Estuarine, Coastal and Shelf Science 133 (2013) 88–96

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Pulses of phytoplanktonic productivity may enhance sea urchin abundance and induce state shifts in Mediterranean rocky reefs

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ARTICLE INFO

Article history:
Received 28 January 2013
Accepted 10 August 2013
Available online 20 August 2013

Keywords:
bottom–up control
Cystoseira brachycarpa
coralline barrens
Diplodus spp.
marine protected areas
Paracentrotus lividus
top–down control
trophic cascades

ABSTRACT

This paper tests the hypothesis that increased planktonic primary productivity may enhance sea urchin recruitment and trigger changes in the structure of benthic communities in oligotrophic temperate regions. Underwater surveys were conducted in the marine reserve of northern Minorca (Balearic Archipelago, western Mediterranean) and an adjoining control area in 2005 and 2012 to assess the abundance of fishes and sea urchins and the cover of macroalgae before and after a natural pulse of planktonic primary productivity. The biomass of most fishes, including that of sea urchin predators, increased significantly in the whole area two years after the productivity pulse, without any effect of management or depth. The abundance of sea urchins also increased throughout the whole area two years after the productivity pulse, but the average test diameter decreased, thus revealing improved recruitment. The aggregated cover of erect algae and that of *Cystoseira brachycarpa* did not change significantly from 2005 to 2012, but the cover of turf-forming algae was negatively correlated with the biomass of sea urchins, whereas the cover of coralline barren was positively correlated with the biomass of sea urchins. The overall evidence indicates that planktonic primary productivity is a key factor in the dynamics of sea urchin populations in oligotrophic regions and that improved sea urchin recruitment after productivity pulses in spring and early summer may result in sea urchin populations sufficiently dense to result in the development of coralline barrens independently on the density of sea urchin predators.

1. Introduction

Marine communities can suffer gradual or sudden significant shifts between alternative stable states. Different mechanisms may underlie the initiation, maintenance and end of a regime and interactions between multiple drivers may be necessary to trigger shifts in state (Rassweiler et al., 2010). Temperate subtidal rocky reefs occur in either of two states: a brown seaweed forest or a coralline algal crust pavement (Graham, 2004; Petraitis and Dudgeon, 2004; Estes et al., 2010). Changes in the intensity of sea urchin grazing is usually the primary force driving shift from one state to the other and sea urchin abundance has been proposed to be controlled primarily by predators (Estes et al., 2010).

The interactions between predatory fishes and sea urchins have been intensely studied within this framework, often revealing the existence of alternative stable states and trophic cascades at local scales (Sala, 1997; Sala et al., 1998; Hereu et al., 2005; Micheli et al., 2005; Guidetti, 2006; Hereu, 2006). However, the pattern proves to be more complex at larger spatial and temporal scales, as dense brown seaweed forests may also exist even when sea urchin predators are scarce (Babcock et al., 2010; Sala et al., 2012). The reason is that sea urchin populations are controlled not only by local factors as predation, habitat complexity and recruitment, but also by factors operating at much larger time scales, such as pathogen outbreaks (Boudouresque et al., 1981; Chapman and Johnson, 1990; Feehan et al., 2012), flash floods (Fernández et al., 2006) and severe storms (Sanchez-Vidal et al., 2012). The return time of these phenomena is usually of several decades and hence they are poorly documented, although may have a large-scale impact on sea urchin populations.

The sea urchins *Paracentrotus lividus* and *Arbacia lixula* are the major native herbivores in the Mediterranean reefs (Sala et al., 1998), as Mediterranean native herbivorous fishes have only a

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http://dx.doi.org/10.1016/j.ecss.2013.08.020

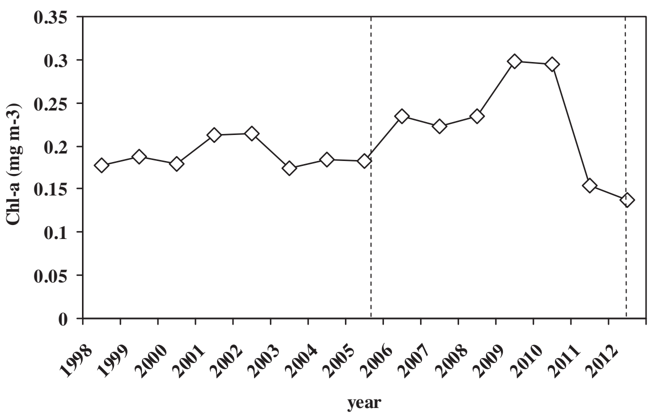

Fig. 1. Average monthly surface concentration of chlorophyll-*a* (mg m^{-3}) off the northern coast of Minorca during spring and early summer (March to July) from 1998 to 2012 according to SeaWiFS and Modis-Aqua data. Dashed vertical bars show when benthic communities were surveyed.

limited impact on macroalgae abundance (Vergés et al., 2009; Tomás et al., 2011) and green turtles *Chelonia mydas* forage primarily on sea grasses (Cardona et al., 2010). Only in the eastern Mediterranean is the Red Sea invasive rabbit fish (genus *Siganus*) also an important macroalgae consumer (Sala et al., 2011).

