Estuarine, Coastal and Shelf Science 214 (2018) 57–63

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

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

Regime shifts and alternative stable states in intertidal rocky habitats: State of the art and new trends of research

Silvia Chemello[a,*], Salvatrice Vizzini[a,b], Antonio Mazzola[a,b]

[a] Dipartimento di Scienze della Terra e del Mare, Università di Palermo, Via Archirafi 18, 90123, Palermo, Italy
[b] CoNISMa, Consorzio Nazionale Interuniversitario per le Scienze del Mare, Piazzale Flaminio 9, 00196, Roma, Italy

ARTICLE INFO

Keywords:
Alternative stable states
Regime shifts
Alternative communities
Resilience
Intertidal rocky habitats

ABSTRACT

The existence of regime shifts and alternative stable states in ecosystems is well known and has very large effects on their structure and dynamics. Since shifts between alternative stable states have significant implications for the ecosystems conservation, their prevention should be an aim of primary interest, and for this reason a particular attention has been paid to their study. Regarding marine ecosystems, rocky intertidal habitats, in particular, represent an ideal system for the study of alternative stable states because of their characteristics: they exhibit strong environmental gradients, are easy to manipulate, and most of the inhabiting species grow rapidly. Given the socio-ecological importance and the vulnerability of intertidal rocky systems to multiple pressures, a specific review on these habitats is valuable for a better understanding of the functioning mechanisms of regime shifts. In this review, we examine the different approaches, both experimental and modeling, used to explore regime shifts and alternative states within rocky intertidal habitats. We also analyse the development and use in intertidal systems of new metrics able to signal in advance an approaching transition. Lastly, we discuss the existing knowledge gaps and highlight the management weaknesses of the study of regime shifts in the framework of ecosystem conservation.

1. Introduction

Ecosystems are subject to multiple pressures (such as climate change, overexploitation of resources, habitat destruction and degradation, and pollution), which act at different spatial scale and profoundly modify their structure and function (Hawkins et al., 2015). Ecosystems and communities can respond to perturbations and changes in environmental conditions in different ways, depending on the strength of the feedbacks that act in the biotic and abiotic compartments: some respond in a smooth and gradual manner, others may remain inert until a critical threshold is exceeded or, alternatively, can suddenly switch from one state to another (Conversi et al., 2014; Kéfi et al., 2014). The last case, defined as "regime shift", takes place when an ecosystem undergoes an abrupt change from one stable state to another one, often greatly different from the original state (Scheffer, 2009). In particular, a transition between alternative stable states occurs when a change in the state variables (properties of the system that respond to changes in the parameters, such as biomass, density, abundance, etc.) or a change in the system parameters (defined as measures that describe behavior and interactions of state variables, such as grazing rate, predation, etc.) exceed a critical threshold, beyond which internal feedbacks that maintain the original stable state are overcome (Beisner et al., 2003; Filbee-Dexter and Scheibling, 2014). There are special cases in which the system transitions to a state where recovery is particularly slow (the system shows hysteresis) or even impossible (in this case the system has alternative stable states) (Scheffer et al., 2001; Scheffer and Carpenter, 2003).

Regime shifts are commonly observed in many marine systems: in particular, coral reefs (Done, 1992; Knowlton, 1992; Hughes, 1994; Norström et al., 2009; Bozec and Mumby, 2014; Jouffray et al., 2015), kelp forests (Simenstad et al., 1978; Steneck et al., 2013; Filbee-Dexter and Scheibling, 2014), and sea urchin-coralline barrens (Sala et al., 1998; Agnetta et al., 2015; Bulleri et al., 2016; Piazzi et al., 2016) are those studied most in-depth.

The first experimental tests of regime shifts were performed in rocky intertidal environments (e.g., Paine et al., 1985), and also in these systems several cases of abrupt shifts between alternative states have been observed and documented (Knowlton, 2004; Petraitis and Dudgeon, 2004a).

One of the first manipulative experiments in the rocky intertidal was carried out by Paine et al. (1985), who evaluated the potential of alternative stable states in mussel bed communities in Chile, Washington

---

[*] Corresponding author.
E-mail address: silvia.chemello@unipa.it (S. Chemello).

https://doi.org/10.1016/j.ecss.2018.09.013
Received 1 March 2018; Received in revised form 3 September 2018; Accepted 14 September 2018

