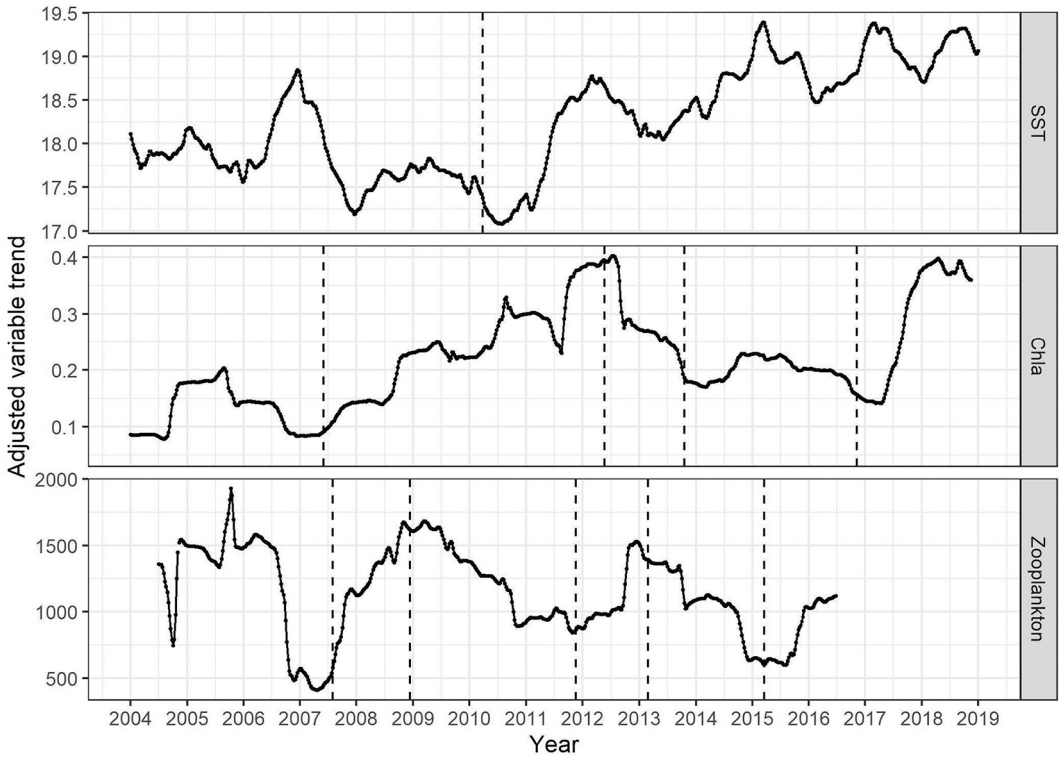


**Fig. 3.** General trends of the SST (in °C), chlorophyll *a* concentration (Chl *a*, in µg.L$^{-1}$) time series between 2004 and 2019 and zooplankton abundance (ind.m$^{-3}$) time series between 2004 and 2016. Dashed points are the significant breakpoints identified over time (p-values <0.05).

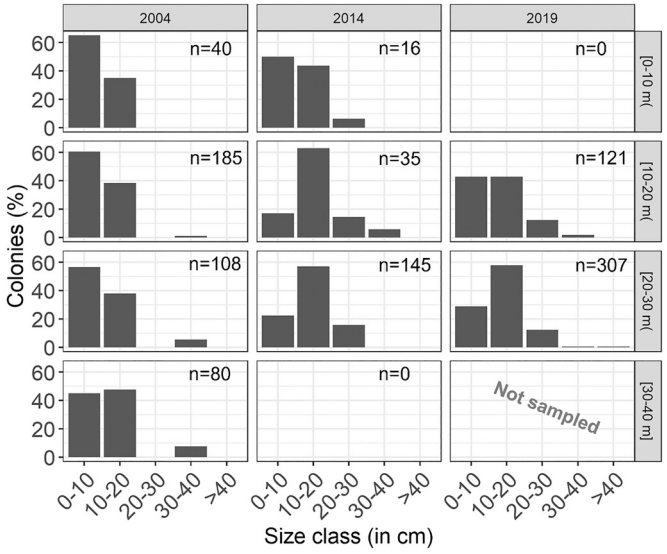


**Fig. 4.** Temporal variation of the proportion of *E. cavolini* in the different size classes (cm) in 2004, 2014 and 2019, in each bathymetric layer (0–10 m, 10–20 m, 20–30 m and 30–40 m).

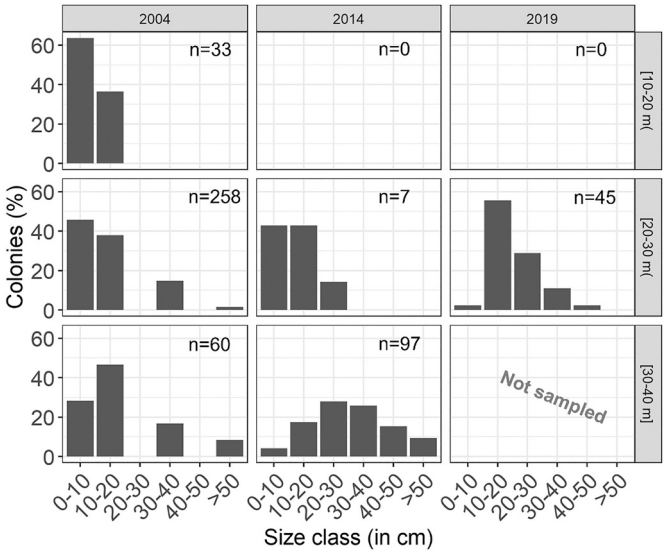


**Fig. 5.** Temporal variation of the proportion of *P. clavata* in the different size classes (cm) in 2004, 2014 and 2019, in each bathymetric layer (10–20 m, 20–30 m and 30–40 m).

