



Improving the construction of functional models of alternative persistent states in coral reefs using insights from ongoing research programs: A discussion paper



Igor C.S. Cruz^{a,*}, Ruy K.P. Kikuchi^b, Joel C. Creed^c

^a Programa de Pós-Graduação em Ecologia e Evolução, Universidade do Estado do Rio de Janeiro, Instituto de Biologia Roberto Alcântara Gomes, Rua São Francisco Xavier 524, PHLC Sala 220 Maracanã, 20559-900 Rio de Janeiro, RJ, Brazil

^b Departamento de Oceanografia, Instituto de Geociência, Universidade Federal da Bahia, Rua Barão de Jeremoabo, s/n – Federação, CEP 40170-115 Salvador, BA, Brazil

^c Departamento de Ecologia, Universidade do Estado do Rio de Janeiro, Instituto de Biologia Roberto Alcântara Gomes, Rua São Francisco Xavier 524, PHLC Sala 220 Maracanã, 20559-900 Rio de Janeiro, RJ, Brazil

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ABSTRACT

Extensive degradation of coral reefs makes it imperative to create functional models that demonstrate ecological processes which occur in alternative states that persist over time. These models provide important information that can help in decision making regarding management measures for both the prevention of further degradation and the recovery of these ecosystems. Development of these models requires identifying and testing the ecological processes that will impose the reduction of coral cover and, preferably, identifying the disturbance that triggers this phenomenon. For this reason, research programs are a useful tool which allows a focus on the production of information for modeling. It should start with survey investigations and tests of hypotheses concerning the cause of the reduction of coral cover. Subsequently, projects should be guided by the most probable hypotheses, focusing on one guild or functional group at a time until the "trigger" process which unleashed the disturbance is identified. Even if incomplete, these models already provide information for focusing management steps.

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1. Introduction

Ever more frequently the consequence of coral-reef degradation is the change of reef communities to alternative states which are persistent over time (Done, 1992a; McCook, 1999; Mumby et al., 2007b). We are using the terminology 'alternative state persistent over time' to define all kinds of persistent community change, which can occur under the same environmental conditions or under a different set of environmental conditions. Over the past 40 years 19% of these ecosystems have been degraded and another 35% are threatened (Wilkinson, 2008), and this problem has drawn considerable attention of scientists, reflected in the large number of publications on the subject (Knowlton, 1992; McCook, 1999; Nyström et al., 2000; Nyström and Folke, 2001; McManus and

Polsenberg, 2004; Bruno et al., 2009; Norström et al., 2009; Dudgeon et al., 2010; Fung et al., 2011). The great majority of these studies discuss alternative states resulting in change to the dominance of macroalgae on coral reefs. However Norström et al. (2009) emphasize the existence of numerous reports worldwide of reef communities that have shifted to stable states dominated by other, non-macroalgal organisms after disturbance; these have received scant attention.

The lack of interest in other alternative persistent states is reflected in recent reviews on the topic. In relation to the dominance of macroalgae, the theme has been discussed from the perspective of human impacts and resilience (Nyström et al., 2000, 2008; Nyström and Folke, 2001), theoretical models (McManus and Polsenberg, 2004; Fung et al., 2011) and meta-analyses (McCook, 1999; Bruno et al., 2009). However few studies deal with this issue from a more general perspective such as Knowlton (1992) did when she discussed the limits of change based on the basic processes of population ecology; Dudgeon et al. (2010), who conducted a conceptual review; and Norström et al. (2009) who carried out a

* Corresponding author. Tel.: +55 7188936062.

E-mail addresses: igoracruz@gmail.com, igoracruz@uerj.br (I.C.S. Cruz), kikuchi@ufba.br (R.K.P. Kikuchi), jcreed@uerj.br (J.C. Creed).

meta-analysis of alternative persistent states in coral reefs other than those dominated by macroalgae.

The lack of attention paid to non-algal alternative persistent states results from a dearth of experimental studies that test underlying ecological processes (Norström et al., 2009), as most of the studies test hypotheses about the processes involved in the dominance shift to macroalgae (Tanner, 1995; Miller and Hay, 1998; Lirman, 2001; River and Edmunds, 2001; Smith et al., 2006). Consequently the only model concerning changes in the ecological processes that lead to dominance that has been tested is the macroalgal one (Norström et al., 2009).

Functional models, (which we define here as conceptual models that show all or the main ecological interactions involved in a phenomenon) which contemplate, in detail, the ecological processes involved in each type of change, are essential tools for managers (Temperton et al., 2004; Norström et al., 2009). These models enable ideas to emerge, which can result in indirect management interventions in the key processes of change. A classic example is the model of trophic cascade of otters in kelp forests. The drastic reduction in sea otter populations due to hunting and other human activities in the 1960s and 1970s triggered a population explosion of sea urchins, herbivores that decimated large areas of kelp forests (Simenstad et al., 1978; Reisewitz and Estes, 2006; Estes et al., 2011). From this model it was possible to infer a functional measure of effective management, that of the protection of otters (Estes et al., 1998; Lorentsen et al., 2010). In coral reefs the best known example is, indeed, the phase shift model to dominance of macroalgae. This is triggered by 1) increasing the level of nutrients in the water and/or 2) overfishing of herbivorous fish (Done, 1992a). The logical management conclusions drawn from this model are to 1) eliminate the discharge of sewage and/or 2) protect herbivorous fish (Done, 1999; Bellwood et al., 2004).

