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The rise of thermophilic sea urchins and the expansion of barren grounds in the Mediterranean Sea

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Recent ecological studies have shown a strong relation between temperature, echinoids and their grazing effects on macro-algal communities. In this study, we speculate that climate warming may result in an increasingly favourable environment for the reproduction and development of the sea urchin *Arbacia lixula*. The relationship between increased *A. lixula* density and the extent of barren grounds in the Mediterranean Sea is also discussed.

Keywords: ocean warming; overgrazing; sea urchin fertilisation and development

Factors influencing the functioning of ecosystems, such as climate change, inputs of nutrients and/or toxic chemicals, groundwater reduction, habitat fragmentation, harvest of biomasses or loss of biodiversity, are never constant. The state of some ecosystems may respond gradually to such changes, whereas others might remain unresponsive over time (or ranges of conditions), and then respond abruptly when conditions reach a critical level. This implies that, for certain environmental conditions, the ecosystem might have two or more alternative stable states, separated by an unstable equilibrium that marks the border between the 'basins of attraction' of the states (the theory of alternative stable states; ASS) [1,2]. This theory also hypothesised that natural systems are often in persistent, resilient, alternative states: alternative combinations of ecosystem states and environmental conditions that may persist at a particular spatial extent and temporal scale.

These states have been shown to be maintained by intrinsic mechanisms involving biotic and abiotic interactions (grazing or predation intensity, storm frequency, pollution, local extinction, invasion, nutrient loading, etc.) which inhibit reversal to the previous community state [3]. In combination with other factors, the loss of a keystone species [4], which results from changes in top-down interactions between (1) predators and herbivores and (2) herbivores and macroalgae, may cause changes in grazing intensity and consequent switches between two or more alternative states in marine ecosystems.

For example, in temperate seas, several species of echinoids play a crucial role, and are even more important than other herbivores (i.e. fishes) as controllers of benthic communities [5–13].

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Variations in the population density of ecologically important echinoderm species can have marked consequences for the ecosystem, with notable examples resulting in major ecosystem changes described as 'phase-shifts' between alternative stable states, or catastrophic shifts [14]. For marine ecologists, the most familiar examples include the changes from coral- to algal-dominated systems associated with the die-off of the tropical sea urchin *Diadema* in the Caribbean [15,16] and the shift from large areas of complex macroalgal beds to areas termed 'urchin barrens' or 'barren grounds' [5,12,17–20], which are dominated by high sea urchin abundance and crustose coralline algae [21,22].

Subtidal urchin barrens are considered a global phenomenon [23,24], reported along temperate coastlines [25], subtropical coastlines [26], as well as in tropical regions [27], and are often considered ASS because they are highly resilient and may persist unless the abundance of sea urchins declines. To date, the factors responsible for their establishment and maintenance remain controversial and poorly understood [19,28–30].

Many authors have highlighted a human role in regulating sea urchin populations, such as overfishing of urchin natural predators [19,23,26,27,31–33]. The generality of this assertion has been a source of contention [34,35], and much of this debate can be summarised in two factors; lack of controlled experimental manipulations [21] and high spatial variability observed in system responses [34,36].

Many environmental factors can potentially decouple the top-down influence of urchins (and indirectly predators) on macroalgae. Environmental stress associated with wave action, sedimentation and low salinity has been shown to restrict the abundance of sea urchins and/or their grazing efficiency [37–39]. These environmental factors can vary at many spatial scales, for example, among regions, sites within regions and across depths within sites. Oceanographic variability can also influence the delivery of propagules and nutrients to near-shore environments [40] and potentially affect the relative importance of urchins in controlling kelp in space and time [41].

Furthermore, we cannot omit the potential impacts of the under-way global warming, causing ocean warming and acidification, in regulating the reproductive cycles and distribution of many sea urchin species [42,43].

There are a number of different life-cycle stages, such as fertilisation, cleavage, planktonic larva, settlement, metamorphosis, juvenile, adult and reproductive stages, which are affected differently by changes in temperature. Many studies hae shown that each sea urchin species has an optimal fertilisation temperature based on the average temperature found in its natural habitat [44]. This optimal temperature is necessary for the successful development of the embryos and pluteus larvae [45]. As recently reported by Byrne et al. [43], studies of thermotolerance in a diverse suite of tropical and temperate sea urchins show that fertilisation and early development are robust to temperatures well above ambient and the increases expected from climate change [46–48]. Thermotolerance in sea urchin fertilisation and early development is conveyed by maternal factors imprinted by ovary temperature [45,49] and potentially include protective heat shock proteins [50,51]. There is strong evidence that adult thermal history, particularly maternal acclimatisation, influences thermal tolerance in echinoderm fertilisation and development due to adaptive phenotypic plasticity with respect to prevailing temperatures [49,52–55].

