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.

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.,

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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
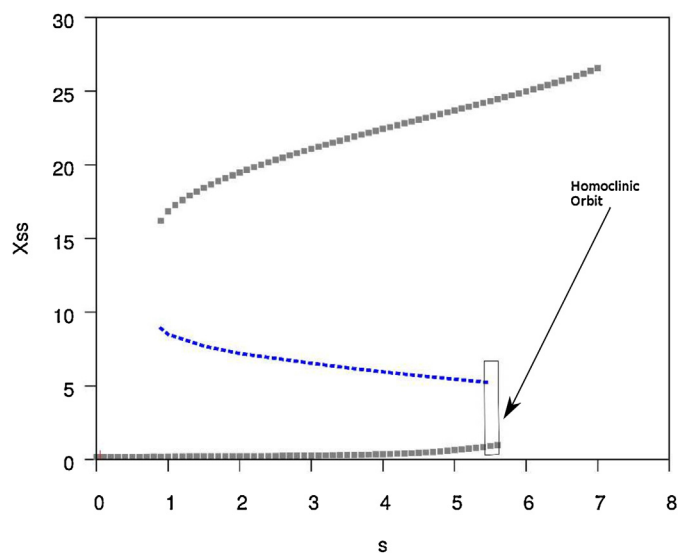
Fig. 1. Bifurcation diagram reporting the prey population steady states (X_{ss}) as a function of s, controlling the fishing pressure in the system. A reversible hysteresis as well as an oscillatory domain is found for $A = B = 1$. $r_X = 4.7$, $r_Y = 2.1$, $K_X = 31$, $K_Y = 26$, $c = 0.95$. Black squares are the stable steady states while the dashed blue line depict the unstable branch separating the low- and high-density solutions.
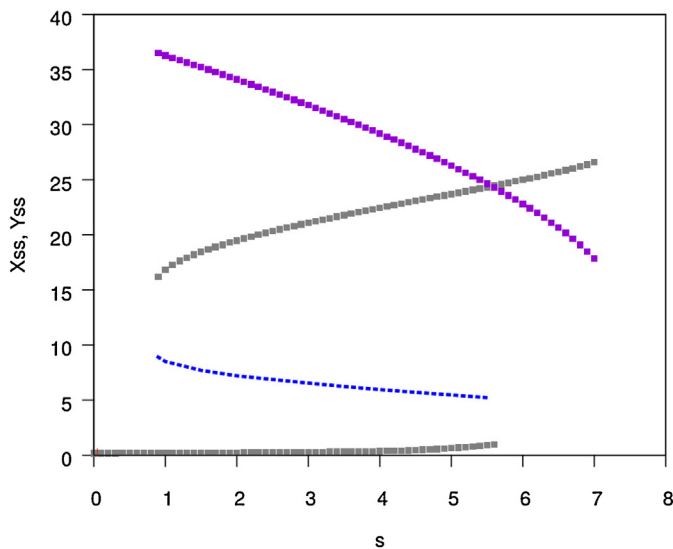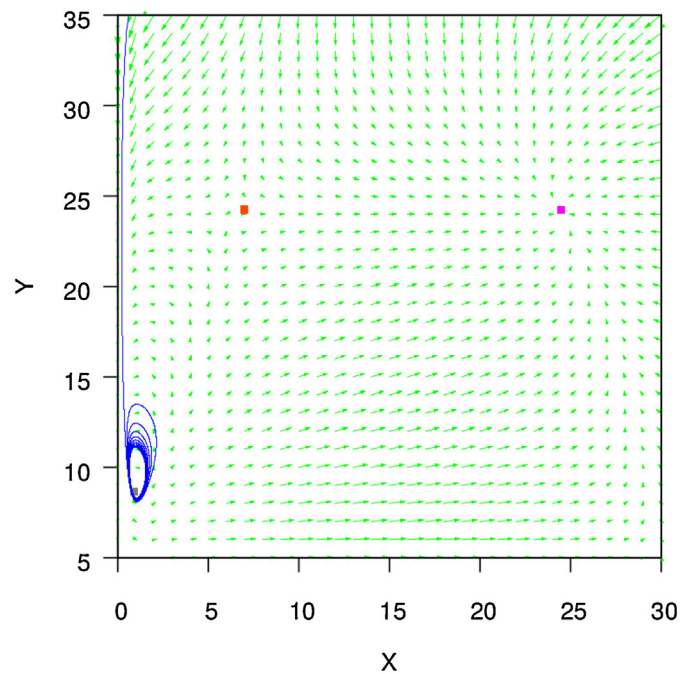
Fig. 2. Bifurcation diagram reporting the prey (X_{ss}) and high level of predators (Y_{ss}) population steady states as a function of s, controlling the fishing pressure in the system. $A = B = 1$. $r_X = 4.7$, $r_Y = 2.1$, $K_X = 31$, $K_Y = 26$, $c = 0.95$. Black squares are the stable steady states for X and the purple squares are the high level steady states for Y, while the dashed blue line depict the unstable branch separating the low- and high-density solutions to the prey. After the bifurcation point ($s = 5.55$) the fish predators steady states drops fast as the pray X increases.

