



## Multiple climate-driven cascading ecosystem effects after the loss of a foundation species

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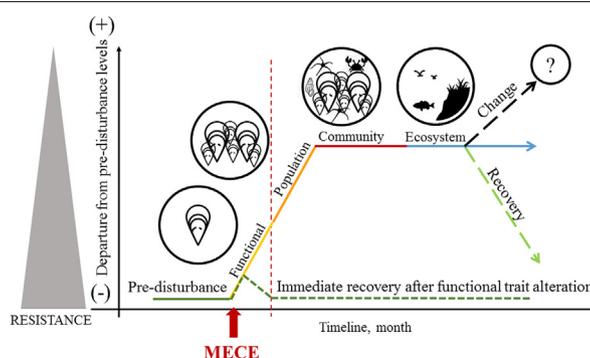
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### HIGHLIGHTS

- Multiple Extreme Climate Events (MECEs) are increasing due to climate change.
- MECEs mechanisms bringing to the loss of biodiversity are poorly described.
- Near-term ecological forecasting sensor networks support MECEs early detection.
- Mixed manipulative and observational studies allow disentangling MECEs effects.
- Foundation species drives habitat functioning, its lost impair the whole system.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Climate change is evolving so fast that the related adverse effects on the environment are becoming noticeable. Thus, there is an urgent need to explore and understand the effects generated by multiple extreme climatic events (MECEs) on marine ecosystem functioning and the services provided. Accordingly, we combined long-term in-situ empirical observations in the Mediterranean Sea with a mesocosm manipulation to investigate the concurrence of increasing temperature and hypoxia events. By focussing on a foundation mussel species, we were able to detect several cascade events triggered by a mass mortality event caused by stressful temperature and oxygen conditions, and resulting in a loss of ecosystem services. The measured rates of chlorophyll-*a*, carbohydrates, proteins and lipids - in both particulate and sedimentary organic matter - were used as proxies of ecosystem functioning during pre- and post- disturbance events (MECEs). In the past, MECEs were crucial for individual performance, mussel population dynamics and biomass. Their effect propagated along the ecological hierarchy negatively affecting the associated community and ecosystem. Our results suggest that the protection and/or restoration of coastal areas requires careful consideration of ecosystem functioning.

**Significance statement:** Our decadal time-series recorded by a near-term ecological forecasting network of thermal sensor allowed us to record and monitor multiple extreme climatic events (MECEs; heat wave and hypoxia events), warning on the environmental change recorded on a pond system. By integrating observational and manipulative approaches, we showed how a MECE triggered cascade events, from individual-based impaired

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functioning up to biodiversity loss (community composition and structure changes). Our results emphasize the key role played by a foundation species in driving ecosystem functioning, and the synergistic effects of climatic drivers acting simultaneously.

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## 1. Introduction

Climate change has triggered complex and, sometimes, catastrophic ecological responses due to the increasing frequency of multiple extreme climatic events (MECEs). This phenomenon calls for a comprehensive understanding of “how” and “when” climate-induced regime shifts modify the ecosystem’s state and the relationship between ecosystem functioning and biodiversity; the aim being to design anticipatory integrated tools (Redmond et al., 2019). The superimposition of natural climate variability and decadal warming trends is increasing the probability of driving ecological systems towards their functioning limits, and unexpected changes in their ecological status. The increasing frequency and intensity of MECEs, and their effects on weather (Smith, 2011), such as drought, wildfires, hypoxic events and heat waves cause rapid cascade events characterised by responses transversally propagating along the ecological hierarchy. The effect always triggers from the lower level of the ecological hierarchy, i.e. the functional level as defined by the hierarchical performance paradigm (Violle et al., 2007; Wong et al., 2019).

By definition, MECEs are multifaceted. For instance, incidences of hypoxia in seas, partly symptomatic of coastal eutrophication, have increased exponentially over the past decades and are strengthened by rising temperatures (Stewart et al., 2013), often further exacerbating the natural functional balance of marine ecosystems. A mass mortality event (Seuront et al., 2019) is usually the first visible catastrophic step, with detrimental repercussions at population level, due to the alteration of natality and mortality rates. Such event in turn, lead to changes in the composition and structure of ecological communities (Cerrano and Bavestrello, 2009; Garrabou et al., 2009). The last visible step is biodiversity loss (Cloern et al., 2011), which undermines the provision of ecosystem services (Worm et al., 2006).

The pressure exerted on ecosystem functioning by climatic events, interacting with natural variability, often increases when more than one stressor is considered, i.e. if the temporal relationships between different environmental drivers are “in” or “out of phase” (Gunderson et al., 2016). Similarly, when a foundation species (Grime, 1987; Hughes, 1994; Avolio et al., 2019) is involved in the process, its loss implies a weaker or declining linear/exponential relationship between biodiversity and ecosystem functioning (Naem, 2002; Cardinale et al., 2012; Strong et al., 2015; Thrush et al., 2017; Daam et al., 2019). In such cases, the severity of the cascade effects increases the speed at which the effects manifest and propagate, from functional alterations - at individual level - to changes in community equilibria through loss of biodiversity and ecosystem functioning (Lohbeck et al., 2015). The first step of this cascade, i.e. mass mortality events, has been widely reported during the last two decades (Hughes, 1994; Seuront et al., 2019). Moreover, the final step, i.e. loss of biodiversity and associated ecosystem services (Worm et al., 2006; Hooper et al., 2012; Şekercioğlu et al., 2019) is well-discussed in the literature. In contrast, empirical, step-by-step reports on a set of sequential events driving the system from an extreme climatic event to the final loss of biodiversity and functioning at ecosystem level, is still poorly explored.

Most experimental studies are manipulative and have the advantage of controlling all possible factors affecting species loss (Smith et al., 2019) although sometimes the outcomes are unrealistic due to flawed assumptions (Korell et al., 2019). In contrast, most of the evidence available in the literature originates from observational studies, even though they are often criticised due to lack of replicability, among other aspects (sensu Smith et al., 2019). Thus, it seems that the full sequence of a cascade, due to and triggered by stressors, is often more conceptualized

(e.g. Burrows et al., 2011; Cloern et al., 2016; Windsor et al., 2018) than experimentally measured under natural conditions (sensu Ettinger et al., 2019). Currently, the mechanisms remain unclear due to a lack of the biological and ecological outcomes needed to improve the anticipatory frameworks. Moreover, the datasets required to parameterize the causal relationships between the effects of climate drivers are also scant (Riedel et al., 2014). Nonetheless, the knowledge of the mechanisms triggering the shift of functioning is crucial for stakeholders and policy-makers to make informed decisions when managing natural resources under extreme climatic events (sensu Mangel and Levin, 2005).

Thanks to our near-term ecological forecasting network of thermal sensors maintained in the field for more than a decade, we were able to detect the environmental change trigger that drove the ecological shift of a shallow pond from one status to another. The alien mussel *Brachidontes pharaonis* (Fischer P., 1870) (Bivalvia, Mytilidae), whose rapid spreading power has been modelled and validated across the Mediterranean (Sarà et al., 2018) was used as model species. By studying a metabolic proxy of functioning, namely oxygen consumption, we tested whether the concurrent increasing temperature and hypoxia events, experienced by the mussel, was behind the cascade of events beginning with mass mortality of the foundation species and culminating in functioning losses.

Our observations support the idea that an ecological system responds according to a hierarchical sequence of steps (sensu Smith et al., 2009, Smith, 2011) and that the loss of a foundation species produces effects that are often more significant than the potential effects due to the loss of related species. The observational information gathered during the case study will be crucial for validating the current theories about the relationship between biodiversity and functioning (e.g. Mulder et al., 2012; Wang et al., 2019), and inform the development of an anticipatory suite of tools to inform environmental managers and thus help them react promptly to extreme climatic events.

