Journal of Sea Research 95 (2015) 132–138

Contents lists available at ScienceDirect

Journal of Sea Research

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

Colonisation processes and the role of coralline algae in rocky shore community dynamics

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ARTICLE INFO

Article history:
Received 26 September 2013
Received in revised form 16 July 2014
Accepted 18 July 2014
Available online 30 July 2014

Keywords:
Recovery
Disturbance
Colonisation Processes
Space Occupancy
Coralline Algae

ABSTRACT

Recovery from disturbance is an important attribute of community dynamics. Temperate rocky shores will experience increases in both the type and intensity of impacts under future expected global change. To gauge the community response to these potential changes in the disturbance regime it is important to assess space occupancy and the temporal dynamics of key species over the recovery process. We experimentally disturbed replicated 1 m^2 plots in the lower intertidal at 5 sites along the Ligurian rocky coast (North-western Mediterranean) and assessed early succession processes over 18 months. To identify colonisation processes and role of key species in affecting species richness on recovery trajectories, we monitored species composition at the cm-scale along fixed transects within the plots. Our results highlighted the role of a limited number of taxa in driving the recovery of species richness across sites, despite site variation in community composition. Settlement of new propagules and overgrowth were the principal pathway of space occupancy. We detected an important role for coralline algae, particularly the articulated *Corallina elongata*, in promoting the colonisation of a diverse range of colonists. The present study highlights the important role played by calcifying coralline macroalgae as substrate providers for later colonists, favouring recovery of biodiversity after disturbance. This pivotal role may be compromised in a future scenario of elevated cumulative disturbance, where ocean acidification will likely depress the role of coralline algae in recovery, leading to a general loss in biodiversity and community complexity.

1. Introduction

Recovery from disturbance is an important attribute of community dynamics and is controlled by a combination of physical and biological features, operating at different spatial scales (Dayton, 1971; Thrush et al., 2008). Coastal ecosystems, threatened by impacts from both marine and terrestrial activities (Halpern et al., 2008), are affected by a wide range of disturbances associated with urbanisation, increased sediment load, global warming and ocean acidification, and, in many locations, physical disturbance associated with extreme climatic events, whose magnitude and frequency are expected to increase in global change scenarios (IPCC, 2007). Recovery dynamics following a physical disturbance event will be modified if key species in the recovery process are affected by multiple stressors (Crain et al., 2008) and, as a consequence of impaired recovery, biodiversity loss and changes in coastal ecosystem functioning will potentially escalate (Airoldi and Beck, 2007).

The removal of plants and animals to expose bare rock in experimental plots is a useful simulation of severe physical disturbance on rocky reefs (Airoldi, 1998, 2000b; Benedetti-Cecchi and Cinelli, 1994; Keough, 1984; Paine and Levin, 1981; Underwood, 1980). Space occupancy processes that follow disturbance result from the interaction of colonist supply (reproduction, dispersal, recruitment), interactions amongst species (growth, competition, facilitation) and variation in local abiotic conditions (Conway-Cranos, 2012; Crowe et al., 2013; Dayton, 1975; Foster et al., 2003).

Settlement and propagation patterns of the habitat forming macroalgal taxa and their positive or negative interactions are at the basis of the successional process in rocky reef systems. Encrusting algae are amongst the first colonisers of bare rocks in euphotic marine habitats (Dethier, 1994; Kaehler and Williams, 1997; Littler, 1972), and coralline species (encrusting and articulated) are usually both early colonists and important understory species that are overgrown by other conspicuous algal taxa in established assemblages on temperate reefs (Airoldi, 2000a; Coleman, 2003; Maggi et al., 2011). Their life-history traits allow crusts to occupy space by the settling of new propagules and lateral vegetative propagation (Airoldi, 2000a; Airoldi

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http://dx.doi.org/10.1016/j.seares.2014.07.012
1385-1101/

and Virgilio, 1998). Encrusting coralline algae are known to facilitate recruitment and settlement of later colonists, providing a substrate more suitable for algal propagules and invertebrate larvae in comparison to bare rocks, because of increased surface rugosity (Arenas et al., 2006; Bulleri et al., 2009). In the later stages of succession, encrusting algae can coexist with epiphytic turf or as an understory to canopies (Bulleri, 2006; Figueiredo et al., 1997; Miles and Meslow, 1990) without being damaged. Overgrowth by turf can limit the biomass of crusts, but does not affect their cover or fertility and does not result in increased mortality (Bulleri, 2006). Turf overgrowth may have possible direct or indirect benefits, protecting underlying crusts from abrasion, desiccation, light and heat stress or relieving crusts from competition for primary space by outcompeting erect and canopy algae (Airoldi, 2000a).

Algal turf, made up of a complex matrix characterised by small Corallinales, Ceramiales and other filamentous algae, is reported to secure space by the encroachment of prostrate axes from the periphery and regrowth of surviving prostrate axes (Airoldi, 1998, 2000a, 2000b), quickly regaining spatial dominance in experimentally cleared patches and persisting over two years after disturbance (Dayton and Tegner, 1984; Kennelly, 1987). The settlement of coralline turfs can be facilitated by ephemeral-filamentous algae (Coleman, 2003). Coralline and non-coralline turf forming algae can inhibit the recruitment of canopy species in clearings caused by storms or human activities (Ambrose and Nelson, 1982; Bellgrove et al., 2010; Connell and Russell, 2010; Dayton, 1975; Kennelly, 1987) and may drive long-lasting changes in community structure (Benedetti-Cecchi and Cinelli, 1992; Bulleri et al., 2002). Inhibition is mostly due not only to competition for space and light, but also by chemical interactions (Kennelly, 1987).