Fig. 3. Representation of the unstable focus-saddle connection in the phase portrait (X, Y) when $r_X = 4.7$, $r_Y = 2.1$, $K_X = 31$, $K_Y = 26$ and $s = 5.62$. Over the green arrows describing the flow field in the phase-portrait, the blue curve traces the homoclinic orbit between the unstable focus (green point at $X = 0.91$, $Y = 8.67$) and the saddle point (red point at $X = 6.97$, $Y = 24.25$) (purple point at $X = 22.5$, $Y = 24.22$) locate the high-density stable node. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

not only on the perturbation amplitude, but also on the size of the attraction basin. The size of the attraction basin gives an estimation of the "resilience" of the related stable state, which corresponds to the maximum perturbation tolerated by the system without switching to an alternative stable state (Fig. 1). A loss of resilience, which is possible when the other parameters of the system are modified, makes the dynamics more vulnerable to these stochastic events.

When the fishing rate reaches the bifurcation value $s = 5.8$, the only steady state possible for the urchin population belongs to the high-density branch. Once more, note that, due to hysteresis, a backwards shift towards the low-density sustainable branch can only occur if s is decreased far enough to reach the first bifurcation point $s = 3$. The steady states corresponding to urchin high-density branch are stable nodes for every value of s. As s is decreased, the topology of the phase portrait changes such that the attraction basins of the saddle characterizing the unstable branch and the stable node points approach one each other and collapse together at $s = 3$. This saddle-node bifurcation leads to the extinction of high-density solutions.

The urchin barren formation is supposed to diminish the abundance of fish since such state much lower primary productivity and habitat structural complexity than kelp beds; consequently, it can be considered a collapse of the kelp state (Simenstad et al., 1978; Filbee-Dexter and Scheibling, 2014; Chapman and Johnson, 1990; Sivertsen, 1996; Christie et al., 2009). The removal of predators through fishing in Kenyan reefs resulted in the expansion of sea urchin population, which apparently led to a decrease in live coral and to loss of topographic complexity, species diversity and fish biomass (McClanahan and Muthiga, 1988; Garcia et al., 2003). Therefore, these experimental results support our model. The collapse of the fish population (Fig. 2) follows the increase of the urchin density. Beyond the bifurcation point, the fish density decreases quickly and goes to zero.

An interesting behaviour that can be isolated close to the second bifurcation point $s = 5.8$ is the occurrence of oscillatory behaviours of the species population. This is accessible over an extremely narrow range of the control parameter, namely $s \in (5.773 \leq 5.80)$,

where the low-density branch states undergo a transition from stable nodes ($s \in (0, 4.8)$) to stable foci ($s \in (4.8, 5.773)$) and then unstable foci ($s \in (5.7743, 5.8)$). The attraction basin of such unstable foci can interact with that surrounding the saddle points of the unstable branch (Fig. 3). As a result of the unstable-focus-saddle connection, when the initial density of the prey is in the range $X \in (0, 7)$, the dynamics is controlled by the homoclinic orbit traced in blue and thus the species show population density oscillations (Fig. 4). A further increment of s leads to the saddle connection break, the loop is destroyed and the system jumps to the high-density branch.

