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Subtle differences in growth rate drive contrasting responses of ephemeral primary producers to recurrent disturbances

Iacopo Bertocci[1,2] | Elena Maggi[1] | Claudia Scirè Scappuzzo[1] | Luca Rindi[1] | Lisandro Benedetti-Cecchi[1]

[1]Department of Biology, University of Pisa, CoNISMa, Pisa, Italy

[2]Stazione Zoologica Anton Dohrn, Naples, Italy

Correspondence
Iacopo Bertocci
Email: iacopo.bertocci@unipi.it

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Abstract

Although the importance of time after disturbance is well established in the ecological literature, studies examining how differences in growth rate affect species recovery and persistence in relation to the interval between recurrent perturbations are rare. We examined the response of two ephemeral primary producers inhabiting high-shore rock pools, epilithic microphytobenthos (EMPB), and green filamentous algae, to disturbance regimes varying for the time interval between consecutive events. Informed from an empirically parametrized growth model's outcomes, we tested the hypothesis that EMPB would be able to recover from more frequent disturbance compared with filamentous algae in a field experiment involving three physical disturbance patterns differing for the clustering degree: high, moderate, and low (20, 40, and 80 days between disturbances). We predicted that: high clustering would prevent the recovery of both taxa; moderate clustering would prevent the recovery of the slower growing taxon only (filamentous algae); both taxa would recover under low clustering. Results showed that EMPB persisted independently of the clustering degree, whereas filamentous algae did not withstand any disturbance regime. Dramatically different effects of disturbance on organisms with subtle differences in their growth rate indicate that even stronger responses may be expected from taxa with more markedly contrasting life histories.

KEYWORDS
climate change, extreme events, filamentous algae, microphytobenthos, recovery, temporal variability

Iacopo Bertocci and Elena Maggi contributed equally to this study.

INTRODUCTION

As climate change involves an increase in frequency and severity of extreme events such as heat waves, hurricanes, droughts, and floods, natural systems are becoming increasingly exposed to multiple and recurrent disturbances (Fischer & Knutti, 2015; Frölicher et al., 2018). Although there is wide evidence that extreme disturbances can drive drastic changes to the structure and functioning of terrestrial and aquatic ecosystems (Benedetti-Cecchi, 2021; Boucek & Rehage, 2014; Garrabou et al., 2009; Voloisciuk et al., 2016), their actual impact depends on several characteristics, including nature, duration, intensity, spatial extent, and return time (Pickett & White, 2013). These are components of the spatial and temporal regime of disturbance, which, together with life history traits of exposed organisms, are key determinants of responses at different levels of biological organization (Capdevila et al., 2022; De Battisti, 2021; Louthan et al., 2022; Ratajczak et al., 2017; Rindi et al., 2017).

Over the last two decades, studies based on the manipulation of the frequency of pulse events or of the alteration of their temporal variance, the interval of time between subsequent events (Benedetti-Cecchi et al., 2006; Bertocci et al., 2005, 2017; Dal Bello et al., 2017; Garcìa-Molinos & Donohue, 2010; McCabe & Gotelli, 2000), provided a direct test of the effects of natural perturbations predicted to increase in intensity and clustering, that is, the degree of separation between consecutive events, under climate change (e.g., Easterling et al., 2000). For instance, meteorological time series spanning the period 1901–2010 revealed a strong clustering of tropical cyclones, with periods of high activity characterized by several recurrent events separated by relative calm periods, along the coasts of the Caribbean Sea and the northern Atlantic region between Africa and the Caribbean (Mumby et al., 2011). In general, such studies highlighted that changes in temporal variance of disturbance can be as important as those in mean intensity to structure natural assemblages. Moreover, there is evidence that time since the last disturbance is a major determinant of fluctuations in population abundance and community structure in tropical regions (Holmgren et al., 2013; Mumby et al., 2011), grasslands (Fuchslueger et al., 2016), and Mediterranean coasts (Voloisciuk et al., 2016). Experiments indicated that the main effects of temporal variance of disturbance depend on how much time is available between two (clusters of) events; this dependency is associated with the recolonization ability and growth rate of different organisms (Benedetti-Cecchi et al., 2006; Bertocci et al., 2005; Dal Bello et al., 2017, 2019; Holmgren et al., 2013). Although growth rate is acknowledged as a key process influencing recovery,

studies examining how differences in growth rate affect species recovery and persistence in relation to the interval between recurrent perturbations are still rare (Hillebrand & Kunze, 2020). This remains a critical gap to understand how species respond to increasingly frequent and intense disturbances (McDowell et al., 2020; Oliver et al., 2018).

