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Assessment of grazing effects on phytobenthic community structure at shallow rocky reefs: An experimental field study in the North Aegean Sea

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ABSTRACT

Overgrazing can deplete macroalgal communities and lead to reduction of habitat complexity and species diversity. To quantify the effects of sea urchin and fish herbivory on the rocky reefs of the North Aegean Sea, a six-month grazer exclusion experiment was conducted at the southeastern part of Lesvos Island at three rocky reef sites at depths between 1.0 and 4.7 m. The aim was to test whether (a) algal growth is hampered by the combined grazing activity of sea urchins and fish, and (b) algal growth is suppressed by the foraging of fish alone. At each site, three replicate cage, cage-control, and control treatments were applied and sampled every two weeks using photoquadrats: (1) fully-closed cages that excluded both sea urchins and large herbivorous fish; (2) open-top cages that excluded sea urchins only; and (3) control surfaces with no restrictions on herbivores. Algal biomass was estimated based on the percentage cover values of the analyzed images. Underwater surveys for the estimation of sea urchin population density (by quadrat sampling) and total fish biomass (by strip transects) were also conducted. The main grazers observed were the sea urchins *Arbacia lixula* and *Paracentrotus lividus*, and the herbivorous fish *Sarpa salpa*. Herbivorous fish dominated fish communities, but the overall fish biomass density was relatively low. The experimental monitoring of algal biomass showed that erect algal growth was significantly higher inside the fully-closed cages in contrast to the respective controls. Overall, algal growth was significantly higher inside both types of cages, when compared to the control surfaces. No significant differences among the two types of cages were found in terms of total algal growth, indicating that urchin grazing was the most important factor causing the hampering of algal growth and altering the structure of the macroalgal community towards a sparse vegetation of low complexity devoid of erect algae, while herbivore fish had a minor effect.

1. Introduction

Macroalgal forests created by large, brown seaweeds of the order Fucales and Laminariales are a fundamental feature of the rocky sublittoral ecosystems. These complex and diverse algal communities are among the most important seabed biotopes (Bennett et al., 2016; Salomidi et al., 2012): they contribute to the regulation of essential biophysical processes, such as primary production and nutrient cycling (Boudouresque et al., 2014), provide refuge for fish and invertebrates, and play a vital role in the conservation of benthic communities (Ballesteros, 1990; Cheminée et al., 2013; Gianni et al., 2013 and references therein). In the Mediterranean Sea, macroalgal species of the genus *Cystoseira* and *Sargassum* (order Fucales) are the main contributors of macroalgal forests, which represent the climax community of the shallow sublittoral zone in well-preserved waters, and are commonly used as indicators of good environmental status (Ballesteros et al., 2007; Orfanidis et al., 2001, 2011). However, these late-successional, perennial species are particularly susceptible to multiple stressors that affect coastal ecosystems, and have suffered major losses in species diversity, area cover, and biomass (Thibaut et al., 2005, 2015; Tsiamis et al., 2013). For this reason, Mediterranean rocky habitats that are dominated by canopy-forming algae were recently classified as endangered in the European Red List of Habitats (Gubbay et al., 2016).

A severe depletion of erect algal cover can eventually lead to the creation of unproductive areas of low complexity, called "rocky-barrens", which are characterized by extended bare rock and the dominance of encrusting algae (Benedetti-Cecchi et al., 1998; Bulleri et al., 2002; Gagnon et al., 2004; Perreault et al., 2014; Sala et al., 2011). The transition from diverse phytobenthic communities to encrusting algae-dominated barrens is considered as a catastrophic drift from a productive state to a non-prolific one that threatens biodiversity (Steneck et al., 2002). The formation of these new impoverished habitats is increasingly common at a global scale along temperate coastal regions

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(Filbee-Dexter and Scheibling, 2014; Vergés et al., 2014). However, the mechanisms that induce these phase shifts are not always straightforward, as there are multiple factors involved in the development of alternative states. Anthropogenic pressures such as illegal fishing practices, marine pollution, habitat fragmentation, and ocean warming, are generally considered the main drivers of the degradation of macroalgal forests (Airoldi et al., 2009; Guidetti et al., 2003; Vergés et al., 2016) and shifts in community structure and function (Airoldi and Beck, 2007; Bianchi et al., 2014). At the same time, food web alterations, sea urchin population explosions, and overgrazing (i.e., when grazing rate overcomes algal growth; Eklöf et al., 2008) are also known to have a detrimental effect on macroalgal species and the associated benthic communities (Pinnegar et al., 2000; Sala et al., 1998).

To understand and confront regime shifts and degradation of rocky reefs, research effort should focus on identifying the mechanisms that produce or aggravate state resilience (Ling et al., 2015). In the western Mediterranean, Boada et al. (2017) examined the effect of nutrients on state resilience. They showed that in oligotrophic ecosystems (as in the eastern Mediterranean), macroalgal communities are more vulnerable to sea urchin overgrazing when compared to nutrient-rich environments where the echinoids must achieve a higher population threshold to outcompete algal growth rates. There is strong evidence that barrens represent a new equilibrium state that is difficult to reverse (Boada et al., 2017; Ling et al., 2015). Sea urchins, in particular, appear capable of maintaining barren areas through the depletion of algal buds and seeds until their population is almost completely decimated, thereby protracting the needed time for the recovery of the macroalgal assemblages.