were positively skewed in 2004, for all bathymetric ranges. In 2014, only gorgonians present between 0 and 10 m show a positive skewness, in contrast to 2019 where gorgonians at 10–20 m and 20–30 m are positively skewed (Table 3). These positive skewness result in a large proportion of smaller colonies (< 10 cm and 10–20 cm) and a decrease in the proportion of larger size classes.

For *P. clavata*, gorgonians present between 20 m and 40 m show positive skewness in 2004 with a predominance of gorgonians of 0–10 cm. In 2019, skewness coefficient indicates that size distributions of 20–30 m were positively skewed, with a predominance of gorgonians of 10–20 cm. In 2004 and 2019 both *E. cavolinia* and *P. clavata* populations displayed positive excess kurtosis (>3) since the distribution has a sharper peak (Table 3).

### 3.3.2. Temporal trend of gorgonian necrosis

Regarding the *E.cavolini* population, the colony's necroses remained quite stable between 2004 and 2014 with <10% of injured colonies (Table 4). However, in 2014, necrosis seems to be getting worse as 5% of

**Table 3**
Characteristics of studied *Eunicella cavolini* and *Paramuricea clavata* populations (year, depth, number of gorgonians (n)) and distribution parameters (skewness and kurtosis). Significance (Sig.) with ns: p > 0.05, *: p < 0.05, **: p < 0.01, ***: p < 0.001.

| *Eunicella cavolini* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Year | Depth | n = | Skew | p value | Sig. | Kurtosis | p value | Sig. |
| 2004 | 0–10 m | 40 | 1.22036 | < 2.2e-16 | *** | 4.755044 | 1.00e-05 | *** |
| | 10–20 m | 185 | 0.45455 | 0.01207 | * | 1.206613 | 0.0223 | * |
| | 20–30 m | 108 | 1.370832 | 1.02e-06 | *** | 4.737 | 0.00711 | ** |
| | 30–40 m | 80 | 1.081364 | 0.000283 | *** | 4.000516 | 0.0708 | ns |
| 2014 | 0–10 m | 16 | 1.240295 | 0.0198 | * | 3.973412 | 0.1199 | ns |
| | 10–20 m | 35 | 0.628746 | 0.0964 | ns | 2.95506 | 0.676 | ns |
| | 20–30 m | 145 | −0.09046 | 0.6423 | ns | 2.497775 | 0.1565 | ns |
| | 30–40 m | 0 | No observation | | | | | |
| 2019 | 0–10 m | 0 | No observation | | | | | |
| | 10–20 m | 121 | 1.193432 | 3.30e-06 | *** | 4.87025 | 0.003718 | ** |
| | 20–30 m | 307 | 2.28 | < 2.2e-16 | *** | 20.16622 | < 2.2e-16 | *** |
| | 30–40 m | No sampled | | | | | | |
| *Paramuricea clavata* | | | | | | | | |
| Year | Depth | n = | Skew | p-value | Sig. | Kurtosis | p-value | Sig. |
| 2004 | 0–10 m | 0 | No observation | | | | | |
| | 10–20 m | 33 | 0.56695 | 0.1391 | ns | 1.3214 | 1.88E-10 | *** |
| | 20–30 m | 258 | 1.7237 | < 2.2e-16 | *** | 7.4263 | 1.00E-08 | *** |
| | 30–40 m | 60 | 1.6492 | 1.18E-05 | *** | 5.8253 | 0.003068 | ** |
| 2014 | 0–10 m | 0 | No observation | | | | | |
| | 10–20 m | 0 | No observation | | | | | |
| | 20–30 m | 7 | | Not enough obs. | | 2.975192 | 0.261 | ns |
| | 30–40 m | 97 | 0.067984 | 0.7709 | ns | 2.2842 | 0.05203 | ns |
| 2019 | 0–10 m | 0 | No observation | | | | | |
| | 10–20 m | 0 | No observation | | | | | |
| | 20–30 m | 45 | 1.3005 | 0.000844 | *** | 5.0537 | 0.01701 | * |
| | 30–40 m | No sampled | | | | | | |

**Table 4**
Summary of the proportions of the colony injury extent (in %). Proportions of uninjured (<10% of necrosis tissue), injured (10–99% of necrosis tissue) and dead (100% of necrosis tissue) colonies and proportions of colonies per type of injury, for *E. cavolini* and *P. clavata*, in 2004, 2014 and 2019.