The development of a functional model for a persistent alternative state requires a focused research effort. Several possible ecological relationships need to be tested with methodological rigor. Unless dominance is monospecific, a whole suite of species within a functional group or guild should exhibit the same behavior in ecological interaction. The results of these tests often generate more questions than answers. For this reason, specific research programs are the most rational and logical way to accelerate the production of the information required to feed the model.

The aim of this review is to propose a standard research program for the collection of the information necessary to build a functional model for alternative persistent states. While the objective is not to discuss concepts of alternative persistent states, the substantial confusion and controversy in the literature regarding this issue (Connell and Sousa, 1983; Rogers and Miller, 2006; Dudgeon et al., 2010) needs a brief evaluation.

2. Alternative persistent states

The community is an ecological level hierarchically situated between the population and the ecosystem (Jax, 2006). Although its level is well defined, the concept is one of the most problematic and controversial in ecology (Looijen and van Anandel, 1999; Parker, 2004; Ricklefs, 2008). There are two predominant schools of thought regarding communities, each of which has distinct objectives and concepts. The biogeographical and phytosociological (vegetation science in a study area that aims to understand the patterns of richness and abundance of plant species in time and space) school aims to describe and explain patterns of diversity at different spatial scales. They define the community as all species in a given area (Jax, 2006). The other school, that of demographic or animal ecology, aims to describe and explain the processes of coexistence, maintenance and change in a community. They define

the community as all species in a given location that interact directly or indirectly (Jax, 2006).

Both schools agree that ecologists still fail in their attempts to define the boundaries of a community (Looijen and van Anandel, 1999; Parker, 2001; Jax, 2006). This problem brings back the old discussion about open vs. closed communities, now from a landscape ecology perspective, which questions whether limits exist, and if so, how they should be defined in spatial and temporal scales (Ricklefs, 2008). Researchers of the biogeographical school, such as Looijen and van Anandel (1999), argue that the interactions at the local level do not explain the patterns of regional and global diversity and therefore the interactions should not define the community. Moreover, while Ricklefs (2008) agreed that on a local scale interaction is irrelevant as it does not represent the ecological unit as a whole, he argues that on a regional scale interaction should integrate the concept of community. Implicit in this argument is the problem of the definition of edge. As an alternative to the problem of defining borders, Parker (2001, 2004) suggests removing the spatial reference from the community concept and only use interaction as the defining feature, so that when species are interacting in time or space they are a community. Finally, Jax (2006) presents a decisive argument for the maintenance of community interaction: all ecological levels should be capable of self-regulation and in a community this process occurs through ecological interactions. In light of the arguments above, in the present study we discuss the maintenance and change in the community using the animal ecology community concept.

The persistence of a community is maintained by its capacity to renew itself. Confirmation of persistence requires monitoring the community for at least as long as the time required for this renewal; older individuals should be replaced by younger ones (Connell and Sousa, 1983). In some cases, it can take decades for the community to reach maturity. However, the prevalence of the environmental impacts of human activities throughout the planet makes for environmental problems and issues that require urgent action and an immediate search for solutions (Vitousek et al., 1997). According to Norström et al. (2009) the change of dominance from corals to macroalgae may be considered persistent when continuous for more than five years; though this period may not be ideal for the renewal of some communities in ecological terms, it is in accordance with the human timeframe required to provide answers. The permanence of an alternative standard of the community for more than five years is therefore a sign that this pattern is persistent and requires management measures.

Understanding disturbance and stability, as well as its attributes resistance and resilience, is needed in order to understand alternative persistent states. Disturbance is fundamentally a change in a physical and/or chemical regime of natural or anthropogenic origin (Minchinton, 2007), which causes injury, displacement or death to one or more organisms or directly or indirectly removes biomass and creates opportunities for other organisms (Sousa, 1984). Connell and Sousa (1983) defined the stability of a community as the variation pattern of their populations around an equilibrium point persistent in time (Fig. 1). This definition differs from “general stability” adopted by the Mccann (2000) review, which is one of more cited in the literature and which assumes that the stability of a population increases as the density moves away from zero. Besides this being a Population Ecology definition and in this paper we address community level issues, is very common that after an outbreak the population density drops to zero or close to it, which leaves doubt about whether the distance from density zero is indeed a good measure of stability. Resistance is the ability of a community to absorb disturbance without changing its natural variation (Fig. 2; Minchinton, 2007). When the intensity of the disturbance is enough to break resistance, it generates a

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