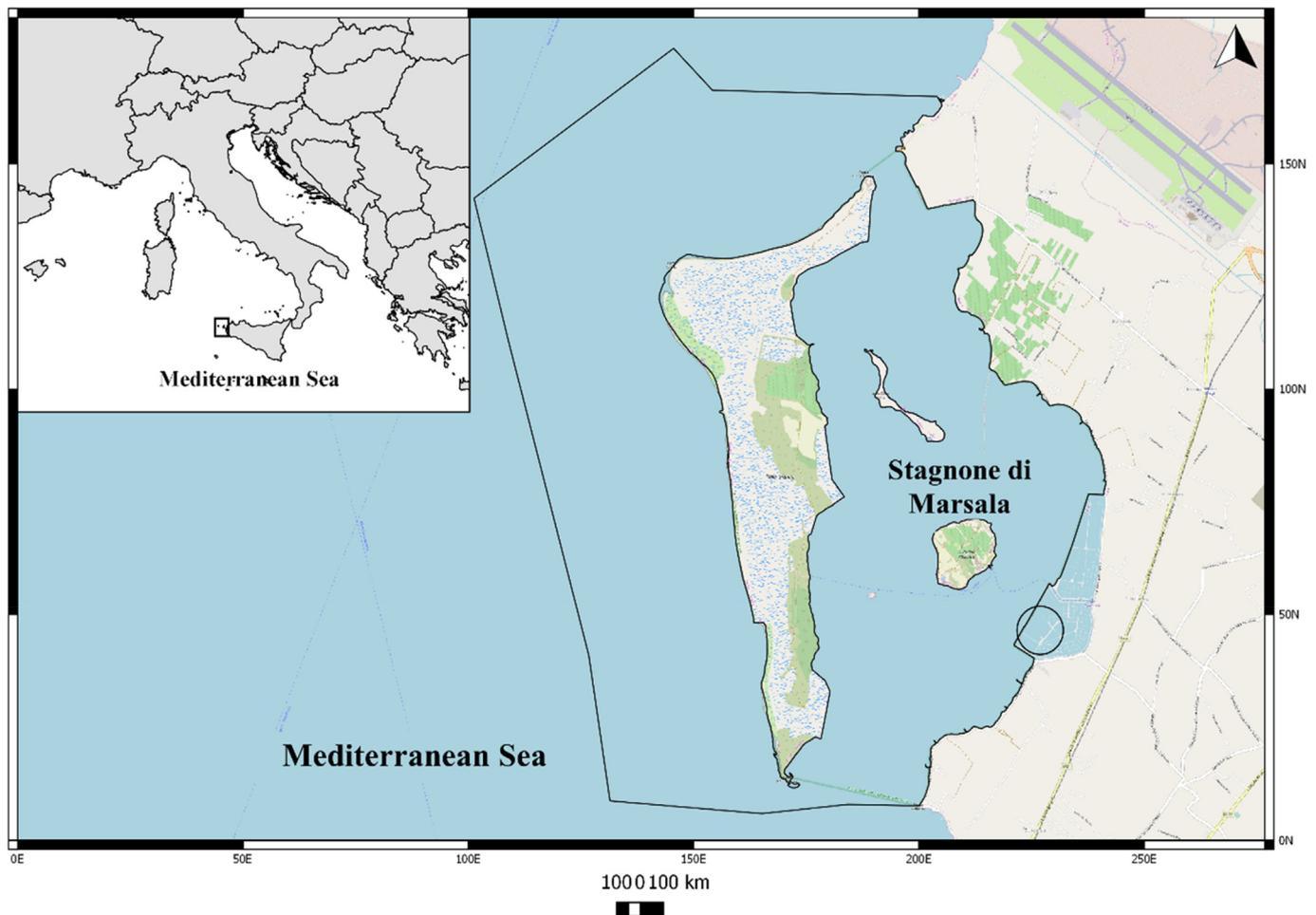
## 2. Materials and methods

### 2.1. The study area

The study was based on a twenty-year monitoring plan focused on the “Stagnone di Marsala”, the largest lagoon in Sicily (~2500 ha, Site of Community Importance since 1995 - ITA010026 EU Habitat Directive 92/43/EEC; Pusceddu et al., 2003, Sarà, 2006) and the adjacent system of man-made ponds (~1500 ha; Bellino et al., 2019) (Fig. 1). Created in the 15th century for salt production, the pond system is connected to the sea through channels, with salinity values similar to, or slightly higher, than seawater (Mannino and Sarà, 2006). The lagoon-pond system is characterised by sand/muddy bottoms largely covered by the seagrass *Cymodocea nodosa* (Ucria) Asch., while the macroalgal community on rocky substrata is mainly characterised by species belonging to the *Chaetomorpha*, *Cladophora*, and *Ulva* genera, *Acetabularia acetabulum* (Linnaeus) P.C. Silva and *Chondria capillaris* (Hudson) M.J. Wynne. The average depth across the lagoon-pond system is ~0.8–1.0 m. The alien mussel *Brachidontes pharaonis* represented the foundation and dominant species in “Ettore” pond (Sarà et al., 2000, 2003, 2008, 2018). Ettore pond (~ 7.5 ha) is separated from the lagoon by an artificial wall (~1.5 m width).

### 2.2. Temperature and dissolved oxygen data logging

Since 2007, the temperature in both the ponds and the lagoon is monitored using temperature data loggers (model: iButton G1, prec.



**Fig. 1.** The study area, the “Stagnone di Marsala” (Site of Community Importance ITA010026 EU Habitat Directive 92/43/EEC, black polygon) and the neighbouring pond systems (Western Sicily, Italy), the black circle indicates the “model” pond named Ettore.

$\pm 1$  °C, res.  $\pm 0.5$  °C, <http://www.alphamach.com>) set at a 1 h frequency. With only few data points missing from the decadal dataset, the long-term data series was crucial for detecting thermal anomalies due to the heat waves that started in June 2017 (data stored at the Laboratory of Ecology, University of Palermo). In addition, dissolved oxygen loggers set at 1 h frequency (HOBO U26 Dissolved Oxygen Data Logger; <https://www.onsetcomp.com/products/data-loggers/u26-001>, sampling frequency at 1 h) were deployed at Ettore pond from autumn 2016 to early July 2017. Data from both sensors were used to build the relationship between in situ temperature and dissolved oxygen. Unfortunately, the oxygen sensors did not completely cover the temperature time series monitored, and thus part of July, August and September were not monitored. Nevertheless, the HOBO sensors recorded a large dataset covering over 6000 h, i.e. a dataset that highlighted the negative relationship between temperature and dissolved oxygen; this dataset was used to set up the mesocosm experiment. This relationship supported the hypothesis tested in the study area, namely, that the juxtaposition between increasing temperature and hypoxia events triggered the cascade events beginning with the mass mortality of the foundation species and culminating in loss of ecosystem services.

### 2.3. Density of foundation species and associated biodiversity

During the last decade, both the density of mussels and of the associated macrofaunal communities were routinely sampled (yearly) and analysed at Ettore pond. The monitoring plan included 9 hard substrata sites inside the pond, of which 3 haphazardly chosen plots were surveyed using quadrats (27 quadrats of 400 cm<sup>2</sup> [20 cm × 20 cm]). The

surface delimited by the quadrats was scraped to collect the specimens (Bellan-Santini, 1969). The samples were transferred to the laboratory, and both live and dead *B. pharaonis* mussels were counted; live mussels were individually measured (valve length, and total and somatic weight; Sarà et al., 2013), and species richness of the associated benthic macrofauna was calculated (see Bellino et al., 2019 for a more exhaustive presentation of seasonal diversity trends). The trophic type of the associated macrofauna was also analysed as a proxy of community functioning, with the final aim being to detect changes due to the MECEs. In addition, the densities of the most abundant seagrasses, *Cymodocea nodosa* and *Ruppia maritima*, were recorded and reported (percentage coverage). Here we specifically refer to a comparison between year 2016 (when *B. pharaonis* dominated the communities all across the monitoring sites) and year 2017 data (sampling performed a week after the heat wave).