| Year | | 2004 | | 2014 | | 2019 | |
|---|---|---|---|---|---|---|---|
| Species | | *E. cavolini* | *P. clavata* | *E. cavolini* | *P. clavata* | *E. cavolini* | *P. clavata* |
| n | | 413 | 351 | 196 | 104 | 428 | 45 |
| Extent of colony injury (%) | Mean | 4.53 | 25.64 | 9.35 | 13.44 | 16.20 | 14.06 |
| | sd | 11.65 | 38.34 | 23.96 | 25.23 | 29.75 | 26.57 |
| Proportion of colonies by degree of injury | <10% | 90.10 | 63.53 | 85.71 | 74.04 | 69.73 | 71.11 |
| | 10–99% | 9.66 | 21.65 | 9.69 | 24.04 | 25.52 | 24.44 |
| | 100% | 0.24 | 14.81 | 4.59 | 1.92 | 4.75 | 4.44 |
| Proportion of colonies per type of injury (%) | A | 44.14 | 15.88 | 32.35 | 2.17 | 20.38 | 0.00 |
| | B | 29.66 | 37.06 | 33.82 | 43.48 | 14.23 | 20.00 |
| | C | 26.21 | 47.06 | 33.82 | 54.35 | 65.38 | 80.00 |

colonies are dead compared to 0.2% in 2004. In 2019, necrosis surface is significantly higher than in 2004 and 2014 (EMMeans post-hoc comparison test, p value <0.001 for both) with 26% of colonies presenting necrosis surface >10% and 5% of dead, fully necrotic colonies (Table 4 and Fig. 6).

In 2004, 44% of the necrosis can be considered as recent (type A) while old necrosis (type C) represents only 26%. The trend reverses over time, with 20% of type A necrosis and 65% of type C in 2019 (Table 4).

Regarding the *P. clavata* population, the proportion of necrosis surface is significantly higher in 2004 with 15% of dead colonies, compared to 2014 with 2% (EMMeans post-hoc comparison test, p value <0.001). In 2019, necrosis increases and affects 24% of individuals with 4% of dead individuals. Without reaching the same level of necrosis as in 2004, necrosis observed in 2019 is still significantly higher than values in 2014 (EMMeans post-hoc comparison test, p value = 0.0172) with 24% of injured colonies and only 2% of dead colonies (Fig. 7 and Table 4).

Regarding necrosis dating, recent necrosis decreases over time with 16% in 2004, 2% in 2014 and no recent necrosis observed in 2019. On the other hand, old necrosis (type C) increased from 47% in 2004 to 80% in 2019 (Table 4).

### 3.3.3. Necrosis and/or mortality of colonies in relation to depth

For *E. cavolini*, while proportion of dead colonies is greatest in the shallowest layer (11%), proportion of damaged colonies (> 10% necrosis surface) is greatest in the 10–20 m bathymetric layer (24.73%). Between 10 and 20 m, colonies are significantly more damaged compared to 20–30 m and 30–40 m bathymetric layers (EMMeans post-hoc comparison test, p value <0.0001 and p value = 0.0081, respectively). At 20–30 m and 30–40 m, the population is dominated by healthy colonies with respectively 81% and 93% of healthy colonies and only 3% of dead colonies at 20–30 m and none dead colony at 30–40 m (Fig. 6).

Regarding *P. clavata*, the opposite is observed with deepest colonies being the most damaged. Between 10 and 20 m, 9% of sampled colonies are affected by necrosis (necrosis surface between 10 and 99%) against 21% and 28% for colonies at 20–30 and 30–40 m, respectively (EMMeans post-hoc comparison test, p value = 0.0273 and p value = 0.0001, respectively). Between 10 and 20 m, no colony showed 100% necrosis while 11% and 13% of individuals were fully necrotic for 20–30 m and 30–40 m bathymetric layers. No individuals of *P. clavata* were observed in the 0–10 m layer (Fig. 7).