3.2. Role of r_X

The stability scenarios described above are strongly affected by a second key parameter of the system r_X, which represents the measure of the rate at which the carrying capacity is reached. Tuning this parameter has the main effect of shifting the bifurcation diagram along the s-domain. As an example, it is shown how, by increasing r_X from 5 to 6 the lower bifurcation point bounding the bistability domain is not accessible any more to the system in the positive range of the control parameter s (Fig. 5). In such a case the system can still jump from the low-density branch to the high-density branch when s is increased beyond the critical ($s = b$) value but it cannot undergo the reverse transition high-to-low-density solution if s is progressively reduced. This is a typical example of an irreversible hysteresis. Note that increasing r_X has also the effect of amplifying the bistability domain ($0 \leq s \leq 5.921$ vs $3 \leq s \leq 5.8$ obtained above).

4. Discussion

In this study fish exploitation of anthropogenic origin was considered as driver of urchin population density transitions, and it
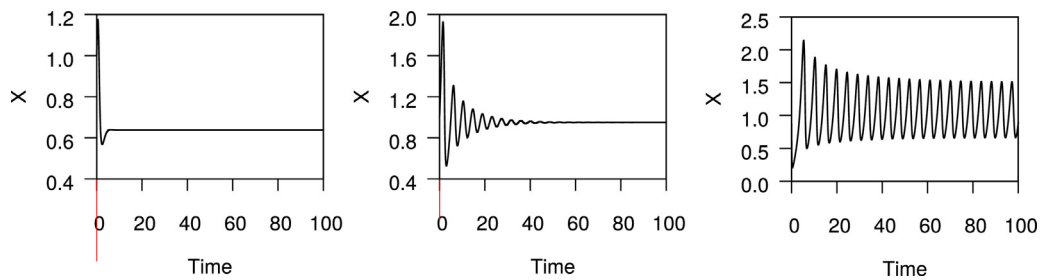
Fig. 4. Transition from smooth to oscillatory behaviours of the prey dynamics when the fishing pressure is increase from $s = 5$ to 5.62. From left to right we observe the dynamics associated with a stable node ($s = 5$), a stable focus ($s = 5.55$) and a homoclinic orbit ($s = 5.62$). The other parameters are $A = B = 1$. $r_X = 4.7$, $r_Y = 2.1$, $K_X = 31$, $K_Y = 26$, $c = 0.95$.

was shown how a jump between the low- and high-density state is possible by varying over a significant range the related critical parameter.

The proposed model is consistent with observed alternative states in Mediterranean subtidal rocky bottom. In fact, the presence of barren state in areas exploited by fishing activity (Guidetti, 2006; Guidetti and Dulcic, 2007) and the hysteresis of barrens (Bulleri, 2013; Piazzi et al., 2016) can be explained by the model.

Evidence of ecosystem collapse have been provided any time kelp forests shifts to barren when fish population collapses (Simenstad et al., 1978; Filbee-Dexter and Scheibling, 2014). Our results (Fig. 2) provide a theoretical support to the studies that describe the loss of complexity of the habitat. Moreover, an irreversible hysteresis was shown to occur when the intrinsic growth rate of the prey increases. In fact, the threshold point for the onset of bistability occurs for $s \leq 0$. In this context, irreversible hysteresis means that, when the system jumps from the low- to high-density solution due to overfishing, the former steady-state solution cannot be recovered via a backward decrease of the critical factor itself. In other terms, stopping fishery, achievable through MPAs institutions, would be necessary but not sufficient to restore urchin population to low density.

Therefore, the only way to reverse the urchin population to a low-density population for the re-establishment of algal forests is by management programs that either includes the urchin and predator populations. The former type should be faced through human harvest of sea urchins and seems one of the feasible actions to be addressed in barren areas. This approach has already been considered to cope with the overgrazed areas (Watanuki et al., 2010) and probably would be acclaimed. In fact, sea urchins may be important commercial resources whose productivity is recently developed through hatcheries worldwide (Couvray et al., 2015). The latter type should be faced by fish restocking (also termed re-introduction or biomanipulation of fish populations) which is has recently been applied to coastal marine ecosystems, although mainly aimed at recovering the yields of target commercial fish populations (Leber, 2013; Lindegren et al., 2010; Lorenzen et al., 2013). Fish restocking is a common tool in the applied management of non-marine aquatic ecosystems, aimed at restoring water quality and vegetation characteristics (Cowx and Gerdeaux, 2004; Angeler, 2010) and has been recently proposed for the recovery of deteriorated coral reefs besides reef gardening (Obolski et al., 2016). Overall, it should be stressed that our proposed dual restoration approach is not presented as an alternative to the removal of the stressor (i.e. fish exploitation) that would cause predator recovery and therefore stabilization of lower trophic levels.