Epilithic microphytobenthos (EMPB) and filamentous algae are fast-growing primary producers that usually characterize the early stages of colonization of disturbed patches on rocky shores (Benedetti-Cecchi & Cinelli, 1993; Jackson et al., 2013). Profound changes in the abundance of these organisms can have dramatic ecological consequences since EMPB provides the main fraction of biomass consumed by herbivores on rocky shores (Underwood et al., 2017), and aquatic microbial biofilms in general are essential for life cycles and metabolic processes of macroorganisms as settlement cues for spores and larvae and part of holobiont associations (Egan et al., 2013; Huang & Hadfield, 2003; Longford et al., 2019; O'Connor & Richardson, 1998). Analogously, green filamentous algae of the order Cladophorales are an essential component of aquatic ecosystems as providers of oxygen to the water and modulators of nutrient cycling (Krause-Jensen et al., 1996, 1999), as well as species of *Cladophora* are a preferred food source for marine invertebrates such as amphipods and isopods (Goecker & Kåll, 2003). EMPB include diatoms, cyanobacteria, and macroalgal spores and germlings, embedded within an extracellular polymeric matrix (Wolfstein & Stal, 2002). EMPB can respond quickly to perturbations owing to its fast growth rates and can withstand repeated shocks from extreme events (Dal Bello et al., 2017; Larson & Sundbäck, 2012; Thompson et al., 2004). Dal Bello et al. (2019) observed EMPB biomass to reach high values in the rocky intertidal when exposed to sediment deposition events separated by 60 days, but it collapsed in response to the same events applied every 15 days. Filamentous macroalgae are also fast-growing organisms that can respond quickly to perturbations (Benedetti-Cecchi et al., 2005). Compared with EMPB, however, such ephemeral algae may take more time to recover, as they appeared to require at least three months to colonize disturbed patches (Airoldi, 2003; Benedetti-Cecchi et al., 2005). Differential responses of EMPB and green filamentous algae to disturbance may have profound ecological implications since, for instance, contrarily to EMPB, the development of filamentous mats may cause marked variations of oxygen concentration associated with their cycles of growth and decay, and reduce the amount of nutrients available to other organisms due to the their great ability to assimilate nutrients from the water column (Krause-Jensen et al., 1996; Risgaard-Petersen et al., 1994; Sfriso et al., 1987).

We combined simulations and experiments to examine the response of EMPB and filamentous algae inhabiting high-shore rock pools to repeated disturbances. These pools are occasionally exposed to extreme events of desiccation and mechanical disturbance by storm waves and provide a tractable model system for manipulative experiments (Hawkins et al., 2020). First, to substantiate the differences in recovery between EMPB and filamentous algae reported in the literature, we developed a simple growth model that was parametrized with field data from previous recovery experiments. In such a context, we did not refer to growth rate as an individual trait, but as a characteristic of sessile taxa including a set of species and individuals, that is, a variable that is often intended as a measure of the fitness of populations in fluctuating environments (reviewed by Metcalf & Pavard, 2007). Second, informed by the outcomes of our simulations and findings of previous studies, we performed a field experiment to test specific predictions about the ability of the two primary producers to recover from disturbances separated by varying recovery periods. We tested the following predictions: (1) an interval of 20 days between consecutive disturbance events would be too short to allow an effective recovery and persistence of both EMPB and filamentous algae; (2) 40 days between disturbances would still prevent the recovery and persistence of filamentous algae, the taxon characterized by lower growth rates, while they would allow the recovery of EMPB; (3) both EMPB and filamentous algae would recover and persist with disturbance intervals of 80 days.

METHODS

Study system

The experiment was carried out between February and November 2021 in rock pools located 30–50 cm above mean low water along the rocky coast of Calafuria, Italy (43°30′ N, 10°20′ E). Pools consisted of shallow depressions of the substrate with an average size of 0.67 ± 0.07 m^2 (mean $\pm$ SE, $n = 40$), periodically exposed to extreme events of disturbance by waves during storms and prolonged desiccation during periods of good weather associated with high barometric pressure and calm sea (Benedetti-Cecchi et al., 2005). Under such harsh environmental conditions, assemblages are simple and dominated, especially in patches of open space, by EMPB, mainly composed of cyanobacteria (Maggi et al., 2017), and filamentous green algae (*Chaetomorpha aerea* [Dillwyn] Kützing and *Cladophora* spp.). At this shore height, the most common grazers are limpets *Patella* spp. and

littorinid snails *Melarhaphe neritoides* (Linnaeus, 1758) (Benedetti-Cecchi et al., 2005; Dal Bello et al., 2017).