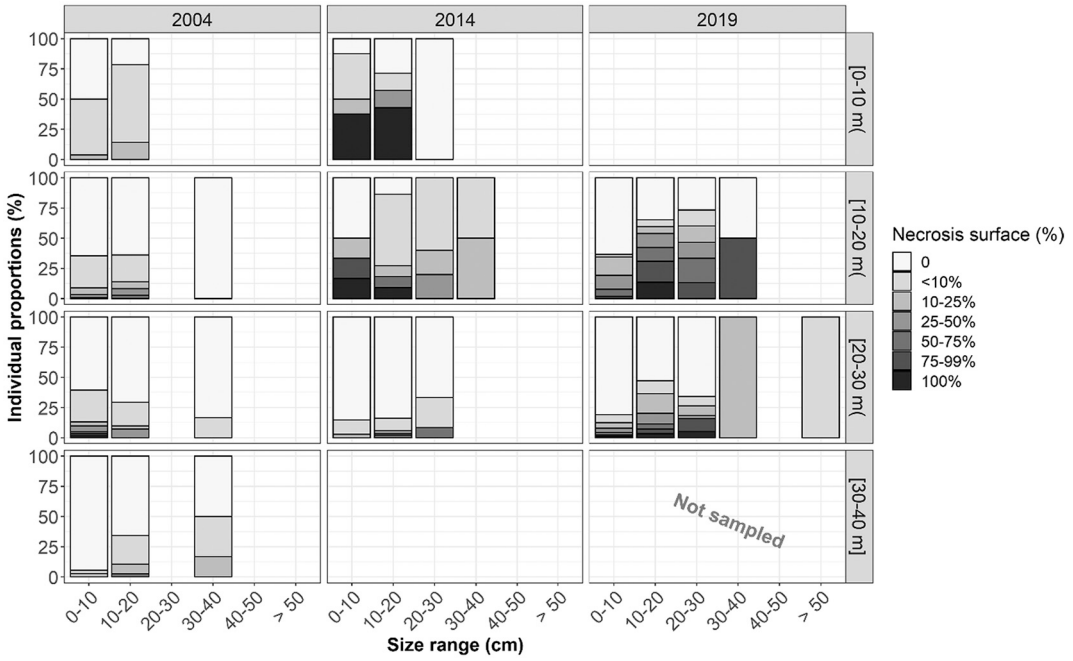


**Fig. 6.** Temporal variation of the proportion of *E. cavolini* with different proportion of necrosis surface (in %) in the six size classes (cm) in 2004, 2014 and 2019.

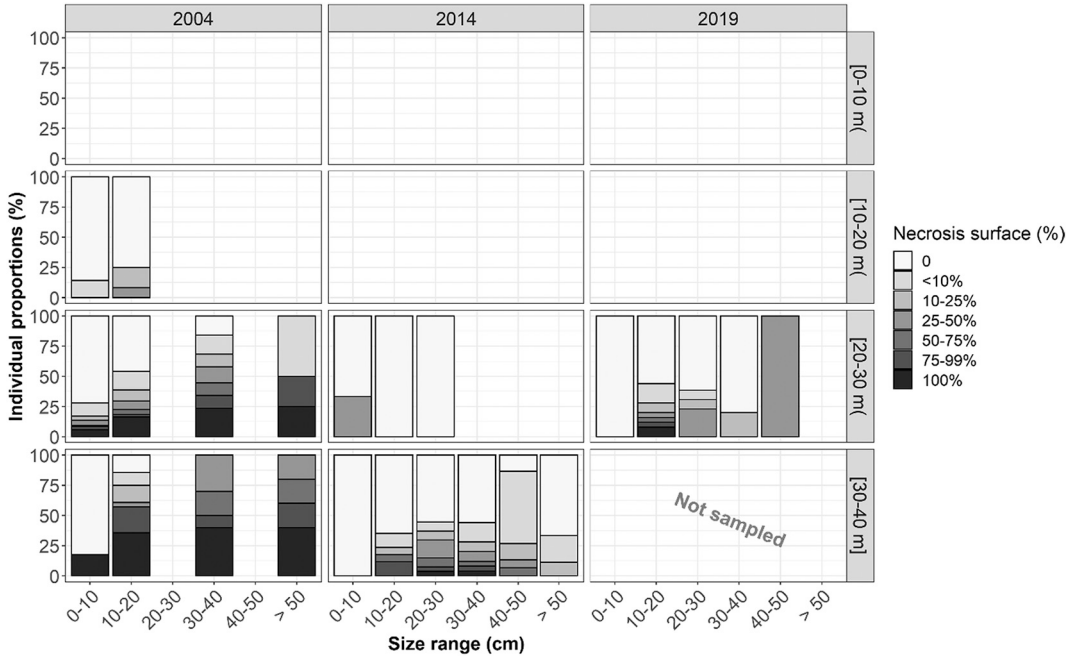


**Fig. 7.** Temporal variation of the proportion of *P. clavata* necrosis surface (in %) in the different size classes (cm) in 2004, 2014 and 2019.

### *3.3.4. Gorgonian size-classes affected by necrosis and/or mortality*

Regarding *E. cavolini*, all years and depths combined, necrosis surface is significantly higher on medium size individuals, 10–20 cm and 20–30 cm, with >20% of colonies affected by partial necrosis, against 12% for 0–10 cm colonies (EMMeans post-hoc comparison test, p value <0.0001 and p value =, 0.0321, respectively) (Fig. 6). On the other hand, there is no significant difference between the necrosis tissue of colonies of 0–10 cm and those of 30–40 cm. Indeed, colonies of 30–40 cm are more affected by necrosis with 27% damaged colonies but average necrosis surface is around 10–25%, lower than colonies of 10–20 cm and 20–30 cm. No colony was identified in size class 40–50 cm and only one colony larger than 50 cm was found and measured.

For *P. clavata*, the same observations as for *E. cavolini* can be made (Fig. 7). Necrosis surface is significantly higher on individuals of medium and large sizes (10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm and 50–75 cm) than on small colonies (0–10 cm) (EMMeans post-hoc comparison test, p value <0.0001, for all). Only 9% of individuals 0–10 cm are affected by necrosis and 6% are dead. In comparison, 30–40 cm gorgonians ($n$ = 78) have 38% damaged colonies and 18% dead colonies.

