Predator exploitation and sea urchin bistability: Consequence on benthic alternative states

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ABSTRACT

In the Mediterranean Sea, such as in other temperate marine areas, the variation in sea urchin density in coastal rocky system may drive switches between one complex state, dominated by erect algae into barren state dominated by encrusting coralline algae and bare rock. The aim of this paper is to mathematically describe how fishing (predator exploitation) affects sea urchin abundance (prey) so that predictions about the effects of fishery restrictions on urchin density could be made. This also would indirectly provide forecast of macroalgal forests from barren. In order to obtain such description, a simple model of prey–predator dynamics in the presence of predator exploitation was evaluated by using a numerical simulation that parametrically explores the impact of external exploitation in the system equilibrium. The proposed model is consistent with observed alternative states in Mediterranean subtidal rocky bottoms. In fact, the presence of barren in areas both exploited and protected from fishing activity can be explained by hysteresis of the system. Moreover, an irreversible transition was shown to occur when the intrinsic growth rate of the prey decreases (predator restoration through fishing restrictions) suggesting that proper and complex management approaches should be considered to address conservation of a benthic habitat.

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1. Introduction

Trophic downgrading worldwide has increased sharply during the last decades leading to reductions in biodiversity, habitat loss and altered ecosystem function (Estes et al., 2011). To appreciate the long-term consequences of these changes and facilitate restoration efforts, it is necessary to understand the mechanisms driving the changes. A particular question of interest is the extent to which changes are easily reversible (Thrush et al., 2009). Ecosystems usually respond to gradual change in a smooth way, but they can also switch abruptly to contrasting alternative states following a loss of resilience (May, 1977; Petraitis and Dudgeon, 2004). Thus, ecosystems can have multiple stable states, separated by unstable equilibria that mark the border between the 'basins of attraction' of the possible states (Scheffer et al., 2001; Folke et al., 2004; Knowlton, 2004; Watson and Estes, 2011). Furthermore, the presence of multiple states can be characterized by hysteresis, in which transitions between alternative states take place at different critical thresholds depending on environmental factors (Balke et al., 2014; Knowlton, 1992; Petraitis and Hoffman, 2010; Scheffer et al., 2001).

Recently, hysteresis has also been supposed to regulate the population dynamics of sea urchins and, in turn, to affect the stability of benthic algal forests (kelps or fucoids). On temperate rocky reefs, catastrophic shifts in dominance from canopy-forming to encrusting coralline macroalgae (barrens), as a consequence of sea urchin overgrazing, have been documented worldwide (Filbee-Dexter and Scheibling, 2014; Ling et al., 2015).

The increase of sea urchin populations can be due to natural changes in environmental factors or reproductive features (Balch and Scheibling, 2000; Hereu et al., 2004).

However, anthropogenic pressure, such as changes in trophic regime that mediate macrophyte systems resilience to urchin grazing and overfishing (i.e. removal of natural urchins' predators), can indirectly regulate sea urchin population dynamics causing severe outbreaks (Guidetti, 2006; Hereu et al., 2008; Pinnegar et al., 2000; Sala et al., 1998; Scheibling, 1996; Shears and Babcock, 2003).

The variation in sea urchin grazing intensity may drive switches between one complex state, dominated by a stratified assemblage of several erect algae into barren state dominated by encrusting coralline algae and bare rock (Bulleri et al., 2002; Bulleri, 2013; Giakoumi et al., 2012; Gianguzza et al., 2011; Sala et al.,

2012). The spatial extent of these barrens can range from 1000s of km of coastline to small patches (100s of m in extent) within kelp bed (Filbee-Dexter and Scheibling, 2014). Theoretically, the reduction of fishing activities leads to the recovery of key fish predators of sea urchins and, indirectly, it allows the restoration of the erect macroalgal-dominated states. However, large barren areas can also be found in Mediterranean Marine Protected Areas (MPAs) (Bevilacqua et al., 2006; Micheli et al., 2005) suggesting the occurrence of factors stabilizing barrens other than predator density (Guidetti and Dulcic, 2007; Piazzi et al., 2016). Unpacking the mechanisms driving transitions between alternative states is crucial for assessing the consequences of anthropogenic pressures on the structure and dynamics of ecosystems. In this context, mathematical models can be useful to define processes that determine persistence of alternative states and levels of perturbation threshold that may cause phase shifts (Marzloff et al., 2011; Montaño-Moctezuma et al., 2007).

Several models have been developed to address the sea urchins–seaweeds relationship (Lauzon-Guay et al., 2008; Montaño-Moctezuma et al., 2007; Marzloff et al., 2011) and the effects of fisheries (i.e. predation pressure) on rocky-bottom ecosystem (Pinnegar and Polunin, 2004), but none of them has focused on the effects of fishing on Mediterranean shift of rocky shallow states through regulation of sea urchin populations. The aim of this paper is to mathematically describe how fishing (predator exploitation) affects sea urchin abundance so that predictions about the effects of fishery restrictions on urchin density could be made. This also would indirectly provide forecast of macroalgal forests from barren. In order to obtain such description, a simple model of prey–predator dynamics in the presence of predator exploitation (here fishing activity) was evaluated by using a numerical simulation that parametrically explores the impact of external exploitation in the system equilibrium.