Model and simulations

We developed a simple growth model to explore temporal dynamics of both filamentous algae and EMPB under different scenarios of temporal clustering of disturbance (time interval between consecutive events). The main feature of the model was that biomass grew logistically following a Gomperzt equation:

$$\frac{dB}{dt} = rB(\log(K) - \log(B)) + \sigma B \frac{dW}{dt},$$

where B is the biomass (percentage cover for filamentous algae and micrograms of chlorophyll a per square centimeter for EMPB), t is time, r is the per capita growth rate, and K is the carrying capacity.

Parameters were estimated separately for filamentous algae and EMPB by fitting the model to time series derived from previous disturbance–recovery experiments conducted in the same study area. Likelihood profiles and 95% CIs were inspected to ensure that parameters were well defined (see, for details, Appendix S1: Table S1 and Figures S1–S4). Maximum likelihood parameter estimates were obtained with the mle2 function of the bmle library in R, assuming lognormal errors (Bolker, 2008). Predicted time series were obtained by integrating over time initial biomass values. We used the ode function of R package deSolve, with backward differentiation formula (Soetaert et al., 2012). We then established three temporal patterns of disturbance consistent with previous experimental evidence on the ability of EMPB and ephemeral filamentous algae to recover in cleared patches in ~1–2 months and 3 months, respectively (Airoldi, 2003; Benedetti-Cecchi et al., 2005): (1) a lowly clustered scenario, in which we imparted repeated disturbances (reduction by 50% of the extant biomass at each event) separated by 80 days; (2) a moderately clustered scenario, where consecutive disturbance events were separated by 40 days; (3) a highly clustered scenario, with consecutive events separated by 20 days. We constructed a set of simulated time series for each scenario starting from 50 different initial biomass values randomly selected out of normal distributions, for a period of 290 days. Simulations were performed using an Euler–Murayama method with Ito calculus (Iacus, 2008) and showed that the growth rate of EMPB ($r = 0.024$) was six times higher than that of filamentous algae ($r = 0.004$). Further details on model derivation and simulations are provided in Appendix S1.
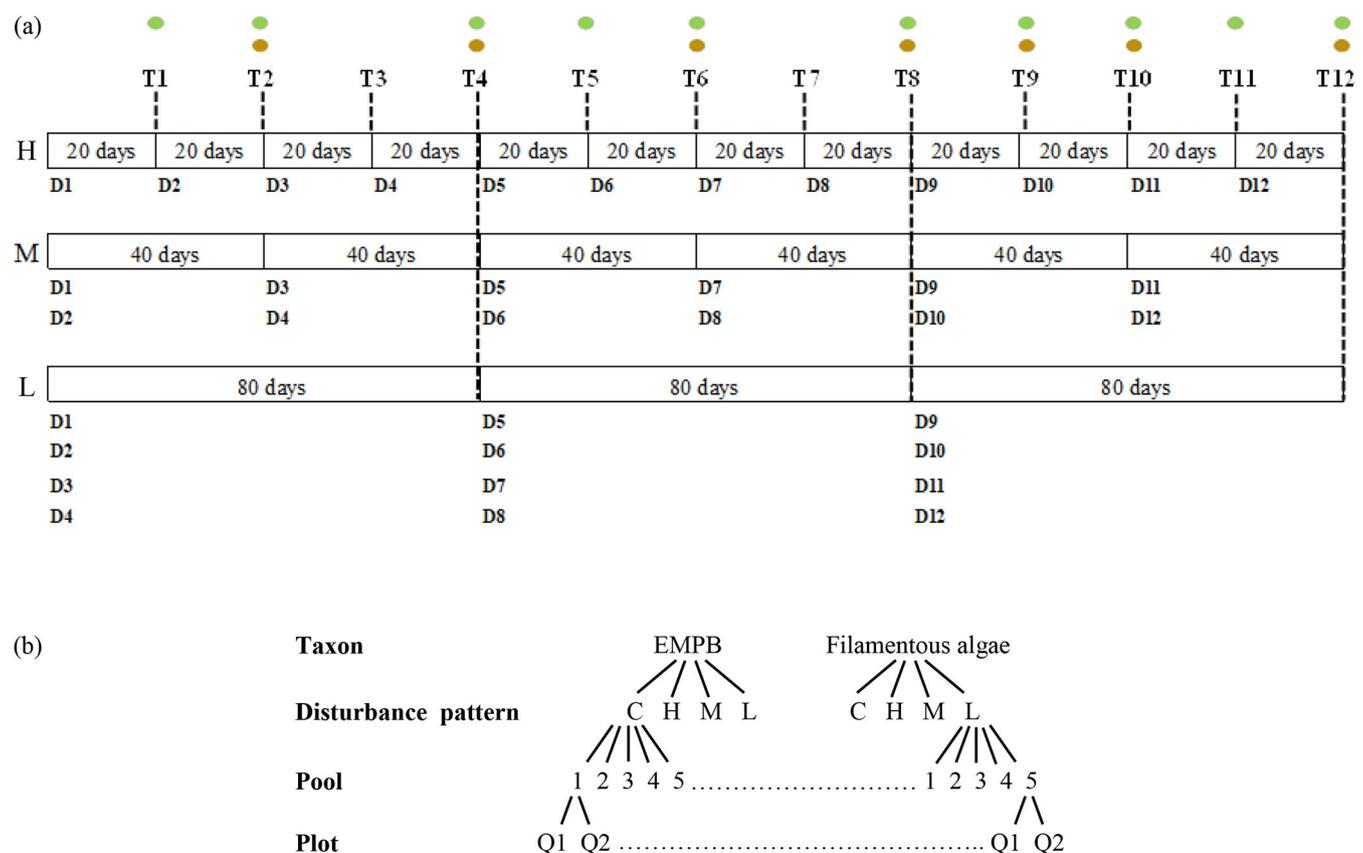
Experimental design