The suggested model is a simplification of the system. In fact, several predator species with different exploiting rate may predate urchins and various environmental variables may influence prey and predator populations. Nevertheless, the model proposed can be a base to describe the influence of human activities on coastal subtidal assemblages suggesting that proper and complex management approaches should be considered to address conservation of a benthic habitat. Moreover, results can stimulate further studies in order to validate the model through correlative and manipulative approaches.

References

Ajraldi, V., Pittavino, M., Venturino, E., 2011. Modeling herd behavior in population systems. Nonlinear Anal.: Real World Appl. 12, 2319–2338.

Angeler, D., 2010. Biomanipulation: a useful tool for wetland rehabilitation. In: Ecology of Threatened Semi-arid Wetlands. Springer Press, New York, USA, pp. 215–228.

Balch, T., Scheibling, R.E., 2000. Temporal and spatial variability in settlement and recruitment of echinoderms in kelp beds and barrens in Nova Scotia. Mar. Ecol. Prog. Ser. 205, 139–154.

Balke, T., Herman, P.M.J., Bouma, T.J., 2014. Critical transitions in disturbance-driven ecosystems: identifying Windows of Opportunity for recovery. J. Ecol. 102, 700–708.

Bevilacqua, S., Terlizzi, A., Fraschetti, S., Russo, G.F., Boero, F., 2006. Mitigating human disturbance: can protection influence trajectories of recovery in benthic assemblages? J. Anim. Ecol. 75, 908–920.

Bulleri, F., 2013. Grazing by sea urchins at the margins of barren patches on Mediterranean rocky reefs. Mar. Biol. 160, 2493–2501.

Bulleri, F., Bertocci, I., Micheli, F., 2002. Interplay of encrusting coralline algae and sea urchins in maintaining alternative habitats. Mar. Ecol. Prog. Ser. 243, 101–109.

Chapman, A.R.O., Johnson, C.R., 1990. Disturbance and organization of macroalgal assemblages in the northwest Atlantic. Hydrobiologia 192, 77–121.

Christie, H., Norderhaug1, K.M., Fredriksen, S., 2009. Mar. Ecol. Prog. Ser. 396, 221–233.
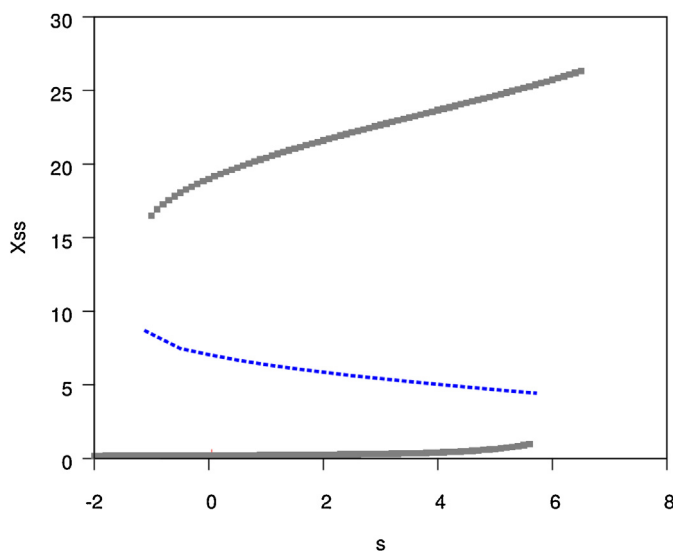
Fig. 5. Bifurcation diagram reporting the prey population steady states (X_{ss}) as a function of s. An irreversible hysteresis is found by increasing r_X from 2.1 to 5.5, with $A = B = 1$. $r_Y = 2.1$, $K_X = 31$, $K_Y = 26$, $c = 0.95$. Black squares are the stable steady states while the dotted grey line depict the unstable branch separating the low- and high-density solutions.