Climate warming is predicted to drive species ranges northwards in the northern hemisphere and southwards in the southern hemisphere [56,57]. From a recent study on climate warming and the range extension of thermophilic sea urchin species, a significant positive relationship between *Centrostephanus rodgersii* (Agassiz) density and the extent of barrens has been unequivocally proven in eastern Tasmania. It is likely that recent warming of the eastern Tasmanian coast results in an environment increasingly favourable for the reproduction and development of this sea urchin, and given prediction of continued warming for this coast, the likelihood of further population expansion of *C. rodgersii* and its associated barren appears considerable [58]. Hart and Scheibling (1988) [59] report evidence of an analogous temperature threshold mechanism for

Strongylocentrotus droebachiensis (O.F. Müller, 1776) along the Atlantic coast of Nova Scotia where sea urchin population booms and associated overgrazing of kelp beds were correlated with a positive ocean temperature anomaly, allowing optimal temperatures for larval development.

Climate warming is perceptible in the Mediterranean realm, where a variety of thermophilic species belonging to macroalgae, plankton, invertebrates and fishes, are extending their distribution towards northern areas [60 and references therein].

In a pioneer study on the ecological consequences of increased mean temperature in the Mediterranean Sea, Francour et al. [61] observed that in Corsica, at Scandola marine reserve, the abundance of *Arbacia lixula* (L.), considered as thermophilous by Kempf [62], increased >12 times over a time span of nine years: from densities of 8 individuals$\cdot$m^{-2} in 1983 to 100 individuals$\cdot$m^{-2} in 1992 [61]. The authors suggested that the increase in water temperature might have favoured population growth of this thermophilic urchin; they also speculated on the impact of this grazer in the formation of barrens, habitats of low primary production and reduced structure that negatively affect several coastal fish that use erect macrophytes for shelter, food, nesting and settlement [61].

A recent study that investigated the relationships among predator fish, sea urchins and barrens in the Mediterranean Sea across latitudes to predict the consequences of the ongoing large-scale changes in the distribution patterns of native thermophilous species through the Mediterranean Sea (including, e.g. *Thalassoma pavo* and *A. lixula*) supports Francour et al.'s hypothesis that *A. lixula* may play an important role in the formation and maintenance of barrens in the Mediterranean [25]. From this point of view, the current expansion of this sea urchin northwards in the Mediterranean could have the potential to induce changes in coastal phytobenthos by enhancing, for example, the chance of transition from macroalgal beds to barrens.

By contrast, a large-scale decline in the abundance of the co-occurring *Paracentrotus lividus* (Lamarck, 1816) is underway in many Mediterranean areas [63–66]. Although human harvesting has been identified as the major factor causing such outbreaks, this species is considered a gastronomic delicacy worldwide [67–69], global warming could play an important role in such outbreaks, facilitating also the proliferation of native warm water species such as *A. lixula*.

In both wild and farmed Mediterranean *P. lividus* populations, the rate of gametogenesis increases with temperature. In general, spawning takes place when the sea surface temperature ranges between 16 and 20 °C. This range is considered optimal for both fertilisation and the survival and development of the larvae of *P. lividus*. At 24 °C, Spirlet et al. [70] observed fleshier but less mature gonads, suggesting that high temperature can inhibit and/or interrupt *P. lividus* gametogenesis.

A. lixula exhibits an opposite trend. From 2003 to 2008 we determined the gonadal somatic index (GSI; the index of gonad mass relative to whole organism size) of this species (10 sea urchins with test diameter 40 mm randomly collected during the summer spawning period) in two sites of Ustica Island (southern Tyrrhenian Sea, Mediterranean, Italy). Results showed a positive correlation between increased surface sea temperature and GSI of *A. lixula* ($r = 0.30\, p < 0.01$). The *A. lixula* GSI was maximum (8.2 ± 1.9; mean $\pm$ SE) in 2008 at 26 °C and minimum (4.07 ± 0.5) in 2007 at 23.5 °C.

Because *P. lividus* gametogenesis is negatively affected by high temperature [71], it is likely that this species might display lower reproductive potential than *A. lixula*, suggesting that climate warming may result in unfavourable environment conditions for its survival. Climate warming acting synergistically with overfishing [72] may allow a shift from a ubiquitous presence in Mediterranean rocky reefs of *P. lividus* and *A. lixula* to a dominant presence of *A. lixula*.

The consequences of this scenario could be serious for the diversity and functioning of the Mediterranean ecosystem. Many authors support the increasing evidence that *A. lixula*, less prone to predation than *P. lividus*, may establish a positive feedback which tends to stabilise and maintain the barren grounds in rocky littoral ecosystems [25,73]. As recently suggested by Privitera et al. [74], this sea urchin is more effective in scraping rocky surfaces and showed a strong preference for encrusting corallines, suggesting a better fit in this habitat where such algal components represent the largest cover.

We encourage future research aimed at understanding the interaction between global warming and reproduction of *A. lixula*. Despite of the commonness and abundance of this species, there are remarkably few studies about its reproductive biology. A reason for the lack of such biological information seems to be that this unpalatable species has never been harvested for consumption and thus has not been of direct economic interest.

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