The experiment was carried out in a total of 40 rock pools, distributed along about 1 km of coastline, which were marked at the beginning of the study with a numbered plastic tag for subsequent relocation. Each pool was photographed, and its surface area was digitally estimated with the ImageJ program (Abràmoff et al., 2004). In each pool, two plots (10 × 10 cm each, 10 cm apart) initially dominated by filamentous green algae were marked at corners with epoxy putty. In 20 randomly selected pools, the two plots were left dominated by filamentous algae, while in the remaining 20, interspersed among the others, each plot was subject to the removal of all macro- and microscopic organisms using a chisel operated by a battery drill. This procedure allowed the subsequent dominance of the substratum by EMPB, which generally represent the earliest colonizers of bare patches.

In each group of 20 pools, five were assigned at random to each of four experimental conditions applied to both plots: (1) control (no manipulation after marking);

(2) high degree of disturbance clustering (a total of 12 events of disturbance applied over 9 months, with a 20-day interval between consecutive events); (3) moderate degree of clustering (same total number of events over 9 months, but with a 40-day interval between groups of two events repeated in consecutive days); and (4) low degree of clustering (same total number of events and experimental duration, but with a 80-day interval between groups of four events repeated in consecutive days). Such a structure of the experiment guaranteed that the total intensity and frequency of disturbance remained constant across all levels of temporal pattern, while varying the recovery time available to each group of organisms (Figure 1a,b).

Experimental disturbance was produced by battering the rock with a chisel operated by a battery drill, analogously to previous studies (Bertocci et al., 2005, 2017). Each event of disturbance consisted in chiseling each plot once, with the caution of keeping the applied force comparable among events and treatments through the use of the same chisel and drill, always operated by the same

FIGURE 1 Diagrammatic representation of (a) three experimental patterns of disturbance with 20 (high clustering, H), 40 (moderate clustering, M), and 80 (low clustering, L) days between events (D1–D12). T1–T12 are the scheduled sampling times. Green and brown circles represent the availability of data for green filamentous algae and epilithic microphytobenthos (EMPB), respectively. Missing data at some sampling times were due to adverse meteorological conditions or instrument failure. In the full experimental design (b), each pattern was crossed with each taxon, and five rock pools were allocated to each combination of factor levels, with two replicate quadrats in each pool.

researcher. The visual inspection of plots indicated that two clustered events of disturbance were able to remove most organisms from the substrate.

Collection and analysis of data

Before the application of the first disturbance event, the size of rock pool was analyzed to guarantee that the mean area was comparable among pools allocated to each experimental condition, a preliminary requirement due to the known ecological effect of rock pool size (Metaxas et al., 1994) (Appendix S2).

We planned to estimate the abundance of filamentous algae and EMPB in the field every 20 days. When sampling coincided with experimental disturbance, it was done immediately before the disturbance event, for a total of 12 planned sampling events (T1–T12 in Figure 2). Unfortunately, bad sea conditions prevented to perform both T3 and T7.