### 2.4. MECE mesocosm experiment

After having analysed the temperature dataset of summer 2017, an experiment was set up, to replicate the two concurring stressors acting in the system using a multiple stressor theoretical framework (Cran et al., 2008; Piggott et al., 2015; Gunderson et al., 2016), and the observations of *B. pharaonis* mass mortality in Ettore pond (end of July 2017). The juxtaposition of stressors is blamed as one of the most important causes of the deviation of ecological processes from common natural patterns in natural ecosystems (Gunderson et al., 2016). Starting from this hypothesis, and supported by our in situ observations, we mimicked the combination of increasing temperature and hypoxia under controlled conditions

at the laboratory in order to investigate “if” and “how” the functional thresholds and mortality of the foundation species could be affected by multiple stressors, as recorded in the field. Specifically, three experiments were designed to mimic the recorded MECEs, to test how single and multiple stressors can: i) affect the functional traits of the foundation species *Brachidontes pharaonis* in the pond, and ii) induce over 50% mortality of the local population. The first experiment investigated the effect of temperature using a 9 h thermal gradient, starting from 26 °C and gradually increasing to 35 °C, and then decreasing again to 26 °C in order to reproduce the 2017 heatwave event. The second experiment examined the effect of hypoxia as a single stressor, at constant temperature (26 °C) and oxygen concentration at 2 mg l<sup>-1</sup>. Finally, the third experiment tested the combined effect of both stressors. In all cases, the highest temperatures, hypoxia and their combination were maintained for five increasing exposure times (2 h, 4 h, 6 h, 8 h, 12 h) during five different independent experiments. The first measure at 26 °C and normoxic conditions was used as a control measurement for each experiment (sensu Gunderson et al., 2016). Thus, we measured the metabolic rates (as expressed by the respiration rate, Sarà et al., 2013) and mortality (in terms of median lethal time, LT50; Duffus, 2009). A Generalized Linear Mixed Model (GLMM) approach was used to test the effect of single stressors, “Hypoxia” and “Heatwave” respectively, while a Generalized Linear Model (GLM) was used to test the effect of multiple stressors (“Hypoxia + Heatwave”) on oxygen consumption. Oxygen consumption recorded before starting the thermal increase was used as a baseline for each model run (GLM and GLMM), as a way for the model to detect the effect of a stressor before exposure (MECE). A Generalized Linear Model (GLM) approach was used to test the oxygen consumption measured before and up to exposure (26 °C and 29 °C) and after exposure (29 °C and 26 °C, the latter measurement was not considered a recovery phase due to its short length); the “before-after” effect was a categorical 3-level variable (before, stressor, after). Details about the experimental design, associated statistics and outcomes are set out in the Supporting Information section.

### 2.5. Trophic and environmental variables

According to the literature, one of the most important roles of bivalves is their capacity to trap food otherwise available to the whole trophic web (e.g. Sarà, 2006). The filtration pressure exerted by bivalves significantly affects the N and C organic cycles, as observed in many shallow water bodies at the same latitude (Manganaro et al., 2009). Mass mortality of these organisms may affect water transparency, particulate (POM) and sedimentary (SOM) organic matter, with clear repercussions on ecosystem functioning. POM and SOM have been routinely sampled and measured during the twenty-year monitoring plan designed for the lagoon-pond system (Sarà et al., 2000; Pusceddu et al., 2003; Sarà, 2006, 2009; Bellino et al., 2019). Specifically, water was collected using Niskin bottles and sediments were collected by scuba diving using hand corers. Chlorophyll-*a* (CHL-*a*), carbohydrates (CHO), proteins (PRT) and lipids (LIP) were measured in both water (POM) and sedimentary (SOM) organic matters. CHL-*a* was measured according to De Jonge (1980), CHO, PRT and LIP were converted into C-equivalents using 0.40, 0.49, and 0.75 g C g<sup>-1</sup> conversion factors, respectively, and normalized according to Pusceddu et al. (2003). The sum of gross PRT, CHO and LIP is usually considered as an estimate of bioavailable fractions in POM and SOM. The sum in C-equivalents represented the biopolymeric organic carbon (BPC), which is usually used as an estimate of the labile fraction of organic C in the water column and sediments, and a reliable proxy (together with the total amount of CHL-*a* in POM and SOM) of ecosystem functioning.

### 2.6. Statistical analysis

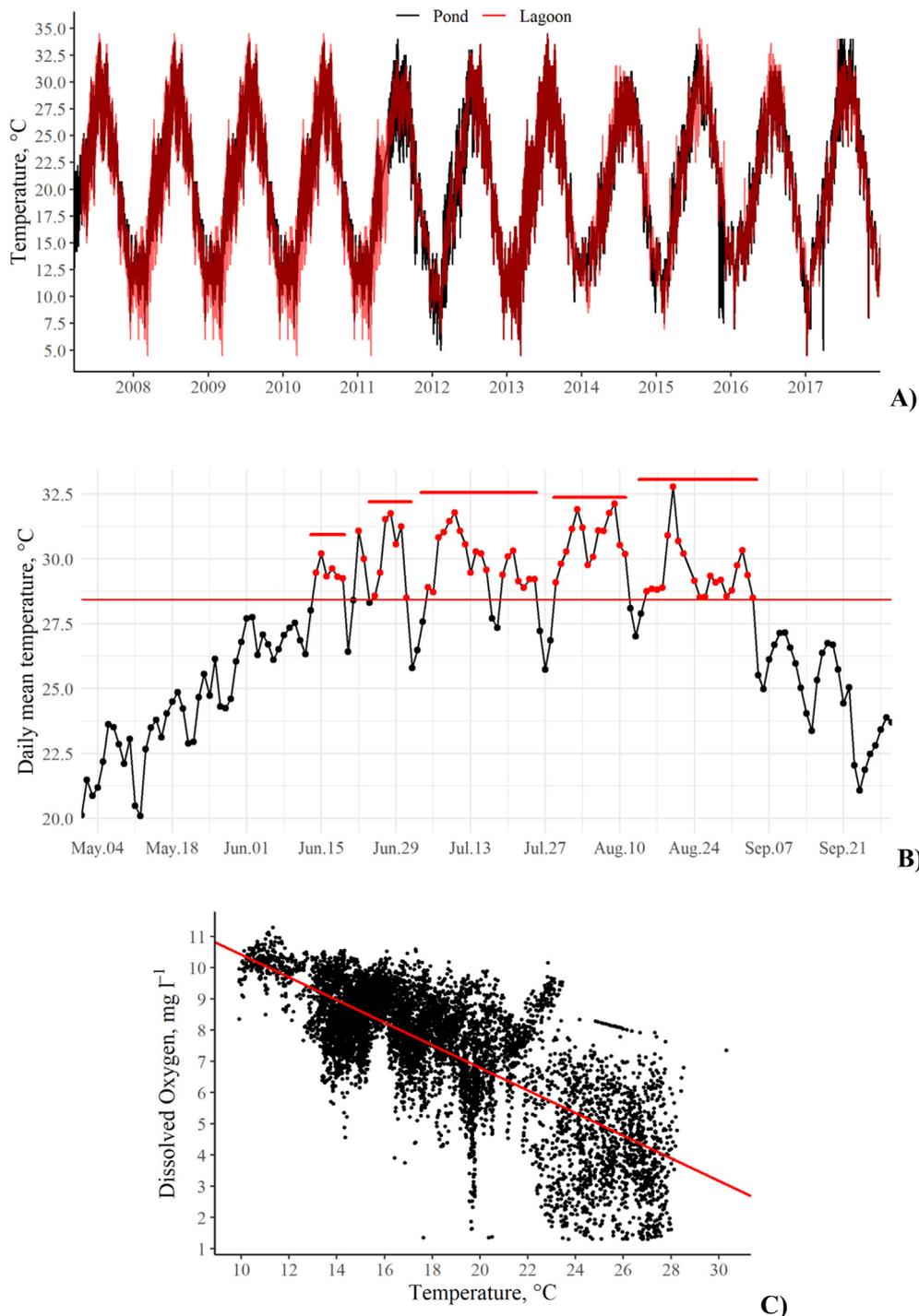
Data from our network of near-term ecological forecasting thermal sensors were analysed to explore temperature thresholds and identify heat waves according to Hobday et al. (2016). The definition was, literally:

“a marine heatwave is defined at locations where an upper locally determined threshold (90th percentile relative to the local long-term climatology) is exceeded for at least a five-day period, with no more than two below-threshold days”. A heat wave can be considered as ended once a temperature under the 90th percentile threshold is recorded on at least three consecutive days (sensu Hobday et al., 2018). To test the differences generated by MECEs at the different levels of the ecological hierarchy, we adopted different methodologies. To test the effect of single (“Hypoxia”, “Heatwave”) and multiple stressors (“Hypoxia + Heatwave”) during the oxygen consumption experiments conducted on *B. pharaonis*, we used a Generalized Linear (GLM) and Mixed Model (GLMM) approach. Four different models were selected through a forward-backward stepwise procedure taking into account the AIC and BIC of different models (see Supporting Information, Tables 2 and 3), one for each experiment and one for the data as a whole, considering all stressors together. Since the Shapiro-Wilk test rejected the normality hypothesis, a gamma distribution was assumed to model the response variables using Log as the link transformation function. Exposure time was used both as a random effect but also explored and tested as a fixed effect. Inter-individual variability within exposure time groups was taken into account as nested random effect (different – independent individuals were used each time, i.e. 9 individuals for 5 exposure times = 45, multiplied by 3 experiments = 135 individuals over a total of 150 sampled individuals). Random slopes were also tested. In order to compare the experiments, the differences in terms of response between the two measures (oxygen consumption) before the thermal increase (26 °C and 29 °C, treatment) and between the two measures after the thermal increase (29 °C and 26 °C, treatment) were tested as control baseline for each Generalized Linear Model (GLM) run. Since there were no significant differences, the measurements were averaged and pooled respectively into before treatment (hereafter: “Before”) and after treatment (hereafter: “After”) to allow the model to detect the effect of the stressor (i.e. thermal increase) before and after exposure. The before-after tested effect represents a categorical variable (with 3 levels: before, stressor, after). Despite the high number of variable levels and the relative complexity of the models, the latter were also tested and we observed that no singularity issues arose (checked through the `is_singular()` function in R). The Kaplan-Meier analysis was used to estimate survival and to plot the three survival functions. The Peto and Peto (1972) modification of the Gehan-Wilcoxon test was used to test differences between them. All statistical analyses were performed using R statistical software (R Core Team, 2019), and the “glmmADMB”, “lme4”, “survival”, “survminer”, and “ggplot2” packages. An ANOVA approach (Underwood, 1997) allowed to test for differences between before and after the MECEs, while assessing the density of bivalves in the field, the quality and quantity of organic matter, or the diversity of associated faunal components. Regression analysis allowed testing the relationship between temperature and dissolved oxygen measured in the field.

## 3. Results

### 3.1. Environmental monitoring to disentangle MECEs

The thermal temporal sequence showed a clear stationarity in both the lagoon and Ettore pond (Fig. 2a). A deviation from the common measured patterns was recorded in the summer of 2017, from June 1st to September 17th (Fig. 2). The heat-wave analysis sensu Hobday et al. (2016) showed that the rough decadal 90th percentile was 28.5 °C, while the smoothed value was 28.4 °C (Fig. 2b). Accordingly, at least five heat wave events were recorded in the summer of 2017, resulting in 68 days of exposure to temperatures ranging from 28.50 to 32.79 °C for the mussels living in the pond (about 120 days of the summer months; Fig. 2, see Supporting Information, Table S1, for more details). The mussels experienced 259 h of temperatures in the sub-lethal range (between ~30 °C and ~32 °C; Sarà et al., 2013) and 141 h of temperatures above the lethal threshold (32.5–32.7 °C, up to 34.5–35.0 °C; Fig. 2b, see Supporting Information, Table S1, for more details). Due to logger data storage issues, we



**Fig. 2.** A) [upper] Decadal chronosequence of water temperature as recorded by thermologger clusters in the study pond (Ettore pond in black) and in the adjacent Lagoon (Stagnone di marsala in red) sites; B) [middle] defined heat waves following Hobday et al. (2016); C) [lower] the relationship between temperature and dissolved oxygen in the waters of Ettore pond.

did not measure the relationship between temperature and oxygen (Fig. 2c) during the entire study period; in fact, the oxygen dataset was not available after the beginning of July. However, we used the available Hobo series to validate and infer the relationship between temperature and dissolved oxygen. A strong negative relationship between these two variables was found and used to design the mesocosm experiments. Our recorded dissolved oxygen series suggested that increasing temperature was associated with an increasing probability of hypoxia events ( $r = 0.5936$   $p < 0.0001$ ). This allowed conceptualisation of the idea

that, under pond conditions, some temperature spikes may overlap with hypoxia events.

### 3.2. Experimental evidence of MECE effects at individual and population level

#### 3.2.1. Heat wave single stressor

Oxygen consumption measured before the thermal increase (“Before”) was used as a baseline for each GLMM run. Estimation

of the heat wave treatment as “single stressor” was significant and positive (Fig. 3a;  $0.2108$ ,  $p = 0.00172$ ), suggesting that the heat wave treatment as “single stressor” positively affected oxygen consumption. Oxygen consumption in the “After” case was not significant. Given the interaction plot (Fig. 3g), random slopes for treatment were investigated as well. Standard deviation differences in intercepts and slopes were explained by clustered structure of exposure time (Fig. 3g). Intra-cluster individual heterogeneity was captured by nested random effect estimates (intercept standard deviation =  $0.312$ ). The results of the heat wave experiment are summarized in the Supporting Information, Table S2.

### 3.2.2. Hypoxia single stressor

The treatment showed a negative and significant value ( $-1.0572$ ;  $p < 0.0001$ ), which indicates that the hypoxia treatment as “single stressor” reduced oxygen consumption (Fig. 3b). The significant value ( $0.2468$ ;  $p = 0.0337$ ) of oxygen consumption in the “After” case indicated full recovery (Fig. 3b). The exposure time (Fig. 3e) was not significant ( $p > 0.05$ ) and was excluded from the model as a fixed effect. When considering exposure time as a random effect for the intercept, the standard deviation was  $\pm 0.04$ , which explained part of the structural differences between exposure time groups (Fig. 3h). A near-to-zero standard deviation (i.e.  $0.0003$ ) of the nested random effect