Pristine Mediterranean rocky reefs are though to be dominated by Fucales (Airlodi and Beck, 2007; Sales and Ballesteros, 2009, 2010; Perkol-Finkel and Airoldi, 2010), but this group of canopy forming macroalgae suffered a long-term decline through the last century (Thibaut et al., 2005; Mangialajo et al., 2008; Perkol-Finkel and Airoldi, 2010; Sales et al., 2011). Although poor water quality was often involved in such a decline (Thibaut et al., 2005; Mangialajo et al., 2008; Sales et al., 2011), sea urchin overgrazing due to intense fishing of sea bream (*Diplodus* spp.) and the resulting predator release was also postulated as a major causal factor (Verlaque, 1984; Frantzis et al., 1988; Sala, 1997, 2004; Sala et al., 1998; Bulleri et al., 1999; Micheli et al., 2005; Guidetti, 2006). However, recent research has failed to demonstrate the relationship between the abundance of sea urchin predators, sea urchin density and Fucales cover in most of the Mediterranean (Micheli et al., 2005; Cardona et al., 2007a; Giakoumi et al., 2012; Sala et al., 2012) and sea urchin barrens have developed within marine reserves where fish abundance has not changed (Coma et al., 2011).

Cardona et al. (2007a) argued that trophic cascades from fishes to sea urchins and Fucales did not operate in most of the Mediterranean Sea because the low planktonic primary productivity typical of most of the basin (Bosc et al., 2004) limited the recruitment of most fish and sea urchin species. The larva of *Paracentrotus lividus* would be particularly sensitive to this limitation, as they spend several weeks in the plankton during spring and early summer (Pedrotti, 1993; Hereu et al., 2004) foraging primarily on phytoplankton (Fenaux et al., 1985).

However, planktonic primary productivity during spring and early summer exhibits a notable interannual variability in most of the Mediterranean (Bosc et al., 2004), which could explain the high interannual variability also observed in the recruitment of *Paracentrotus lividus* (Hereu et al., 2004). Improved recruitment of sea urchins has been postulated to cause the formation of coralline barrens if sea urchin abundance increases beyond a certain threshold (Hereu et al., 2004; Coma et al., 2011) and hence pulses of intense phytoplankton productivity during spring and early summer may result in the improvement of sea urchins recruitment and promote the development of coralline barrens in oligotrophic regions, independently of fish abundance. Furthermore, the large-scale increase in the nutrient load of freshwater runoff during the 1970s and the 1980s and the resulting increase in the planktonic primary productivity in most Mediterranean coastal regions (Ludwig et al., 2009) could have enhanced sea urchin recruitment and contributed to the decline of Fucales at that time.

This tests the hypothesis that increased planktonic primary productivity may enhance sea urchin recruitment and trigger changes in the structure of benthic communities, by comparing fish and sea urchin abundance and macroalgae and coralline barren cover in northern Minorca (Balearic Archipelago, western Mediterranean) before and after a natural pulse of planktonic primary productivity. If sea urchin populations were recruitment limited, the increased levels of chlorophyll-*a* reported from 2009 to 2010 off northern Minorca (Fig. 1) would have resulted in an increase in the abundance of sea urchins, particularly of the smaller size classes. Furthermore, a larger sea urchin population would have reduced the abundance of the dominant canopy-forming algae *Cystoseira brachycarpa* J. Agardth var. *brachycarpa* emendavit Giaccone and other erect seaweeds. Finally, these changes would be independent on the abundance of sea urchin predators, unless trophic cascades operated in the area.

2. Material and methods

2.1. Site description and experimental design

The study was conducted in the northern coast of Minorca (Balearic Archipelago), where the most extensive infralittoral ecosystems are rocky bottoms and seagrass meadows, with a few areas of bare sand. A marine protected area (MPA) was established in 1999 in the northern coast of Minorca (Fig. 2), although enforcement and monitoring began only in 2000 (Coll et al., 2012). The MPA covers 5199 ha and most of it can be classified as partial reserve, as some fishing is still allowed (Coll et al., 2012). Fishing has been totally banned in only two no-take areas, the first covering 838 ha of rocky bottoms in the west and the second one covering 217 ha of soft bottoms in the innermost part of Fornells bay (Coll et al., 2012). Fish biomass increased steadily both in the no-take and the partial reserve areas after the establishment of the MPA and was close to carrying capacity in 2005 (Coll et al., 2012).

Satellite data (SeaWiFS 9 km and Modis-Aqua 4 km; http://reason.gsfc.nasa.gov/Giovanni/) was used to determine the chlorophyll-*a* levels from 1998 to 2012.

A factorial design was used, comparing the abundance of sea urchin predators, sea urchins, erect algae and coralline barren before (2005) and after (2012) the productivity period in the partial reserve and control areas. The effect of fishing protection on the stability of the system was further explored comparing the abundance of sea urchin predators and sea urchins and the cover of erect algae, turf-forming algae and coralline barren and in the no-take, partial reserve and control in 2012, after the period of enhanced productivity. A perfect factorial design (year × protection) was not possible because the no-take area was not surveyed in 2005. Furthermore, the cover of turf-forming algae was not recorded in 2005.

2.2. Field census

Field censuses were conducted from May 25th to June 13th in 2005 and from June 9th to June 15th in 2012. Only areas with non-carbonated rocks were sampled in 2012, as carbonated rocks do not exist within the no-take area (Rosell and Llompart, 2002) and rock type has a large-scale influence on fish abundance (Cardona et al., 2007a). Thus, all comparisons were limited to areas with non-