The percentage cover of filamentous algae was estimated visually using an 8×8 cm grid, placed in the center of each plot to avoid edge effects. An indirect estimate of EMPB biomass was obtained through in vivo measurements of minimum chlorophyll a fluorescence following a period of dark adaptation (F_0), using a portable underwater pulse-amplitude-modulated fluorometer (Diving-PAM, Walz). Two measurements were taken in each plot from pools assigned to the EMPB condition after 5 min of dark adaptation (Maggi et al., 2015). The two values were then averaged to obtain a single value of biomass of EMPB for each plot.
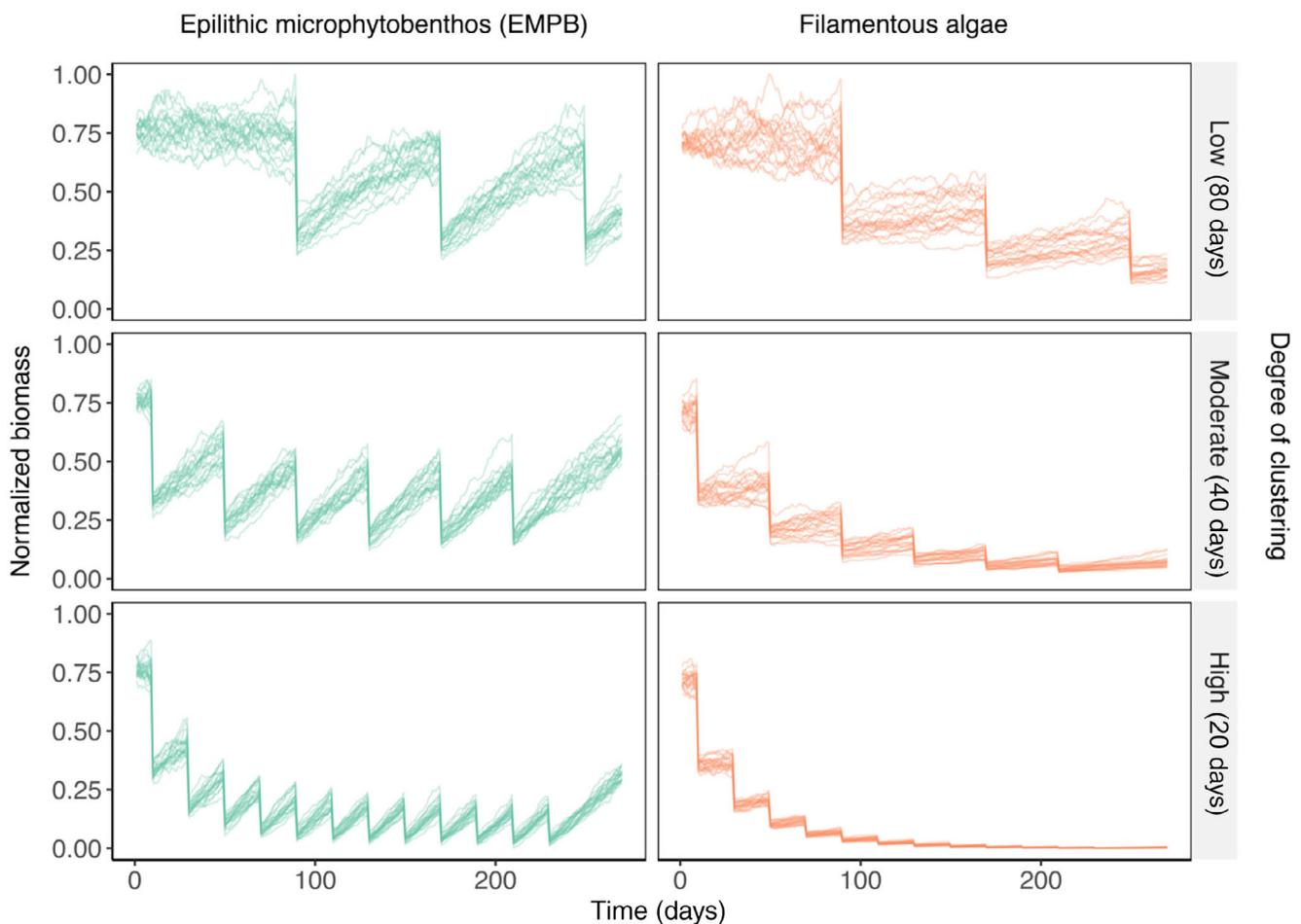
FIGURE 2 Modeled temporal trends of recovery of epilithic microphytobenthos (EMPB) and green filamentous algae under different degrees of disturbance clustering (low, 80-day interval; moderate, 40-day interval; high, 20-day interval). Each disturbance event removed 50% of total biomass of each taxon. Low clustering of disturbance events allowed both groups to recover and maintain relatively large biomass during the interval between clustered disturbances, although EMPB increased in abundance faster than filamentous algae. Moderate clustering of disturbance maintained the abundance of filamentous algae consistently low over the experiment, while allowing EMPB to increase in abundance during the interval between clustered disturbances. High clustering of disturbance maintained the abundance of both taxa consistently low (almost null) over the experiment.