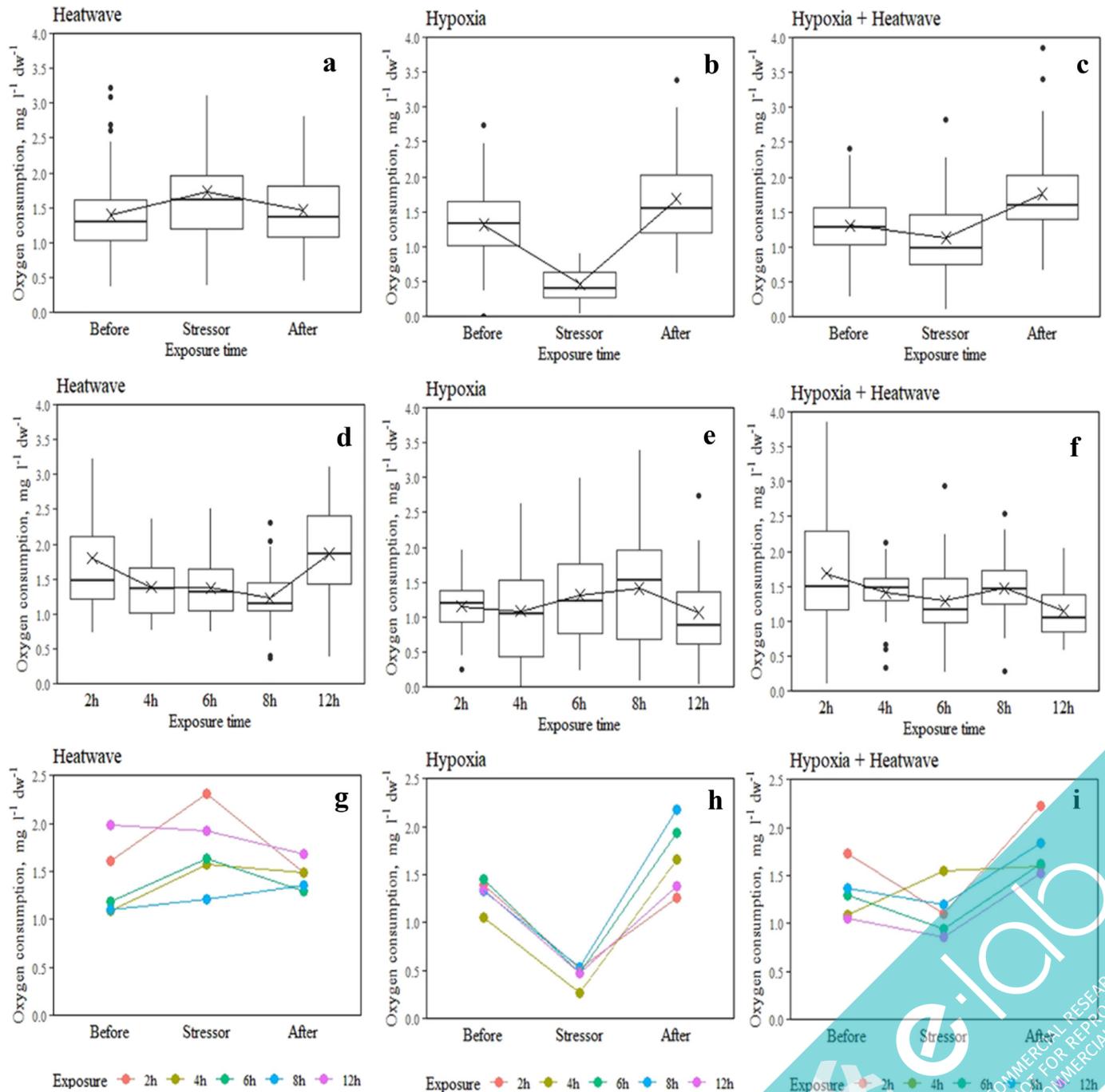


Fig. 3. - Oxygen consumption ( $\text{mg l}^{-1} \text{dw}^{-1}$ ) of *B. pharaonis* across the experimental time relative to Heatwave (left panels, a, d, g) and Hypoxia (central panels, b, e, h) as single stressor treatments respectively and “Hypoxia + Heatwave” treatment (right panels, c, f, i).

indicated that there were no significant differences between individuals. The results of the final model for the hypoxia experiment are summarized in the Supporting Information, Table S3.

### 3.2.3. Heatwave + hypoxia multiple stressors

The treatment value was not significant, while a positive and significant recovery value (0.3093;  $p < 0.0001$ ) was observed (Fig. 3c). As regards exposure time, it was tested both as a fixed and a random effect in the final model. This allowed to measure the overall treatment effect (through the considered categories: before, stressor and after) and as a random effect to study if that effect varied among individuals, nested in time exposure groups, and among time exposure groups. The estimates were negative with respect to 2 h exposure with the strongest effect, and significant for 12 h exposure ( $-0.3906$ ;  $p = 0.0049$ ) (Fig. 3f). Differences between exposure time clusters were detected by slopes from control to treatment (standard deviation = 0.3115). Higher intra-cluster heterogeneity between individuals was detected (intercept standard deviation = 0.2274; slope standard deviation = 0.4391; Fig. 3i). The results of the heatwave + hypoxia experiment are summarized in the Supporting Information, Table S4.

### 3.2.4. Survival analysis

No mortality was detected in mussels until day 3; the “Hypoxia”, “Heatwave” and “Hypoxia + Heatwave” treatment curves did not intersect (Fig. 4). Heatwave alone did not affect survival; LT50 - corresponding to survival probability (=0.50) - was reached after 6 days of exposure to the Hypoxia + Heatwave treatment, showing that multiple stressor treatment was effective in addressing mortality. All the differences between curves were significant ( $p < 0.0001$ ); the control was not visualized because it overlapped with the Heatwave curve. Such findings corroborated our main hypothesis, i.e. that a multiple stressor condition significantly affected the foundation bivalve in Ettore pond, inducing higher mortality than under single stressor conditions. A possible consequence of this finding under mesocosm conditions, when translated in the field, was that the density of the foundation species recorded before the MECES was significantly higher than after the Summer 2017 events (Fig. 5a).

### 3.3. Consequences at community and ecosystem level

The abundance and species richness of the associated macrobenthos significantly changed when the density of mussels decreased, as described by the relationship estimated before the MECES ( $r = 0.76$ ;  $n = 36$ ;  $p < 0.0001$ ) compared to after the MECES (Fig. 5b; see Table S5, Supporting Information, for comprehensive species inventories; data from both before and after the MECES event recorded in Summer 2017). Thus, in line with the well-known density-species relationship, which is typical of many other species-area studies (e.g. the positive

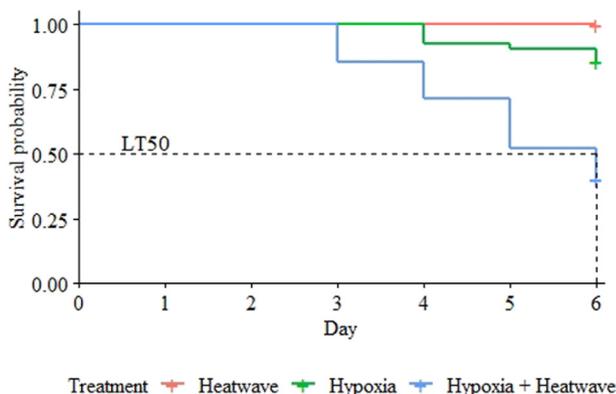
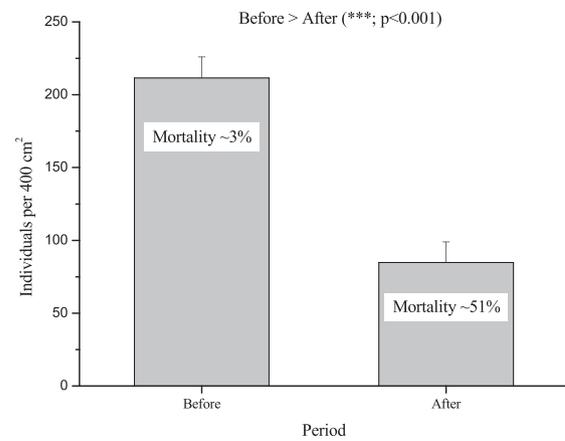
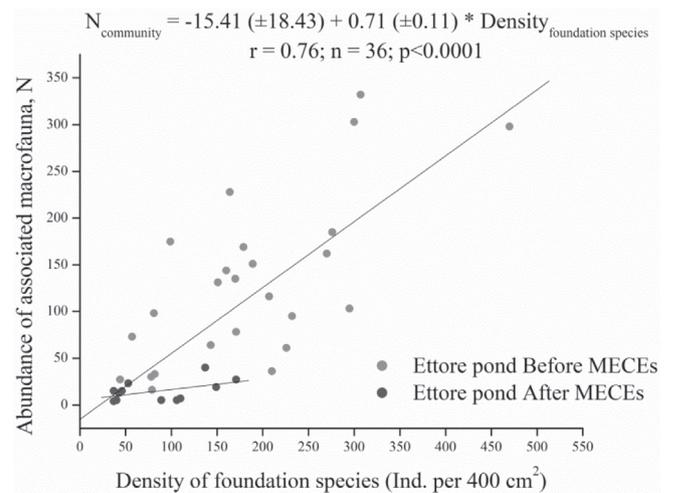