Couvray, S., Miard, T., Bunet, R., Martin, Y., Grillasca, J.-P., Bonnefont, J.-L., Coupe, S., 2015. Experimental release of juvenile sea urchins (*Paracentrotus lividus*) in exploited sites along the French Mediterranean coast. J. Shellfish Res. 34, 555–563.

Cowx, I.G., Gerdeaux, D., 2004. The effects of fisheries management practises on freshwater ecosystems. Fish Manag. Ecol. 11, 145–151.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. Science 333, 301–306.

Filbee-Dexter, K., Scheibling, R.E., 2014. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Mar. Ecol. Prog. Ser. 495, 1–25.

Folke, C., Carpenter, S.R., Walker, B., Scheffer, M., Elmqvist, T., Gundersonand, L., Holling, C.S., 2004. Regime shifts, resilience and biodiversity in ecosystem management. Annu. Rev. Ecol. Evol. Syst. 35, 557–581.

Garcia, S.M., Zerbi, A., Aliaume, C., Do Chi, T., Lasserre, G., 2003. The Ecosystem Approach to Fisheries. FAO Fisheries Technical Paper 443, pp. 1–71.

Giakoumi, S., Cebrian, E., Kokkoris, G.D., Ballesteros, E., Sala, E., 2012. Relationships between fish, sea urchins and macroalgae: the structure of shallow rocky sublittoral communities in the Cyclades, Eastern Mediterranean. Estuar. Coast. Shelf Sci. 109, 1–10.

Gianguzza, P., Agnetta, D., Bonaviri, C., Di Trapani, F., Visconti, G., Gianguzza, F., Riggio, S., 2011. The rise of thermophilic sea urchins and the expansion of barren grounds in the Mediterranean Sea. Chem. Ecol. 27, 129–134.

Guidetti, P., 2006. Marine reserves re-establish lost predatory interactions and cause community changes in rocky reefs. Ecol. Appl. 16, 963–976.

Guidetti, P., Dulcic, J., 2007. Relationships among predatory fish, sea urchins and barrens in Mediterranean rocky reefs across a latitudinal gradient. Mar. Environ. Res. 63, 168–184.

Hereu, B., Linares, C., Zabala, M., Sala, E., 2004. The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. Mar. Biol. 146, 243–249.

Hereu, B., Zabala, M., Sala, E., 2008. Multiple controls of community structure and dynamics in a sublittoral marine environment. Ecology 89, 3423–3435.

Holling, C.S., 1959. The components of predation as revealed by a study of small mammal predation on the European pine sawfly. Can. Entomol. 91, 293–320.

Kempf, A., Floeter, J., Temming, A., 2008. Predator–prey overlap induced Holling type III functional response in the North Sea fish assemblage. Mar. Ecol. Prog. Ser. 367, 295–308.

Knowlton, N., 1992. Thresholds and multiple stable states in coral reef community dynamics. Am. Zool. 32, 674–682.

Knowlton, N., 2004. Multiple 'stable' states and the conservation of marine ecosystems. Prog. Oceanogr. 60, 387–396.

Lauzon-Guay, J.S., Scheibling, R.E., Barbeau, M.A., 2008. Modelling phase shifts in a rocky subtidal ecosystem. Mar. Ecol. Prog. Ser. 375, 25–39.

Leber, K.M., 2013. Marine fisheries enhancement: coming of age in the new millennium. In: Sustainable Food Production. Springer Press, New York, USA, pp. 1139–1157.

Lindegren, M., Mollmann, C., Hansson, L.A., 2010. Biomanipulation: a tool in marine ecosystem management and restoration? Ecol. Appl. 20, 2237–2248.

Ling, S.D., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., Connell, S.D., Salomon, A.K., Norderhaug, K.M., Pérez-Matus, A., Hernández, J.C., Clemente, S., Blamey, L.K., Hereu, B., Ballesteros, E., Sala, E., Garrabou, J., Cebrian, E., Zabala, M., Fujita, D., Johnson, L.E., 2015. Global regime shift dynamics of catastrophic sea urchin overgrazing. Philos. Trans. R. Soc. B 370, 20130269.

Lorenzen, K., Agnalt, A.-L., Blankenship, H.L., Hines, A.H., Leber, K.M., Loneragan, N.R., Taylor, M.D., 2013. Evolving context and maturing science: aquaculture-based enhancement and restoration enter the marine fisheries management toolbox. Rev. Fish. Sci. 21, 213–221.