To compare the abundance of filamentous algae with F_0 of EMPB, we estimated biomass from percentage cover values using linear regression based on the least squares method, eventually rescaling values to vary in the range [0,1] to express the biomass of both groups under the same unit (see Appendix S3 for details).

Since EMPB biomass was almost null until the end of the second 80-day period, we analyzed only data collected during the last 80-day period (from T8 to T12, across which each pool had received the same intensity of disturbance, i.e., four events, preceded by a total of seven events). Rescaled $\log(x + 0.1)$-transformed biomass data were analyzed with linear mixed-effects models (LMEMs; Singer & Willett, 2003). A first analysis included both control and disturbed pools and tested how the effect of disturbance, compared with controls, varied between taxa. The fixed part of the model included the a priori contrast between control and disturbed pools (control vs. disturbed), crossed with "taxon" (fixed, two levels: EMPB and filamentous algae). A second analysis included disturbed pools only and tested how effects of disturbance clustering (low, moderate, and high) varied between taxa. The fixed part of the second analysis included the factor "Disturbance clustering" crossed with "taxon", while the factor "pool" was included in the random part of both models. This allowed to test for the effect of experimental treatments on mean biomass values over T8–T12, taking into account the correlation due to the sampling of each pool and plot at subsequent times. All statistical analyses were performed in R v3.6.1 (available at: https://www.r-project.org). Statistical assumptions were checked graphically using the check_model function in the performance package. LMEMs were run using the lmer function in the lme4 package and summarized results were reported as ANOVA output, while post hoc comparisons were run using the emmeans function of the emmeans package.

RESULTS

Model simulations revealed divergent patterns of recovery of EMPB and filamentous algae exposed to a moderate level of clustering of disturbance, with EMPB recovering within the time interval between disturbances of 40 days and filamentous algae maintaining low biomass (Figure 2). Both filamentous algae and EMPB showed a full recovery within the time interval of 80 days (low level of clustering), while a time interval of 20 days (high level of clustering) hindered the recovery of both taxa (Figure 2). Both groups showed qualitatively similar temporal patterns of recovery over a wide range of disturbance intensities (Appendix S1: Figure S5a–i).

In agreement with simulations, experimental results showed that the differences in biomass between control and disturbed pools were significantly smaller for EMPB than for filamentous algae during the last 80 days of the experiment (control vs. disturbed × taxon, MS = 2.089, $F_{1,1} = 11.39$, $p < 0.05$; see Figure 3 and Appendix S4). The normalized biomass of filamentous algae remained very low and lower than that of EMPB when any disturbance pattern was applied (taxon, MS = 3.667, $F_{1,2} = 18.05$, $p < 0.001$). Interestingly, the difference between pools disturbed every 40 days and those disturbed every 80 days (disturbance clustering, MS = 0.739, $F_{2,2} = 3.64$, $p < 0.05$) was clearly driven by the difference in EMPB biomass, while values for filamentous algae remained comparable among levels of clustering of disturbance (Figure 3 and Appendix S4).

DISCUSSION

Our findings showed that two ephemeral taxa with slightly different growth rates differed drastically for their ability to persist under recurrent disturbances. Specifically, while EMPB exposed to any disturbance pattern could persist with relatively large biomass during the last 80-day period, the consistently low and decreasing biomass of green filamentous algae indicated that they were unable to withstand even a regime of disturbance characterized by 80 days between events. Over the entire duration of the experiment, however, neither EMPB nor filamentous algae could reach the biomass values observed in the corresponding control, regardless of the applied disturbance pattern.