## 4. Discussion

### 4.1. Temporal evolution of marine heat waves and influence of depth

The Mediterranean Sea is an important climate change hotspot with a marked increase of surface temperatures (Bo et al., 2017; Diffenbaugh and Giorgi, 2012; IPCC, 2013; Lionello et al., 2014). It has been proven that global average sea surface temperatures (SSTs) have increased since the beginning of the 20th century (IPCC, 2013). In the Gulf of Calvi, mean monthly surface water temperature ranges from a minimum of 12.4 ± 0.3 °C in February to a maximum of 26.6 ± 0.6 °C in August (Gazeau et al., 2016). The water column is stratified between May and October, and well-mixed during the rest of the year. The mean depth of the thermocline is *ca.* 25–30 m. The depth of the warm layer and the temperature gradient depend on meteorological events (Gazeau et al., 2016). In this study, the recent temperature data (2015–2019) do not show a short-term change in the water column structure. At the different studied depths, no significant increase is observed between 2015 and 2019. On the other hand, according to subsurface temperatures recorded during the last 32 years (from 1987 to 2019), a significant increase in the frequency of extreme weather events and thermal anomalies were observed: MHWs are more numerous every year, even if their intensity and duration remain stable. Indeed, MHW frequency was found to increase by 44% and the annual cumulative duration of MHWs, which combines both high temperatures and duration, also increased by 50% from the 1987–2004 period to 2005–2019 period. In addition, MHW are detectable down to 36 m, even if their duration and intensity are less marked than at the subsurface.

In addition, a recent study has shown that MHWs frequency and mean duration increased by 34% and 17% between 1925 and 2016, respectively, these two factors combined led to a 54% increase in the total number of annual MHW days (Oliver et al., 2018). Unfortunately, forecasts predict a general increase in the frequency, duration, intensity, depth penetration and spatial scale of MHWs in the near future resulting in more and more impacts on the organisms with low or no mobility in shallow or relatively shallow waters (Galli et al., 2017; Rivetti et al., 2014).

So, on the one hand gorgonians are subjected to thermal stress, and on the other hand to energy stress because high temperatures induce a strong stratification of the water column, a low availability of resources but also a high respiratory demand of gorgonians (Ezzat et al., 2013; Previati et al., 2010).

### 4.2. Food availability

In addition to direct effects on gorgonian populations, MHWs frequency and SST increases also generate significant modifications of other biotic and abiotic factors that lead to an impoverishment in food availability for filter feeders. Indeed, periods of stratification of the upper water layers are increasing causing a surface depletion of dissolved nutrients (Cocito et al., 2013), which impacts on the development of phytoplankton (Thomas et al., 2012; Toseland et al., 2013) and zooplankton, by significantly decreasing their biomass. Yet, gorgonians feed on these broad planktonic groups. Although no significant relationship between phytoplankton and zooplankton was found in our study, it is accepted that a decrease in phytoplankton biomass actually leads to a decrease in zooplankton biomass through bottom-up trophic control (Behrenfeld and Boss, 2014). In addition, a recent study carried out in Calvi Bay on zooplankton communities over a 13-year time series showed a significant decline in zooplankton between 2004 and 2016 (Fullgrabe et al., 2020).

Gorgonians trophic ecology studies revealed that they feed on a wide range of Particulate Organic Matter (POM) from pico- and nanoplankton to microplankton (Coma et al., 1994; Coma and Ribes, 2003; Ribes et al., 1999). In fact, gorgonians can play a significant role in carbon and nitrogen cycles of the water column by capturing planktonic prey and filtering a large amount of POM and Dissolved Organic Matter (DOM), or by releasing mucus or other metabolic waste in the seawater (Gili and Coma, 1998; Wild et al., 2004). Like most anthozoans, they can also feed on organic matter contained in the resuspended sediment (Anthony and Fabricius, 2000; Mills and Sebens, 2004; Orejas et al., 2001). It has been shown that the isotopic signature of *P. clavata* is close to the one of Sediment Organic Matter (SOM) in summer and winter, periods during which SOM would represent about 75% of the diet of *P. clavata* (Cocito et al., 2013). Ribes et al. (1999) observed that diet of *P. clavata* is mainly related to detrital and live POM. Catch rate of POC and zooplankton is subject to seasonality, with increasing catch rates in winter and spring (Coma et al., 1994; Ribes et al., 1999). Several studies have shown that gorgonians exhibit low biological activity during the summer (*i.e.* non-reproductive investment, (Coma et al., 1995); low growth investment, (Coma et al., 1998); higher percentage of colonies with contracted polyps, (Coma et al., 1994)). The decline of gorgonian species activity in summer is, therefore, strongly linked to trophic energy limitations (Ribes et al., 1999). In addition, Coma et al. (2009) showed that gorgonians exposed *ex situ* to high temperatures with an ambient food treatment showed an 83% increase in partial mortality (development of damage tissue) after 49 days, while colonies exposed to high temperatures and a high food treatment exhibited a partial mortality of only 55% after 130 days. Furthermore, in this case, partial mortality was first observable after 84 days. Therefore, a high food intake would push back necrosis by about 45 days. The lengthening of summer conditions (high temperatures and vertical stratification of water column) combined with a decrease in food availability are all factors that directly threaten gorgonian populations. Indeed, food availability strongly affects ecology and physiology of coral and gorgonian species as well as their resistance to stressors (Gori et al., 2013). Colonies already weakened by a lack of food in the summer season are therefore less resistant to MHW and other disturbances of anthropogenic or natural origin.