2. Model

The description of the interaction between sea urchins and fishes is based on a simple prey–predator model with equations

$$\frac{dX}{dt} = r_X X \left(1 - \frac{X}{K_X}\right) - Y \frac{AX^2}{X^2 + B} \tag{1}$$

$$\frac{dY}{dt} = r_Y Y \left(1 - \frac{Y}{K_Y}\right) + cY \frac{AX^2}{X^2 + B} - s\sqrt{Y}. \tag{2}$$

Here variables X and Y represent the sea urchin and fish density (number of individuals per surface), respectively. c is a coefficient of conversion from prey to predator. Each Ith species of the prey–predator module (namely X and Y) is assumed to be a generalist and ruled by a logistic growth with the form $r_I I(1 - I/K_I)$, where r_I is the species intrinsic growth rate and K_I its carrying capacity. The predation term is modulated via a Holling III type functional response

$$XR(X) = X \frac{AX}{X^2 + B} \tag{3}$$

where the positive constants A and B are related to the prey handling time and encounter rate, respectively (Holling, 1959; Kempf et al., 2008). Term (3) allows us to incorporate in the model saturation effects due to a large availability of the prey. Moreover, to take into account predators depletion due to fishing activity, we introduce an exploitation term $g(Y)$ into Eq. (2), proportional to the predators abundance Y. The simplest function that can be assumed in this context is a linear form $g(Y) = sY$. However this type of function makes the system too sensible to fishing activity and, since there is no experimental evidence of which form is the most suitable. In analogy to the new symbiotic model (Ajraldi et al., 2011) we

consider here the nonlinear contribution $g(Y) = s\sqrt{Y}$. From a qualitative point of view, the nonlinear contribution $g(Y) = s\sqrt{Y}$ does not change the results but the latter allows us to vary the fishing parameter s over a wider range.

In our numerical study, we explore parametrically the combined influence of fishing pressure and urchin intrinsic growth rate in the prey–predator equilibria, by varying s and r_X, respectively. The other parameters are set as follows: $r_Y = 2.1$, $K_X = 31$, $K_Y = 26$, $A = B = 1$, $c = 0.95$.

3. Results

3.1. Role of s

The influence of predator exploitation on the prey–predator system was evaluated by running simulations of Eqs. (1) and (2)), varying the control parameter s in the range [0, 6.5] with r_x fixed to 5, keeping fixed the initial population of the predator close to its carrying capacity ($Y = 27$) and spanning X initial values between 0 and K_X. This has allowed finding a particular focus on possible threshold phenomena that may lead to uncontrolled growth of the prey (urchin) population X.

The bifurcation diagram of the system dynamics is highlighted by reporting the prey stationary points X_{ss} as a function of s (Fig. 1. There is an initial domain ranging between $s = 0$ and 3 where a unique stable low-density equilibrium can be found. Beyond the threshold $s = 3$, apart for low-density solutions, new high density stable steady states emerge. The low- and high-density solution branches are separated by an unstable manifold (saddle points represented with dotted line) and, thus the final equilibrium state accessible to the system is sensitive the initial density of species X and, in other words, hysteresis occurs. Therefore, because high densities of urchin population may challenge kelp forests, in order to recover the sustainable low-density of this species after it stabilizes to the high-density branch, the fishing pressure should be drastically reduced below the threshold $s = 3$.

However, in the bistability domain, a sufficiently severe demographic perturbation of the species may also change the stability of the ecosystem from one to the other basin of attraction, modifying the final steady state. The likelihood of these events depends
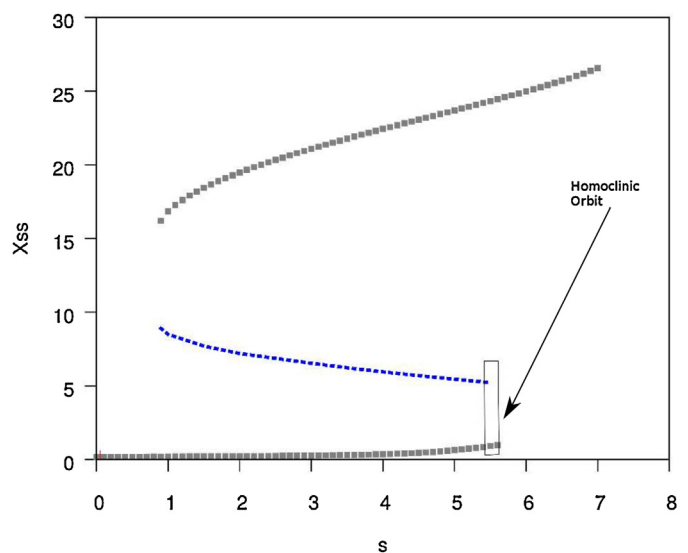

Fig. 1. Bifurcation diagram reporting the prey population steady states (X_{ss}) as a function of s, controlling the fishing pressure in the system. A reversible hysteresis as well as an oscillatory domain is found for $A = B = 1$. $r_X = 4.7$, $r_Y = 2.1$, $K_X = 31$, $K_Y = 26$, $c = 0.95$. Black squares are the stable steady states while the dashed blue line depict the unstable branch separating the low- and high-density solutions.