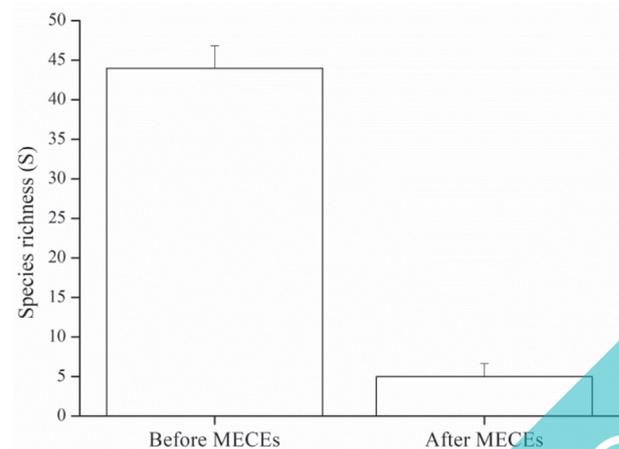
Fig. 4. Kaplan Meier survival functions of *B. pharaonis* across the exposure time of Heatwave, Hypoxia and Hypoxia + Heatwave treatment.



A)



B)



C)

Fig. 5. A) Density (Ind. per m²) of foundation species (the invasive bivalve *Brachidontes pharaonis*) live individuals before (dark grey) and after (light grey) Summer 2017 MECES; B) the relationship between density (before and after) and diversity of associated macrofauna, and C) species richness (S) before and after the MECES.

curvilinear relationship between the number of macroinvertebrate species inhabiting clumps of mussels; Peake and Quinn, 1993 and references therein), we observed a decrease in both taxonomic and functional richness. Interestingly, the pattern was confirmed by the response of mussel density to a MECES event; Species richness (S) decreased once *B. pharaonis* density collapsed (Fig. 5c). The change

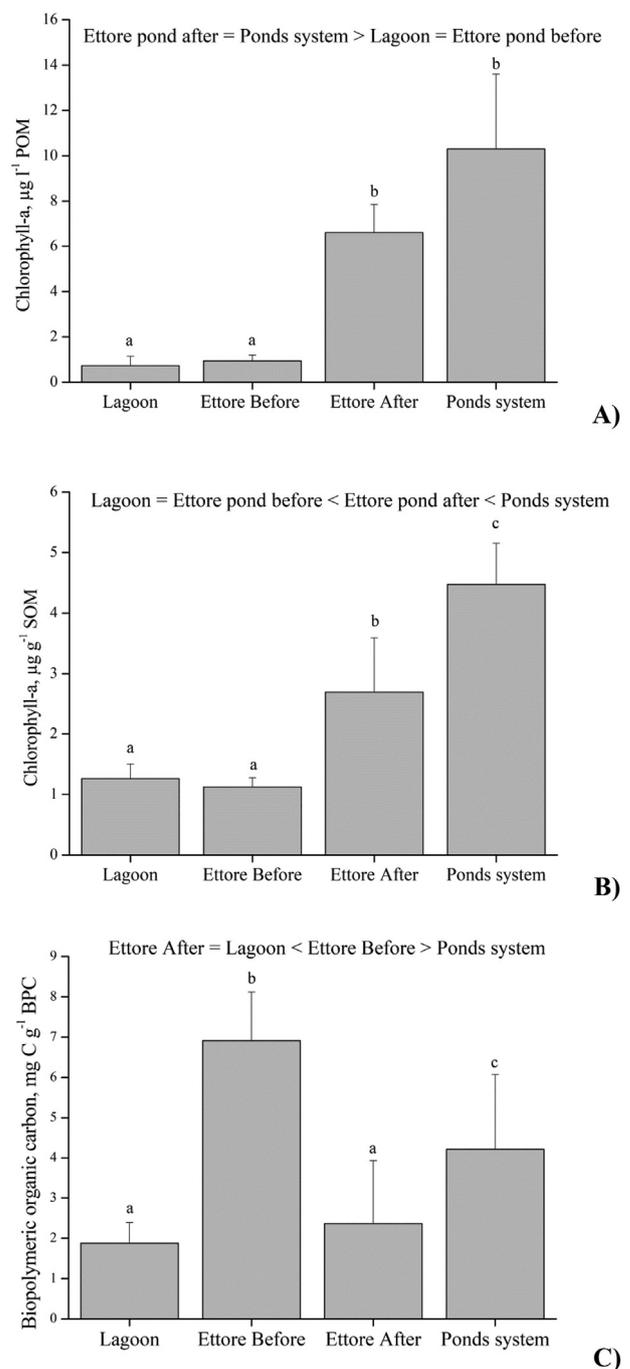
in the pond's trophic asset caused a functional reordering of the pond's community, both in terms of structure (i.e. due to the absence of the foundation species substratum caused by mass mortality) and functioning (i.e. the trophic role and feeding behaviour of the associated macrofaunal community changed between before and after the MECES; see Table S4, Supporting Information, for more details). Before the MECES, the macrofaunal community associated with *B. pharaonis* in Ettore pond displayed five main feeding behaviour types/roles: carnivorous (19 species, 9692 individuals), deposit feeders (14 species, 450 individuals), microalgal grazers (6 species, 408 individuals), suspension feeders (2 species, 44 individuals), grazers (1 species, 1 individual). After the MECES, the number of feeding behaviour types dropped to only two: carnivorous (2 species, 57 individuals) and deposit feeders (2 species, 25 individuals). This finding shows that the presence of the bivalve was the main driving factor influencing biodiversity (and related functioning) associated with the foundation species. Once the density of the foundation species collapsed (i.e. biomass removal due to the mass mortality event), trophic control of pond's ecosystem collapsed due to the decline of the mussel filtration machinery. While suspended material (CHL-POM) and sediment (CHL-SOM) before the MECES were similar in Ettore pond and the adjacent lagoon, mass mortality of *B. pharaonis* caused a loss of trophic control in the pond. Thus, CHL-POM and CHL-SOM tended to reach the typical values of other adjacent ponds where the foundation species was not recorded during the twenty-year monitoring period (Fig. 6a–b). BPC values after the MECES were equal to those of the adjacent lagoon, while before the MECES higher values were recorded in Ettore pond compared to the adjacent ponds (Fig. 6). Before the summer 2017 MECES, percentage coverage of the most abundant seagrasses in the pond, *Cymodocea nodosa* and *Ruppia maritima*, was constant over time (~60% coverage in Ettore pond) but subsequently collapsed and disappeared.

### 3.4. The relationship between biodiversity and ecosystem functioning

In this study, ecosystem functioning is described using descriptors of organic matter available to secondary consumers. Thus, we used CHL-POM and BPC to show the relationship between biodiversity and ecosystem functioning (BEF), a relationship that changed significantly after the MECES (Fig. 7). Biodiversity loss due to the MECES and the loss of the foundation species caused accumulation of suspended chlorophyll-*a* (CHL-POM) in the system. Chlorophyll-*a* concentration was about 7 times higher than before the extreme 2017 climatic event while a significant reduction of BPC (biopolymeric carbon is a reliable proxy of benthic feeding) was noted in sedimentary organic matter (SOM). Such an opposite relationship shows that the trophic control exerted by the suspension feeding foundation species collapsed after the climatic-driven cascade induced by the MECE. Thus, the collapse of filter feeders resulted in the following: i) accumulation of fresh suspended organic matter of pelagic origin and ii) significant reduction of the benthic component in the sedimentary organic matter, caused by the interruption of continuous provision of egested pseudofaecal organic matter produced by the foundation bivalve; before the MECES, the foundation bivalve was the main source of organic matter for the benthic system, when the foundation species had reached its maximum density (Sarà, 2006, 2007).