### 4.3. Temporal trend of gorgonian populations

The two studied gorgonian species *E. cavolini* and *P. clavata* showed different evolutions in proportion of necrosis surface over time. In *E. cavolini* population, proportion of necrosis surface significantly increase since 2004. Moreover, shallow colonies (0–20 m) were more damaged than deeper ones. Previous studies have shown that, in laboratory conditions, *E. cavolini* colonies are highly thermotolerant, mainly those from the 0–20 m bathymetric layer (Fava et al., 2010; Pivotto et al., 2015). However, it has also been demonstrated that laboratory experimental results can, sometimes, differ from *in situ* thermotolerance levels (Pivotto et al., 2015). Populations would be more or less sensitive according to the period at which these temperature anomalies occur because of either abnormal climatic events repetition (like MHW) that exceeded their thermal tolerance, or because it can be coupled with food depletion which may weaken them further. Indeed, a longer stratification period can induce a reduced food availability (Doney, 2006; Sini et al., 2015; Smetacek and Cloern, 2008) with consequences on long-term viability for benthic suspension feeders.

For the red gorgonian *P. clavata*, proportion of necrosis tissue increased between 2014 and 2019. However, it did not reach the same degree as in 2004 when gorgonians were particularly affected by partial or total damage. In fact, in 2004, many colonies were entirely necrosed with highly developed epiphytes (type C necrosis). This suggests that necroses were at least one year old. This would correspond to the mass mortality event of benthic populations including gorgonians measured in 2003 throughout the Mediterranean Sea, where many colonies were affected by a temperature-dependent bacterium of genus *Vibrio* identified as being responsible for gorgonians disease (Bally and Garrabou, 2007; Garrabou et al., 2009; Vezzulli et al., 2010).

Our results indicate that deep colonies of *P. clavata* appear to be more impacted than the shallow ones. This trend is already observed for other species of gorgonians but mainly for symbiotic species of gorgonians

such as *Eunicella singularis* (Ferrier-Pagès et al., 2009). The red gorgonians present between 30 and 100 m are larger because the depth range corresponds to their ecological optimum. Moreover, for the two gorgonian species, colonies larger than 10 cm are more damaged than the small ones (<10 cm) which is consistent with results in other parts of the Mediterranean Sea (Cerrano et al., 2005; Linares et al., 2005) and seems to confirm that the sensitivity of colonies is strongly dependent on the size of the colonies: the larger, the more prone to necrosis. To explain this, several hypotheses have been proposed, including the fact that older colonies being more prone to parasite accumulation, are more likely to be partially damaged (Cerrano et al., 2005; Petes et al., 2003). In addition, Dube et al. (2002) show that small sea fans have more chemical defenses than large sea fans when they are attacked by pathogens. In particular, they point out that antifungal activity decreases with increasing colony age. Patterson (1992) suggests that small colonies may preferentially survive as they have a better mass-transfer capacity, whilst Hoegh-Guldberg (1999) reported enhanced protective capacity of their tissue. Finally, small colonies may have better resistance to disturbances due to a stronger metabolism and a greater production/biomass ratio (P/B) that decreases with age (Coma et al., 1994; Mistri and Ceccherelli, 1994; Weinbauer and Velimirov, 1995a). Similarly, different sensitivity among size classes have also been described for corals involved in bleaching events (Loya et al., 2001).

The loss of *E. cavolini* in the 0–10 m range, between 2014 and 2019, as well as the loss of *P. clavata* in the 10–20 m bathymetric layer, between 2004 and 2014, could be explained by the number and duration of heat waves being more important in these bathymetric layers, but also by the increase of storms in recent years (Jiménez et al., 2012) which can have negative consequences on certain benthic species up to 30 m (Gori et al., 2017; Navarro et al., 2011; Teixidó et al., 2013). However, this study does not confirm these hypotheses and it will be necessary to continue the monitoring on a regular basis in order to correlate, or not, the extreme climatic events to the observed changes.

### 4.4. Temporal trend of gorgonians size-classes distribution

Recruitment refers to the first age class in a population, includes the settlement and survival of settled individuals, and is influenced by events occurring during the planktonic stage and settlement processes, as well as post-settlement mortality (Bramanti et al., 2003; Keough and Downes, 1982). For both species individuals of <10 cm are considered to be non-breeding and recently established colonies (Coma et al., 1995; Linares et al., 2008a). The patterns of *P. clavata* and *E. cavolini* size distribution in this study may suggest a change in population dynamics and a potential disturbance in recruitment success.

*E. cavolini* population is always characterized by the predominance of small individuals (<10 cm and 10–20 cm) and few large colonies. This distribution is consistent with the observations carried out for numerous northwestern Mediterranean populations (Sini et al., 2015). While this could be explained by a recently formed or expanding population, our results also suggest that recruitment (proportion of individuals <10 cm) was halved between 2004 and 2019. Furthermore, the decrease in juvenile colonies (<10 cm) is also particularly marked for *P. clavata*, characterized by a mature population in 2019 (colonies >10 cm), but shows low recruitment.