Canopy species are reported to occupy space mostly by the colonisation of propagules released in the surroundings and are consequently affected in their attachment by physical, chemical and hydrodynamic conditions, and by timing and location of disturbance (Airoldi, 1998, 2000b; Bellgrove et al., 2010). Macroalgal canopies are often important ecosystem engineers: they may regulate community structure in a number of ways, exerting positive (*i.e.* providing refuges and shelter from wave action, solar radiation, extreme temperatures or desiccation; Bertness et al., 1999; Figueiredo et al., 2000; McCook and Chapman, 1991) or negative (*i.e.* limiting light and space availability, *e.g.* Kennelly, 1989; Reed and Foster, 1984) effects on other species.

In the present study, we performed a multi-site disturbance-recovery experiment along the eastern Ligurian coast (North-western Mediterranean) at five sites, encompassing over 80 km of coastline. Macroalgal communities of the infralittoral shallow fringe along this stretch of coast are mainly characterised by articulated and encrusting Corallinales and turf forming species, with the dominance of individual species varying between sites. Species of the genus *Cystoseira*, canopy forming assemblages in this microtidal system (Mangialajo et al., 2012), are generally present in the studied area and dominant in two of our sites, whilst in another two they are absent (see Asnaghi et al., 2009). Nevertheless, in the sites dominated by canopies, articulated and encrusting Corallinales and turf forming species dominate the understory. In the Mediterranean Sea, recovery dynamics after experimental clearings are usually monitored for a period of 1–2 years (Airoldi, 2003a; Bulleri, 2005; Bulleri and Benedetti-Cecchi, 2006; Perkol-Finkel and Airoldi, 2010) encompassing the time scale for the recovery of most of the taxa, even though it is known that communities dominated by canopy species may take longer to recover (Perkol-Finkel and Airoldi, 2010). Our work assessed early succession processes of temperate reef communities over 18 months after the perturbation event. We experimentally cleared 1 m^2 plots, much larger than those commonly used for disturbance–recovery experiment on intertidal rocky shores (*e.g.* Airoldi, 1998, 2000a; Benedetti-Cecchi, 2000), in order to discount edge effects associated with lateral growth from the plot edge.

Considering communities as a dynamic mosaic of species whose patchiness results from microsite differences and disturbances (Pickett and White, 1985), recovery processes were followed at a very small scale (centimetre) along fixed transects to precisely document species-specific space occupation patterns over time. This approach allowed us to take into account different colonisation pathways and test two different hypotheses regarding space occupation dynamics during the initial 18 months of recovery: 1) occupancy at the centimetre scale changes through replacement/overgrowth from free propagules; *versus* 2) changes occur through lateral encroachment from patches of already settled species. This small-scale measurement approach prevents spatial variation from confounding temporal patterns in species replacement. It also allows us to assess the biodiversity enhancement effects of early colonists that can occur when taxa are replaced/overgrown by a larger number of species. This locally enhanced diversity can provide a wider range of species to support recovery and response to changing environmental condition.

2. Materials & methods

2.1. Study area

Sampling sites were distributed along the eastern side of the Ligurian coast: one site near Genoa city (Pontetto — PON), one in the C zone of Portofino Marine Protected Area (Punta Chiappa — POR), one close to Framura (FRA) and two in the A zone of Cinque Terre MPA (Monterosso — MES and Montenero — MON) (Fig. 1). Tidal range in this region is small (30 cm) and the barometric tide may dominate water level. All sampling sites exhibited similar wave exposure and wind-driven currents, which are the major hydrodynamic forces in this area. Sampling sites were also similar in terms of slope (around 60–70°), but showed differences in terms of the dominant macroalgal assemblage. In particular, the local macroalgal community in Pontetto was dominated by canopy forming species of the genus *Cystoseira*, followed by *Corallina elongata* (articulated Corallinales; the name of this species is currently under review, and is regarded as a taxonomic synonym of *Ellisolandia elongata*, see Hind and Saunders, 2013, although Walker et al., 2009 postulate that this species from the Mediterranean Sea may have been misidentified and may belong to *Corallina caespitosa*, sp. nov.); in Punta Chiappa the dominant taxa were articulated Corallinales and fleshy red *Laurencia* spp.; in Framura the assemblage was dominated by *Cystoseira compressa*, articulated and encrusting Corallinales and turf forming species (made up of a complex intricate matrix of small Corallinales, Ceramiales and other filamentous algae); in Monterosso and Montenero algal turf and articulated Corallinales were dominant.

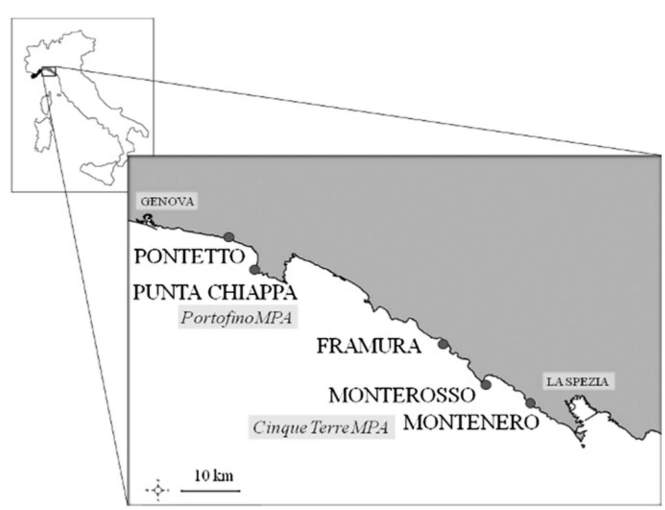

Fig. 1. Location of the 5 sampling sites along the eastern Ligurian coast, North-western Mediterranean.