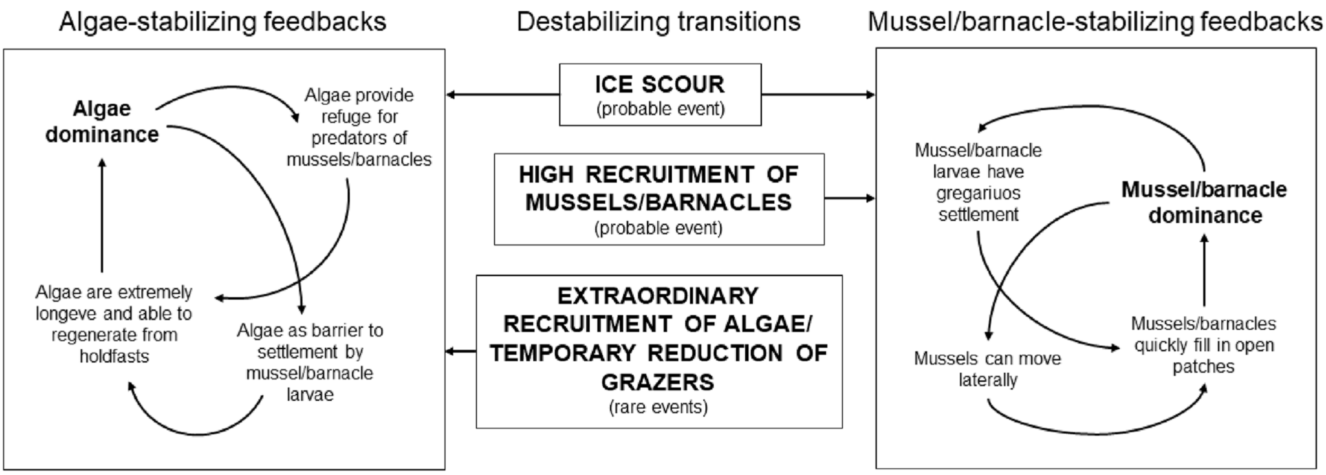

Fig. 1. Conceptual model of North Atlantic alternative stable states. The model illustrates feedback mechanisms that act to return small patches to the original state or to maintain alternatively *Ascophyllum* stands or barnacle-mussel beds (figure redrawn from Petraitis and Latham, 1999).

State (USA) and New Zealand, through removal of a key predator (different species of starfish depending on the geographic location).

In the North Atlantic, it has been proposed that mussel (or barnacle) beds and macroalgae-dominated assemblages (*Fucus* and *Ascophyllum*) represent distinct communities and that each of them, potentially dominating rocky intertidal shores, represents a single alternative stable state (Fig. 1; Petraitis and Dudgeon, 1999; Petraitis and Latham, 1999; Petraitis and Dudgeon, 2004b). Experimental evidence provided by a series of experiments (Petraitis and Dudgeon, 1999; Dudgeon et al., 2001; Dudgeon and Petraitis, 2001; Petraitis et al., 2003, 2009), although challenged by Bertness et al. (2002), support this hypothesis. These experiments represent a strong test of the theory of alternative stable states, proving that the same location can be occupied by different persisting communities which, once established, are maintained by site-specific top-down controls and are influenced by wave motion and exposition (Petraitis et al., 2009).

Another example relates to the Pacific coasts in southern California, where Barry (1988) identified another typology of alternative states: the presence of a community dominated by chitons or algal turf was described, as a function of coast height and slope.

In Washington State rocky intertidal, instead, Ruesnik (1998) took into account predator-prey interactions between hermit crabs and diatoms, which can lead to two alternative stable states: one in which diatoms and crabs coexist and the other where diatoms are eliminated.

Attention has been focused recently on the globally significant decrease in canopy macroalgae (Perkol-Finkel and Airoldi, 2010). These have fundamental roles in rocky intertidal systems: they provide nourishment and protection, enhance the structural complexity of habitats and increase biodiversity and productivity of coastal systems (Chapman, 1995). With the loss of the canopy, macroalgae are replaced by species with lower structural complexity, such as turf, filamentous and ephemeral algae. Once established, turf algae populations inhibit recolonization of space from canopy macroalgae, thus forming a real alternative stable state (Strain et al., 2014). In this case, it was hypothesized that transitions between the two stable states are synergistically driven by anthropogenic local disturbances (urbanization, overexploitation of species that regulate the food web, eutrophication, increased sedimentation, pollution, invasive species, trampling) and environmental and climate stresses (Fig. 2).

Rocky intertidal habitats are complex systems with unique characteristics: these open ecosystems are subject to steep environmental gradients and characterized by a high associated biodiversity (Thompson et al., 2002), which gives them considerable ecological, socio-economic, and conservation value (Raffaelli & Hawkins, 1996). Furthermore, rocky environments are constantly exposed to natural and anthropogenic pressures, which makes the occurrence of regime shifts in these environments more likely. Although transitions in marine ecosystems are a well-known issue and several reviews have already been produced (e.g. Knowlton, 2004; Petraitis and Dudgeon, 2004b; Petraitis and Dudgeon, 2016), a specific review focused only on rocky intertidal systems has not yet been published. A comprehensive analysis of the fundamental aspects of regime shifts in these habitats would therefore be a valuable contribution to understanding the overall phenomenon.

The aim of this review is, thus, to synthesize existing knowledge on alternative stable states and regime shifts in rocky intertidal habitats, taking into consideration all the different approaches used to explore the issue over time.

This review analyses recent research trends, especially the development and use of early-warning indicators to detect an approaching transition, and concludes by outlining the knowledge gaps and management deficiencies in the examination of regime shifts in the context of marine ecosystem conservation.

2. Approaches adopted to study alternative stable states and regime shifts in rocky intertidal environments

2.1. Experimental approach

In theory, experimental tests demonstrating the existence of alternative stable states in natural communities must satisfy three conditions (Petraitis and Dudgeon, 2004b; Petraitis et al., 2009): 1) alternative states exist in the same environment or habitat; 2) experimental manipulation consists of a pulse perturbation that mimics spatial extension, temporal duration and effects on species of a possible natural event; 3) experiments and observations are carried out for a long period and on an appropriate spatial scale, in order to demonstrate that the alternative stable states can be self-maintained.

Experimental tests for alternative stable states usually take place either by monitoring events that occur after a perturbation (whether natural or induced through manipulation) or by evaluating the responses of a system to an inverse perturbation: in both cases, if the new state into which the community is pushed is stable, cessation of perturbation will not imply any return to initial conditions (Beisner et al., 2003).

Rocky intertidal shores represent an ideal system for the study of alternative stable states and regime shifts: they present well-defined environmental gradients, inhabiting species mostly compete for the available space and most of them have high growth rates, thus making these habitats accessible and easy manipulative systems (Hawkins et al.,