Gorgonians are generally described as species with low population dynamics and low recruitment rates (Gotelli, 1988; Lasker, 1991; Linares et al., 2007), which recruitment success depends on several factors such as larval behavior, environmental factors (currents, temperature, food availability), substrate composition and the reproductive capacity of the population (Hughes et al., 2000; Kipson et al., 2015; Vermeij, 2005). Reproductive capacity is determined by fertility, sex ratio, size / age structure and density of each population (Coma et al., 1995; Santangelo et al., 2003). Polyp fecundity increases with age of colonies (Coma et al., 1995), sexual maturity being reached for individuals >20 cm, so that small colonies contribute little to reproductive capacity (Coma et al., 1995; Linares et al., 2008b). The results of this study show that large colonies, which are of capital importance for recolonization thanks to their important contribution to reproductive yield (Santangelo et al., 2015, 2003), are also the most damaged. Additionally, decreased fecundity of polyps appears to be common in recently impacted colonies (Michalek-Wagner and Willis, 2001), which can also lead to a decrease in recruitment in following years. In case of a damage at population level, recovery is mainly the result of recruitment by sexual reproduction, asexual reproduction being less common (Coma et al., 1995).

In general, the mortality rate of small colonies (< 10 cm) is higher than that of large colonies with changing environmental conditions (Coma et al., 2004; Coma et al., 2001). However, extraordinary climatic events, such as MHW, can lead to mass mortalities which mainly affect large colonies (Cerrano et al., 2005; Cupido et al., 2012; Cupido et al., 2008; Garrabou et al., 2001; Huete-Stauffer et al., 2011; Santangelo et al., 2007). Positive temperature anomalies, as well as prolonged exposure to these abnormal temperatures, act at different levels on gorgonian populations. Exposure to lethal temperatures (> 25 °C) causes metabolic dysfunctions as it may cause an increase in coenchymal necrosis and a decrease in polyps' activity and calcification rates (Torrents et al., 2008). Exposure to sublethal temperatures (23–25 °C) can also cause physiological stress resulting from a lack of energy due to the increase of respiration rates (Coma et al., 2009; Coma and Ribes, 2003), but also a decrease of immune system efficiency (Coma and Ribes, 2003; Cossins and Bowler, 1987). Such impact indirectly promotes pathogens development (Banin et al., 2003; Israely et al., 2001; Toren et al., 1998), as it was the case in 2003 for *P. clavata* ultimately leading to elevated mortalities (Bally and Garrabou, 2007). Even though cases of rapid recovery after a significant mortality (as MME in 2003) have been observed in the northwestern Mediterranean Sea (Cerrano et al., 2005), situations in which recruitment remains low after a period of significant mortality, as highlighted by the present study, can also occur in gorgonian population (Coma et al., 2006; Petes et al., 2003).

Asexual reproduction, generally considered to have little influence on gorgonian populations dynamics, could become an important factor in local recolonization capacity of impacted populations (Lasker, 1990). In addition, some studies have also shown that when a population faces mortalities affecting its large individuals, earlier sexual maturity could be observed which could enhance reproductive capacity (Gallmetzer et al., 2010; Santangelo et al., 2003; Tsounis et al., 2006). A significant recovery in gorgonian populations was observed following MME in 2003, with a 4-fold increase in the recruitment rate in four years (Cupido et al., 2009). However, under repeated stress conditions, an energetic budget could be focused on the recovery of dead tissue rather than on reproduction (Cupido et al., 2009, 2008). Despite the existence of a recolonization process, because MHW are more and more frequent, populations may not be able to recover between two major events.

Kipson et al. (2012) also demonstrated that thermostress has a severe impact on *P. clavata* embryos and larvae by reducing their survival, disrupting normal embryonic development, and altering their metamorphosis. Thus, the reduced viability of larvae would jeopardize *P. clavata* species, which relies on efficient recruitment for the recovery of its populations.

Therefore, the decrease of small colonies over the years is probably due to a decline in recruitment given the thermal context. Reproductive capacity might be affected by the increased mortality of large individuals during marine heat waves and remaining larvae and young colonies are potentially also impacted by heat stress.

However, the sampling protocol used in this study only allows to highlight trends and hypotheses. As we have seen previously, recruitment is known to be a variable phenomenon in these species, depending on larval production and connectivity with distant populations (Aurelle et al., 2020; Costantini et al., 2016; Padrón et al., 2018). The differences between the population structure between 2004 and 2014–2019 are mainly due to the differences in the proportions of small colonies. These

differences could also be due to a natural fluctuation in recruitment. To have a more robust view of the recruitment dynamics and annual variability, it is therefore essential to conduct demographic monitoring every year.

### 4.5. Other potential effects associated with climate change

Climate change is also modifying some species distributions and, thus, promoting invasion of coastal ecosystems by exogenous species. This is the case of certain invasive algae such as *Caulerpa cylindracea*, *Lophocladia lallemandii*, *Womersleyella setacea* and *Acrothamion preissii*, which have some overlap with spatial and vertical distribution of gorgonians (Cebrian et al., 2012; Kersting et al., 2014; Kružić et al., 2008; Linares et al., 2012). In addition, a recent study has shown that MHWs and the associated MME can induce a change in a structurally complex habitat, dominated by long-lived species (such as gorgonians), towards a simplified habitat with a significant loss of diversity and specific richness, dominated by turf-forming species (Verdura et al., 2019). Through experimental studies, the presence of *P. clavata* has been observed to mitigate effects of warming by maintaining the assemblage dominated by macroinvertebrates and by retarding proliferation of the invasive algae *C. cylindracea*. However, gorgonians mass mortality events caused an increase of sedimentation, and the proliferation of turf-forming species causing recruitment and larval settlement decreases, an increase in mortality rates of juveniles and a significantly decrease in biomass of gorgonians (Arnold et al., 2010; Birrell et al., 2005; Cebrian et al., 2012; Linares et al., 2012; Vermeij and Sandin, 2008).