Herbivore exclusion is a common experimental approach that provides insights on ecological processes and biological interactions between algae and grazers (Baggini et al., 2015; Lotze et al., 2001; Sala and Boudouresque, 1997). The experimental exclusion of herbivores offers a direct comparison between two different dynamic states: one exposed to herbivory (control) and one with reduced grazing pressure (experimental exclusion of grazers). The wide application of this approach at a global scale (Poore et al., 2012) suggests that the algal groups most heavily affected by grazing pressure are the fleshy algal species with an upright structure of the orders Fucales and Laminariales (i.e., species responsible for the creation of algal forests). In the western and central Mediterranean Sea, the sea urchins *Paracentrotus lividus* and *Arbacia lixula* are considered as the primary grazers responsible for the creation and persistence of rocky barrens (Bonaviri et al., 2011; Bulleri et al., 1999; Guidetti and Dulcic, 2007), while native herbivorous fish such as *Sarpa salpa* are also known to cause strong algal declines (Gianni et al., 2017; Vergés et al., 2009). In the eastern Mediterranean Sea, the role of the alien herbivorous fish *Siganus luridus* and *S. rivulatus* has been detrimental and has led to extensive areas of rocky barrens (Sala et al., 2011). However, there is an overall scarcity of experimental studies that evaluate the impact of grazers on primary producers, especially in the eastern parts of the Mediterranean (e.g. Baggini et al., 2015; Sala et al., 2011); there is no such published work in the North Aegean Sea, where *Siganus* spp. are either absent or scarce.

The objective of this study is to investigate the potential effects of fish and sea urchin grazing on the macroalgal communities of shallow sublittoral rocky reefs at southeastern Lesvos Island (NE Aegean Sea). To this end, a herbivore exclusion caging experiment was conducted in order to test the following hypotheses: a) algal growth is hampered by the combined grazing activity of sea urchins and fish, and b) algal growth is suppressed by the foraging of fish alone. Algal growth was quantified using a photographic method, while complementary visual surveys were conducted to estimate the abundance of sea urchins and fish in the study area. This combined information provided insights into the processes that shape the current state of macroalgal assemblages.

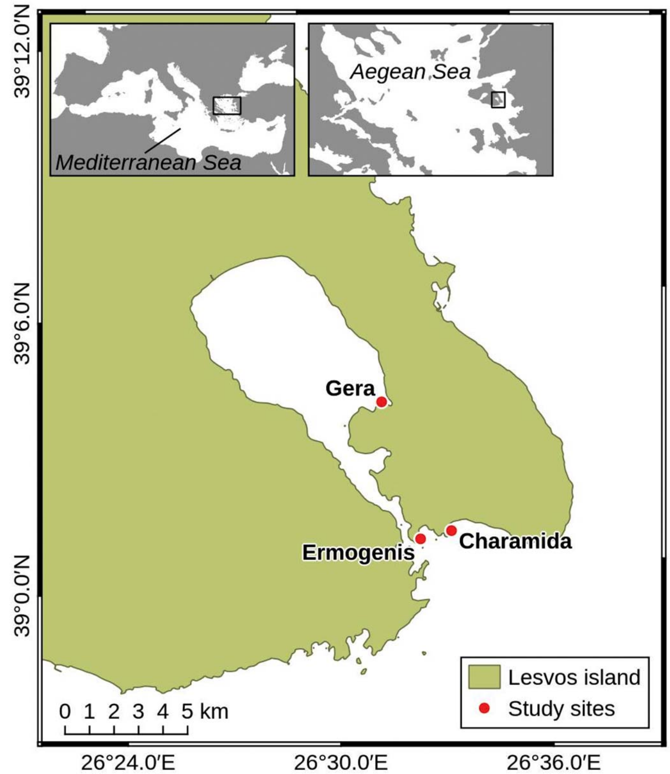

Fig. 1. Location of the study sites at the southeastern part of Lesvos Island, North-East Aegean Sea.

2. Materials and methods

2.1. Study area

The study took place in the southeastern part of Lesvos Island, located in the North Aegean Sea, Greece, Mediterranean Sea (Fig. 1). A herbivore exclusion caging experiment was conducted at the rocky reefs of three sites: Charamida (39.014° N, 26.557° E), Ermogenis (39.013° N, 26.543° E) and Gera (39.063° N, 26.528° E). Charamida and Ermogenis are southward-facing coastal areas that are exposed to the open sea, and are primarily affected by south and southeastern winds. In both sites, rocky reefs form part of the coastline and are adjacent to extensive *Posidonia oceanica* meadows. The site of Gera is located in a semi-enclosed, shallow-water gulf (max depth: 18 m) that is characterized by high seasonal variability in terms of physico-chemical and hydrodynamic conditions (Kolovogiannis and Tsirtsis, 2005). Rocky reefs are primarily found in the southeastern coasts of the gulf, neighboring with soft-bottom substrates.

2.2. Experimental design

The herbivore exclusion experiment included two types of treatment and one type of control surfaces: (1) fully-closed cages that excluded both sea urchins and large herbivorous fish (Fig. S1e); (2) open-top cages that excluded sea urchins, but were exposed to fish grazing (Fig. S1f); and (3) control surfaces without cages which were delimited by permanent markings. Three replicates of each treatment were applied at each site. The cages were constructed using PVC frames (40 × 60 × 25 cm) and plastic mesh (2 × 2 cm opening), following Sala and Boudouresque (1997), and were installed on horizontal or gently-sloping rocky surfaces at a depth range of 1.0–4.7 m (mean depth: 2.8 m). A manual drill was used (Fig. S1a) to permanently fix stainless steel bolt anchors onto the rocky surfaces (Fig. S1b, c), and a system of ropes and hangers secured the cages in place (Fig. S1d). Cages