This study spanned different seasons and phases of development of target organisms, and results could be explained as potentially driven by the interaction between effects of the variable regime of disturbance and those of other exogenous factors (see also Dal Bello et al., 2019). Despite previously observed fast and large temporary increases in abundance associated with favorable environmental conditions, the morphology of green filamentous algae does not confer great resistance to the direct physical impact of extreme disturbance events (Malkin et al., 2008). So, their low recovery in the present study is consistent with the findings of recent meta-analyses revealing that recovery to pulse disturbances tends to be faster and more complete when systems have high resistance (Hillebrand & Kunze, 2020). Indeed, the high growth rate during spring (coinciding with the first 80-day period in this experiment), which is typical of filamentous algae on temperate coasts (Benedetti-Cecchi & Cinelli, 1996), was not enough to allow these algae to recover even under the longest intervals of time between consecutive disturbances. Likely, the
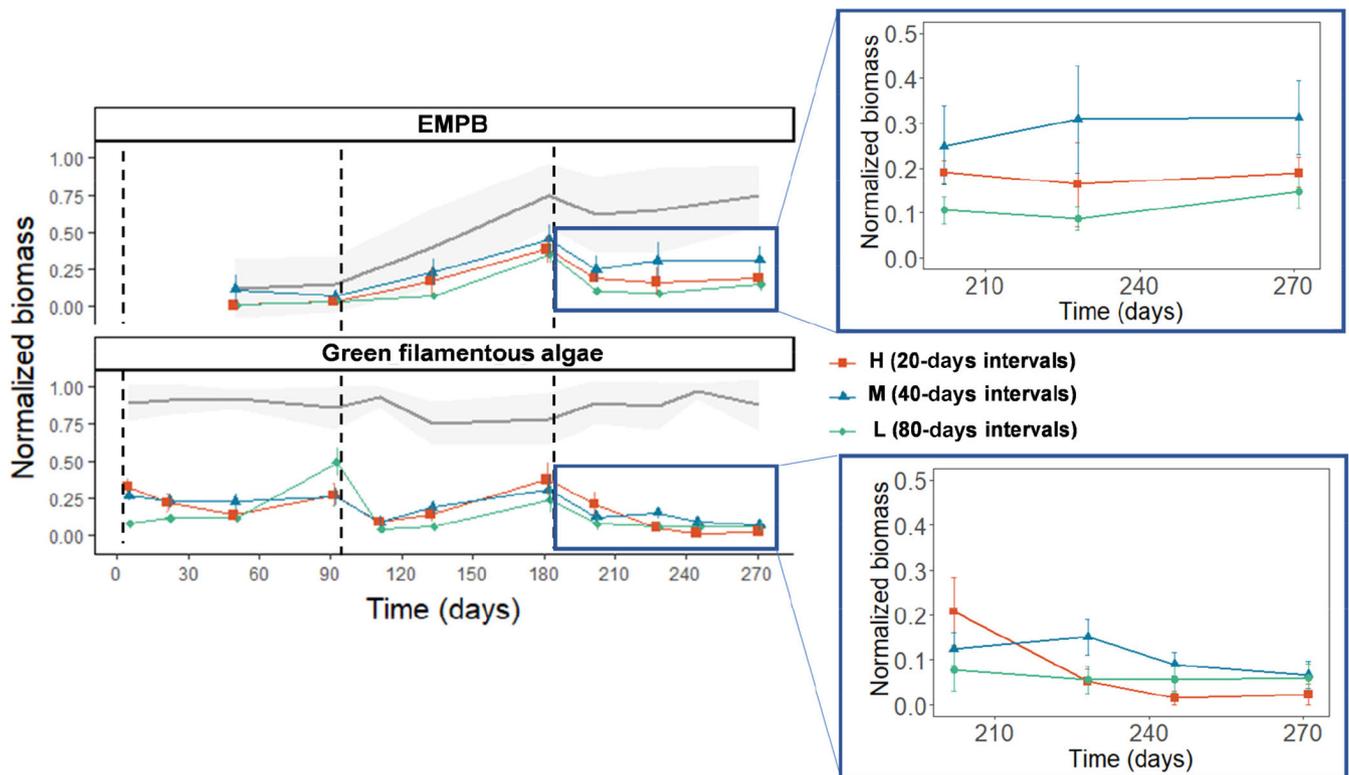
FIGURE 3 Temporal variation of normalized biomass (±SE, $n = 10$) of epilithic microphytobenthos (EMPB) and green filamentous algae in control rock pools (black line, with gray area indicating 95% CI) and pools allocated to high (H), moderate (M), and low (L) clustering of disturbance (as in Figure 1). Vertical dashed lines mark disturbance events occurring at the beginning of each of three 80-day periods over which H, M, and L received the same total number of events.

effects of disturbance were even more negative later in summer, associated with extremely high temperature, irradiation, and variation in salinity, oxygen, and pH (e.g., Huggett & Griffiths, 1986). Under such extreme environmental conditions, green filamentous algae may have been characterized by a stressed physiological state (Gray et al., 2007), resulting in their almost disappearance from disturbed pools.