All these factors ultimately facilitate the extension of *C. cylindracea* and other exogenous species (Bulleri and Benedetti-Cecchi, 2008; Verdura et al., 2019). *C. cylindracea* is particularly present on the Revellata site so it is possible that the decrease in gorgonian juvenile colonies (<10 cm) may also be partly due to its proliferation (Fig. 8A).

Blooms of mucilaginous algae caused by the proliferation of several phytoplanktonic species have increased considerably in the northwestern Mediterranean Sea, including in Corsica and Calvi Gulf. Their dense carpets can sometimes completely cover benthic communities, such as gorgonian forests (Giuliani et al., 2005) and cause lesions and necrosis due to prolonged anoxic conditions (Fig. 8B) (Piazzi et al., 2018).

### 4.6. Local anthropogenic disturbances

Coralligenous reefs form essential habitats on Mediterranean coasts by playing an important role for fishery resources and tourist attraction (Ponti et al., 2014). Despite tourism economic benefits, excessive diving activities can have negative effects on gorgonian and coral populations (Betti et al., 2019; Casoli et al., 2017; Di Franco et al., 2010; Di Franco et al., 2009). The Revellata site, where gorgonians were followed for this study, is a site particularly popular for scuba divers. Despite clubs and practitioners' awareness, it is still common for colonies to be voluntarily or involuntarily touched or hit by divers (Iborra et al., unpublished data), whether with hands, fins or other diving instruments, thus potentially damaging the colonies (Betti et al., 2019). This threat mainly concerns shallower populations (down to the limit of recreational diving at 40 m depth) (Bo et al., 2017; Coma et al., 2004; Di Franco et al., 2009). Finally, other mechanical damage can affect gorgonian populations such as professional or recreational fishing. Although trawling is not practiced on the west coast of Corsica, professional fishermen may have to set nets on or near drop-offs of coral. Also, gorgonians can be pulled out while fishing nets are being recovered (Pers. Com.). Recreational fishing is also a very popular activity on the Revellata cape (Iborra et al., unpublished data). Fishing lines, by catching or wrapping around gorgonians, can cause lesions such as abrasions of colonies tissues or uprooting of entire colony (Bavestrello et al., 1997; Bo et al., 2017; Bo et al., 2014; Tsounis et al., 2012) (Fig. 8C).

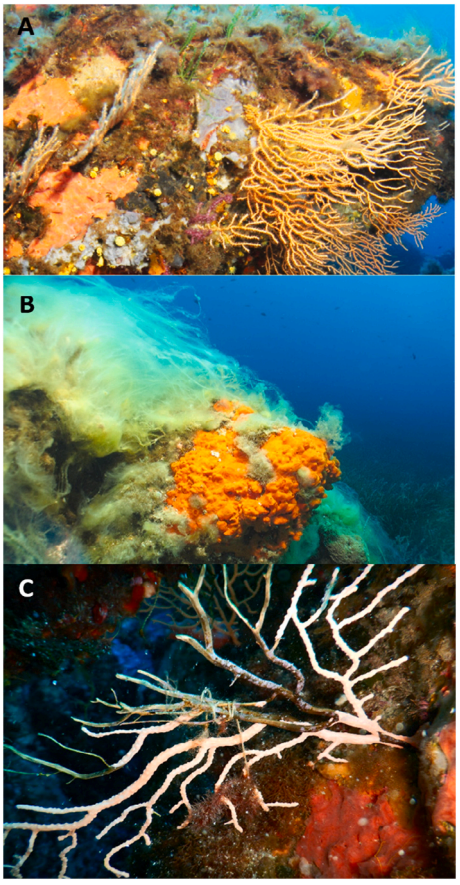


**Fig. 8.** A. Yellow gorgonians *Eunicella cavolini* and invasive algae *Caulerpa cylindracea* at Revellata cape, in 2016. B. Bloom of mucilaginous algae at Revellata cape, in 2012. C. Monofilament line lost by recreational fisherman and entangled in a yellow gorgonian affected by a recent necrosis at Revellata cape, in 2019.

## 5. Conclusion

This study has shed light on long-term trends of two gorgonian species *E. cavolini* and *P. clavata* discussed with regard to climate change, marine heat waves, and food availability. Our results and identification of all these cumulative threats show the need to continue to monitor these populations on a regular basis. Although these two sea fans species are widely distributed in the Mediterranean Sea, the increased threats have severely affected their populations in recent decades. A study of the frequentation of the Revellata site by fishermen and divers would enable a better understanding of the local anthropogenic impacts on these populations. In addition, it could be interesting to study the density of gorgonian populations on this site according to wall orientations and turbulence because these factors can be correlated with gorgonian fitness (Sini et al., 2015; Weinbauer and Velimirov, 1995b). Thus, suitable routes could, for example, be offered to divers to avoid disturbance of areas favorable to recruitment. Consequences of these global and local disturbances are to be followed in short and long term to develop or improve the protection and/or restoration of these iconic and patrimonial species.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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