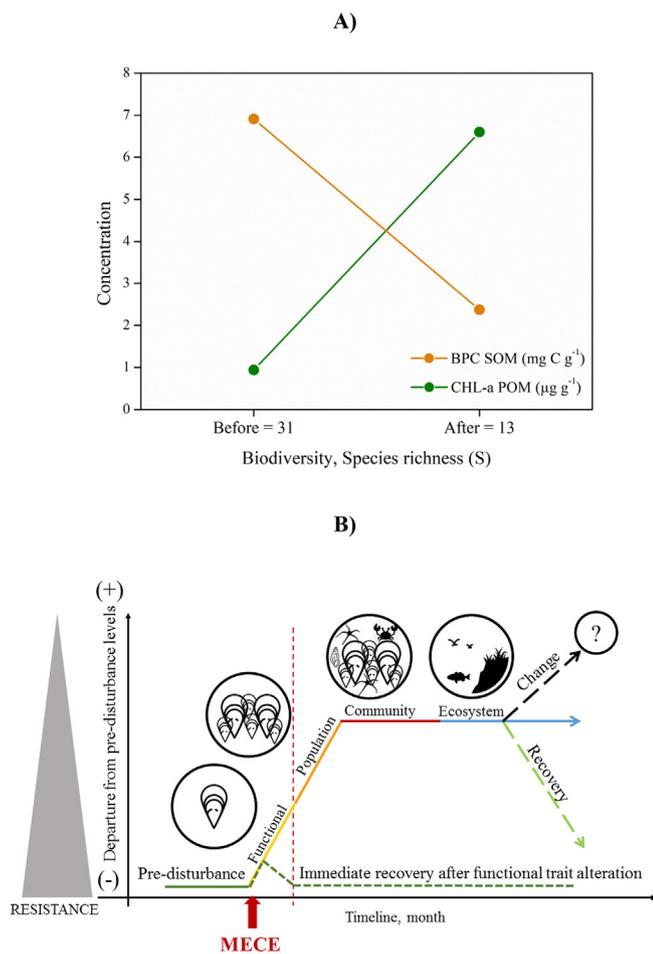
## 4. Discussion

This observational study offered the opportunity to depict the magnitude of the loss of a foundation species; it affected functioning and propagation along the ecological hierarchy. As pointed out by Smith (2011), as regards information on environmentally-driven effects of species loss, opportunistic studies are subject to many limitations (e.g. lack of replication; no control of type, timing, magnitude of climate extremes; no check for other covarying factors such as disturbance regimes, pest outbreaks etc.; Smith, 2011) compared to experimental



**Fig. 6.** The indirect effect at ecosystem level through alteration of the concentration of some trophic components before and after the MECES; A) suspended chlorophyll-*a* from POM; B) chlorophyll-*a* from SOM; C) the amount of biopolymeric carbon in the sediments (as sum of carbon fractions of proteins, lipids and carbohydrates, BPC).

(manipulative) studies (e.g. random vs. non-random species loss; Smith et al., 2019). Nevertheless, this opportunistic observational study has an advantage; it displays the succession of events triggered by the loss of a foundation species. Although the information gathered within the framework of this study cannot be experimentally controlled as in the case of manipulative experiments, observational studies significantly increase our understanding of how natural ecosystems respond to MECES and the temporal unfolding of (expected) consequences. Such information represents an added value if used as a validation measure for data obtained from manipulative experiments. Hence, we suggest an integration of observational and manipulative outcomes in order to obtain robust and validated frameworks for mechanistically



**Fig. 7.** A) The biodiversity–ecosystem functioning BEF relationship as extrapolated by the relationship between the associated biodiversity to the foundation species and suspended chlorophyll-*a* (CHL-*a* from SOM) in the sediments and the amount of biopolymeric carbon (BPC) in the sediments, both proxys of ecosystem functioning; B) conceptual chronosequence of hierarchical responses as observed in our model ecosystem (Ettore pond) representing the role of extreme events (MECEs red arrow) in eliciting the regime shift cascade through the impairment of the functional traits of a foundation species (sensu Dayton, 1972) that, recording the stress at individual (functional) level (e.g. effect on the metabolic machinery), translates in terms of population (e.g. mortality), community (i.e. biodiversity loss) and ecosystem effects (e.g. sudden collapse with loss of ecosystem services delivery).

disentangling the responses of natural systems to anthropogenic pressure.

#### 4.1. Top-down effect due to climate drivers and the interplay with bottom-up effects

Our research deeper into the effects of how a climate extreme can cause a loss of species through displacement of a functional trait of the most abundant species in a pond. Indeed, the dominant species in the pond (an invasive marine bivalve) is a primary filtering consumer, feeding mainly on detrital organic matter of autotrophic and heterotrophic origin (Sarà, 2006). Besides, it does not only provide nutrients to autotrophs, mainly seagrasses, but also offers shelter (crevices) to many other associated species (Burge et al., 2016). These functions, which sustain the entire food web in the pond, were changed by an interaction between environmental stressors. Specifically, heat waves and hypoxia altered the traits of the foundation species and thus the Eltonian trophic equilibria, thus triggering cascading events across trophic levels. Although

a primary consumer, bivalves are known to exert strong top-down control due to their large biomass (e.g. Schmitz et al., 2008). In our case study, the biophysical conditions in the pond were also influenced, as was the amount and quality of organic matter entering the detrital pool; as testified by the remarkable amount of deposit feeders among the associated macrofauna. High water temperatures – within physiological tolerable ranges – typically increase the filtration rates of such bivalves (Gosling, 2003, Burge et al. 2019). When the bivalve was lost due to mass mortality events, the top-down effect was also lost as observed in other environmental contexts of marine mass mortalities (e.g. Garrabou et al., 2009, Seuront et al., 2019).

This had a strong influence, which transversally involved all ecosystem components (Fig. 7) such as: i) light availability to primary producers (a lower bivalve filtration rate causes water turbidity), ii) the quality and quantity of particles for other associated consumers (reduction of ejected and egested organic matter) and iii) loss of habitat complexity (reduction/loss of spatial and microclimate refuges for the associated macrofauna). Such a set of effects supports the idea that climate-driven environmental change can produce effects on community structure and ecosystem functioning (Rosenblatt and Schmitz, 2016), confirming previous studies that show the extent to which aquatic invertebrate bioturbation/feeding traits can actually mediate detritus processing, redox chemistry and bacterial assemblages (Hunting et al., 2012). While we did not gather direct evidence, we can infer that these bivalves indirectly controlled the rates of microbial conversion of organic matter as well, thus exerting additional bottom-up control on ecosystem functioning (sensu Schmitz, 2013). Thus, this invasive bivalve controlled time, space and resources available to most organisms in the pond, suggesting a key role in maintaining species richness (Stachowicz, 2001) and playing a positive role of ecosystem engineer (Ellison et al., 2005). The sequence of hierarchical responses explored here started with a change in bivalve homeostatic responses to heat waves that likely worsened because of the hypoxia events. Temperature was the main factor causing changes in the quality and quantity of resources available for other consumers belonging to the same food web. According to the Arrhenius Break Point of this foundation species, estimated at ~30 °C, a mass mortality of 50% of the population – as evidenced by our mesocosm experiment – would have meant that several millions of bivalves that normally filtered water and particulate organic matter were no longer able to ensure water transparency and continuous provision of organic matter to sediments through egestion. The collapse of the bivalve filtering machine due to the observed MECEs triggered cascading events resulting with species loss and collapse of ecosystem functioning. Accordingly, when the density of this foundation decreased, species richness and abundance of the associated community also decreased. The results are even more relevant considering that other bivalves, such as *Mytilus* species, have a very strong compensatory capacity to mitigate negative effects caused by changes in temperature and chlorophyll-*a* (Telesca et al., 2019).