McClanahan, T.R., Muthiga, N.A., 1988. Changes in Kenyan coral reef community structure and function due to exploitation. Hydrobiologia 166, 269–276.

Marzloff, M.P., Dambacher, J.M., Johnson, C.R., Little, L.R., Frusher, S.D., 2011. Exploring alternative states in ecological systems with a qualitative analysis of community feedback. Ecol. Model. 222, 2651–2662.

May, R.M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269, 471–477.

Micheli, F., Benedetti-Cecchi, L., Gambaccini, S., Bertocci, I., Borsini, C., Osio, C.G., Romano, F., 2005. Cascading human impacts, marine protected areas and the structure of Mediterranean rocky-reef assemblages. Ecol. Monogr. 75, 81–102.

Montaño-Moctezuma, G., Li, H.W., Rossignol, P.A., 2007. Alternative community structures in a kelp–urchin community: a qualitative modeling approach. Ecol. Model. 205, 343–354.

Obolski, U., Hadany, L., Abelson, A., 2016. Potential contribution of fish restocking to the recovery of deteriorated coral reefs: an alternative restoration method? PeerJ 4, e1732, http://dx.doi.org/10.7717/peerj.1732.

Petraitis, P.S., Dudgeon, S.R., 2004. Detection of alternative stable states in marine communities. J. Exp. Mar. Biol. Ecol. 300, 343–371.

Petraitis, P.S., Hoffman, C., 2010. Multiple stable states and relationship between thresholds in processes and states. Mar. Ecol. Prog. Ser. 413, 189–200.

Piazzi, L., Bulleri, F., Ceccherelli, G., 2016. Limpets compensate sea urchin decline and enhance the stability of rocky subtidal barrens. Mar. Environ. Res. 115, 49–55.

Pinnegar, J.K., Polunin, N.V.C., 2004. Predicting indirect effects of fishing in Mediterranean rocky littoral communities using a dynamic simulation model. Ecol. Model. 172, 249–267.

Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.L., Hereu, B., Milazzo, M., Zabala, M., D'Anna, G., Pipitone, C., 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environ. Conserv. 27, 179–200.

Sala, E., Boudouresque, C.F., Harmelin-Vivien, M., 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos 82, 425–439.

Sala, E., Ballesteros, E., Dendrinos, P., Di Franco, A., Ferretti, F., Foley, D., Fraschetti, S., Friedlander, A., Garrabou, J., Guclusoy, H., Guidetti, P., Halpern, B.S., Hereu, B., Karamanlidis, A.A., Kizilkaya, Z., Macpherson, E., Mangialajo, L., Mariani, S., Micheli, F., Pais, A., Riser, K., Rosenberg, A.A., Sales, M., Selkoe, K.A., Starr, R., Tomas, F., Zabala, M., 2012. The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications. PLoS ONE 7, e32742.

Shears, N.T., Babcock, R.C., 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Mar. Ecol. Prog. Ser. 246, 1–16.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596.

Scheibling, 1996. The role of predation in regulating sea urchin populations in eastern Canada. Oceanol. Acta 19, 421–430.

Simenstad, C.A., Estes, J.E., Kenyon, K.W., 1978. Aleuts, sea otters, and alternate stable-state communities. Science 200, 403–411.

Sivertsen, K., 1996. Incidence, occurrence and distribution of the nematode *Echinomermella matsi* in its echinoid host, *Strongylocentrotus droebachiensis*, in northern Norway. Mar. Biol. 126, 703–714.

Thrush, S.F., Hewitt, J.E., Dayton, P.K., Coco, G., Lohrer, A.M., Norkko, A., Norkko, J., Chiantore, M., 2009. Forecasting the limits of resilience: integrating empirical research with theory. Proc. R. Soc. B 276, 3209–3217.

Watanuki, A., Aota, T., Otsuka, E., Kawai, T., Iwahashi, Y., Kuwahara, H., Fujita, D., 2010. Restoration of kelp beds on an urchin barren: removal of sea urchins by citizen divers in southwestern Hokkaido. Bull. Fish. Res. Agency 32, 83–87.

Watson, J., Estes, J.A., 2011. Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. Ecol. Monogr. 81, 215–239.