Unlike green filamentous algae, EMPB could persist with relatively large biomass throughout the experiment and, during the last 80-day period, with significantly larger values under disturbance events applied every 40 days than every 20 or 80 days. Regarding our hypotheses, a question would be why EMPB biomass did not increase to reach control values even after 80 days since the preceding disturbance. Previous studies indicated that increasingly stressful environmental conditions in summer can make EMPB assemblages more susceptible to collapse in response to a subsequent disturbance (Dal Bello et al., 2019; Nagarkar & Williams, 1999). In addition, temporal changes in EMPB composition could have played a role, analogously to what was observed in grassland communities, where plant diversity increased stability through its positive effects on species asynchrony, implying the ability

of increases in biomass of some species to compensate the loss of other species (Hector et al., 2010; Isbell et al., 2009). Our sampling procedures, in particular, focused on autotrophic organisms, thus neglecting other components of microbial biofilms, which commonly comprise a range of other metabolic modes (Dang & Lovell, 2016; Maggi et al., 2020) whose potential increase could not be captured. Assessing the response of nonautotrophic components of biofilms to disturbance was beyond our goals, but it represents a future direction of research.

Nevertheless, the ability of EMPB to persist independently of any interval between disturbances could be related to both biotic and abiotic processes. Large fluctuations in EMPB biomass are driven by changes in abundance of grazers (Christofoletti et al., 2011; Maggi et al., 2020; Skov et al., 2010). In our study habitat, one of the main grazers of EMPB is the littorinid *M. neritoides*, which is more abundant in autumn–winter than spring–summer, and mainly active under wet conditions (Dal Bello et al., 2017). This behavior may explain the very low biomass until T4 and the subsequent increase when grazing likely started to weaken.

Although EMPB and ephemeral green algae are the only dominant organisms in our rock pools and can play

a similar role in terms of primary production and food for grazers, their contrasting responses to disturbance can become of great ecological importance in systems where other macroalgae can potentially settle with high rates or where blooms of ephemeral green algae can exert adverse effects. For example, our findings suggest that relatively frequent disturbances could maintain the biomass of filamentous algae consistently low, eventually preventing oxygen depletion due to excessive respiration during the night or intense decomposition of large algal biomasses (Anderson, 2009; Lyons et al., 2014; Valiela et al., 1997). By contrast, the same disturbance regime could allow microbial biofilms to become dominant, which could potentially affect biological interactions through direct and indirect mechanisms. In some cases, for instance, extant biofilms enhanced the settlement of ephemeral green algae, eventually buffering the negative effect of disturbance on the same species (Eriksson et al., 2006; Lotze et al., 1999; Worm et al., 2001). In other cases, instead, green algal blooms were indirectly inhibited by biofilms that accelerate the settlement of competing macroalgae (Park et al., 2022). Moreover, on rocky intertidal shores comparable to the present one, a number of small invertebrates were found within mats of green filamentous macroalgae (Best et al., 2014), a habitat that would clearly become unavailable if recurrent disturbances prevent the persistence of these forms in favor of a biofilm-dominated substrate, with consequent loss of biodiversity.

The present study aimed at deepening current knowledge on which characteristics of organisms are key to drive their resilience and recovery under recurrent pulse disturbances, rather than gradual changes in environmental conditions. Life history traits were often discussed as potentially responsible for changes in sensitivity to and recovery from disturbance, but the actual driving role of such changes was not yet identified (Hillebrand & Kunze, 2020). Answering this question has important implications for the management of populations and assemblages exposed to environmental changes, such as those associated with extreme events (Geist & Hawkins, 2016). For instance, it was reported that just small differences in life histories of similar coral species may result in persistent large differences in their population growth and abundance, although monitored over six years with no major disturbances (McWilliam et al., 2022). In this respect, both our target taxa could be considered ephemeral and early colonizers of disturbed patches. Our results, however, show that relatively small differences in growth and recolonization ability can drive dramatically different responses to the same regime of disturbance (see also Louthan et al., 2022). This suggests that biological responses and ecological implications would be even stronger when involving taxa with more markedly contrasting growth rates. Such taxon-specific features could greatly contribute to changes in patterns of abundance of organisms developing after various disturbances and eventually to recovery in assemblage composition, a key requirement for full functional recovery (reviewed by Hillebrand & Kunze, 2020). Indeed, the possibility of species to persist after increasingly severe disturbance events, such as those associated with climate change, depends on their intrinsic ability to resist to and recover from such events (Capdevila et al., 2022). Understanding these dynamics is needed to develop effective management strategies and can substantially benefit from their evaluation at relatively low levels of biological organization (Capdevila et al., 2020).

In this respect, our results suggest that profound changes to the structure of natural assemblages can occur through contrasting responses to recurrent disturbances of similar constituting taxa in terms of trophic position, longevity, and growth rate.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data and R codes (Bertocci et al., 2023) are available from Figshare: https://doi.org/10.6084/m9.figshare.22819718.v1.

ORCID
Luca Rindi https://orcid.org/0000-0002-2279-4214

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.