#### 4.2. A support to hierarchical response framework and the mass ratio hypothesis

Even if jeopardised, studies on the relationship between the density and biodiversity of foundation species in marine ecosystems, provide crucial evidence to inform management actions and plans in a context of predictive science. Indeed, density is the most important variable describing the role of a species in a community, given that ecological relationships are usually driven by the density of involved actors (Costelli, 2008). The consequences of the bivalve mass mortality event were visible in the short term (only a few weeks) at ecosystem level as the collapse of the filtering machine affected water transparency, impairing the ecological function of photosynthesis in the seagrasses colonising the pond (*Cymodocea nodosa* and *Ruppia maritima*; Mannino and Sarà, 2006), which disappeared.

The cascade of events triggered by the displacement of the functional trait of the pond's foundation species is in agreement with the mechanistic hierarchical sequence of responses described by Smith et al. (2009) and Smith (2011), when dealing with ecosystems under pulsing pressure (climate extremes). Our study shows that effects caused by climate extremes, and propagating hierarchically across an ecosystem, are influenced by the biomass of the foundation species. This dominant species was pushed towards the edge of its physiological tolerance limits and triggered a series of cascading events, from individuals through populations up to communities, thus affecting ecosystem functioning. Such results are in accordance with the Mass Ratio Hypothesis (MRH; Grime, 1998; Mokany et al., 2008; Vaughn, 2010; Smith et al., 2019). The MRH suggests that ecosystem processes and stability, and the rates of ecosystem functioning are mostly determined by the identity and traits of dominant species (Avolio et al., 2019). There are many examples of MRH in the current literature but most of them deal with the role played by autotrophs (e.g. Vile et al., 2006; Smith et al., 2009; Bílá et al., 2014; Sonkoly et al., 2019). Instead, the current case study can help in solving conflicts regarding the generality of the MRH in heterotrophs, given that a large part of the effect on species loss in our natural system is indirect, via mass ratio effects (Grime, 1998), which may alter species richness through cascading (Smith et al., 2019). Indeed, there is little evidence against the generality of the MHR in invertebrates. For instance, Tsafack et al. (2019) who studied insects (carabids), showed a significant negative correlation between the relative abundance of the most dominant species and the corresponding stability, which counteracts the MRH (Valone and Balaban-Feld, 2018).

Furthermore, our work suggests that when a foundation species is involved in the provision of materials and energy, and in the processes involving time and space, the community depending on these functions is undermined as a consequence of the loss of ecological functions supported by the physiological traits of the foundation species (Suding et al., 2008; Vaughn, 2010). Collectively, these findings corroborate the idea that ecological changes are universally and substantially dependent on a species-identity effect (Crowl et al., 2001; Bjelke and Herrmann, 2005; Taylor et al., 2006; Vaughn et al., 2007; Wojdak and Mittelbach, 2007; McIntyre et al., 2007; Smith et al., 2009). As a main consequence, given that in most natural communities only few species dominate (Whittaker, 1965) and that when they are lost a series of catastrophic events may occur (Ellison et al., 2005), we suggest strengthening the integrated view of how natural ecosystems actually work. This is critical for increasing our predictive understanding of the nature and pace of ecosystem change under both anthropogenic pressing and pulsing drivers.

Indeed, species responses manifest through modifications of biological traits such as body size, fecundity, dispersal ability, thermal tolerances, etc. (Payne et al., 2016; Heilpern et al., 2018). Unfortunately, despite ample scientific consensus on the mechanisms underpinning the link between species processes, biodiversity and ecosystem functioning, most biodiversity-ecosystem functioning experiments rarely explore the causes and mechanisms of the modifications in species richness rather than fluxes of nutrients through the communities of an ecosystem (Heilpern et al., 2018). Actually, environmental drivers (of any origin, from biotic to abiotic, such as physical, chemical, climatic, etc.) remain "imprinted" in the community traits, even after disturbance, the so called ecological memory (Ogle et al., 2015 and reference therein). If the environmental change is so strong as to push most individuals of a population close to the edge of biological (functional) tolerance, and affect individual fecundity and survival, and natality and mortality rates, there will be a measurable effect on local density and consequent implications at ecosystem functioning level. Thus, depending on: i) species abundance at local level, i.e. if the species is important species (dominant, foundation) or rare, uncommon or subordinate (sensu Avolio et al., 2019) and/or ii) whether response and effect traits covary positively or negatively (Heilpern et al., 2018), ecologists will

measure - at the end - a different magnitude of effects in response to ongoing environmental change/biodiversity loss; the higher the functional role and/or the larger the biomass, the greater the effect involving more functions (Grime, 1998; Suding et al., 2008; Cardinale et al., 2012).

On the one hand, after an environmental change generating biodiversity loss altered the functional traits of foundation species also, mussel beds and other self-organized communities are likely to be able to compensate for species loss (sensu Suding et al., 2008; Heilpern et al., 2018). On the other hand, given that foundation species are known to contribute to connectedness and energy storage, these species facilitate the propagation of disturbances (Massé Jodoin and Guichard, 2019). Furthermore, foundation species, such as bivalve, not only aggregate and offer many habitats to other species but also influence many (micro)organisms through their passive feeding behaviours (Gosling, 2003; Burge et al., 2016; Telesca et al., 2019). In all these cases, foundation species are essential for the delivery of ecosystem services and ecosystem functioning.

#### 4.3. Implications for the development of an anticipatory science

Developing a systemic ability to follow the temporal sequence of events in most ecosystems - especially when they are under anthropogenic pressure - is a real challenge. It can be time-consuming and expensive, but it is what scientists and managers should strive for. Our case study shows that a near-term ecological forecasting network of thermal sensors in the field, coupled with a voluntary twenty-year monitoring plan, represents a winning strategy. The information collected disentangled the propagation of induced disturbance caused by the MECes across all the levels of the ecological hierarchy. Moreover, it may prove useful for proactively detecting environmental changes, at temporal scale, in terms of detecting functional trait alterations (response trait) and providing effective early warning management measures, and thus reducing the propagation of negative effects to the upper ecological levels (effect traits; Lavorel et al., 2013; Mulder et al., 2012). Such information constitutes an added value when developing an anticipatory science - i.e. using scientific evidence to inform early warning systems - to inform resources management actions (Bradford et al., 2018).

In this perspective, conservation science should address research efforts to identify dominant species in every ecosystem, from algae to vascular plants and animals, or species showing traits responsible for sustaining/maintaining functions that support biodiversity and ecosystem functioning. Nonetheless, most conservation plans, for the Mediterranean Sea in particular, do not focus on the dominant species that support the ecosystem as a whole, but on charismatic/iconic species. According to the current well-known ecological theories and given the empirical evidence to support them, conservation plans should integrate knowledge on foundation species, by adding ad hoc monitoring plans that should be crossborder as in the case of invasive species (Sarà et al., 2018), coupled with experimental monitoring plans to measure the functioning of individuals and identify the breaking points of crucial associated functions (early warning system). The implementation of local monitoring plans at relevant temporal and spatial resolution is necessary to detect potential deviations from natural patterns (both temporal and spatial). Thus, targeted monitoring of the functional traits of dominant species will be crucial to develop anticipatory tools to prevent biodiversity loss. The management and/or restoration of functionally important species rather than the collection of information on the number of species and community evenness will ensure the maintenance of ecosystem functioning and services in view of global environmental change (Smith et al., 2019).

#### CRedit authorship contribution statement

GS together with CG and MCM designed the study. GS drafted the ms. and provided lab and field funds to support surveys and

experiments. AG contributed to the maintenance of the sensor network in the field, and performed the mesocosm experiment together with CG. All co-authors critically revised the later versions of the ms.

### 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.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.144749>.

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