

«NATURAL» POPULATION DENSITY  
FLUCTUATIONS OF ECHINOIDS. DO THEY  
HELP PREDICT THE FUTURE?

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CLIMATE CHANGE PERSPECTIVES FROM THE ATLANTIC:  
PAST, PRESENT AND FUTURE

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## ABSTRACT

In order to determine whether future changes in population density of sea urchins are caused by anthropogenic increases in temperature, acidity, or sea level it is necessary to have baseline data of how populations change in response to natural causes. I review cases of species with relatively stable populations over a decade, of species in which populations are known to have expanded and denuded the benthos of algae, and of species in which populations have crashed. Such documented cases are rare, because there is a dearth of information regarding long-term changes in population parameters for most echinoid species. An alternative method of deciphering past population fluctuations on the basis of genetic diversity of populations is used to show that *Diadema antillarum* became abundant long before human colonization of the Caribbean. The mass mortality suffered by this species in 1983-1984 was thus not due to abnormal population density due to the removal of its predators and competitors by humans. The existing data do not permit firm predictions regarding the future of echinoid populations under global change, but they do establish that some species are subject to boom-bust fluctuations accentuated by disproportional effects of adult population changes upon recruitment and juvenile survivorship.

KEYWORDS: sea urchins, population fluctuations, *Diadema*

## INTRODUCTION

The impending global changes due to the accumulation of carbon dioxide has worried scientists during the last two decades. Concern about marine ecosystems has understandably focused on the future of coral reefs in light of increased ocean temperatures and in sea water acidity (e.g., Kleypas *et al.* 1999; Hoegh-Guldberg *et al.* 2007; Knowlton and Jackson 2008; Kiessling and Simpson 2011; Pandolfi *et al.* 2011). A number of models have attempted to forecast changes in these ecosystems (e.g., Halpern *et al.*, 2008; Anthony *et al.*, 2011). Curiously, these models do not explicitly consider the effects of higher temperature and decreased pH on echinoids, even though echinoids are known to be important in coral reef ecosystems as herbivores that keep corals from being overgrown by algae (Carpenter, 1986; Hughes, 1994; McClanahan *et al.*, 1996) and as agents of bioerosion (Hunter, 1977; Scoffin *et al.*, 1980; Bak, 1990, 1994). The present compendium thus fills a need in that it focuses attention

on a subject well-worth discussing. As oceans change, what will happen to sea urchin populations, and how will such changes affect ecosystems in which sea urchins play a role?

Although some attempts have been made to predict the future of certain sea urchin species under impending changes in temperature (Francour *et al.*, 1994; Guidetti and Dulcic, 2007; Gianguzza *et al.*, 2011; Privitera *et al.*, 2011) or acidity (Catarino *et al.*, 2012; Doo *et al.*, 2012), the straight-forward answer to the question of future changes in echinoid populations is that we do not know what will happen. This is, of course, true for all organisms; however, for those that have a good fossil record, such as corals, informed guesses can be made on the basis of past changes in their abundance that have resulted from environmental change, as documented from proxies of temperature and carbon dioxide concentration (e.g., Kiessling, 2009). Such efforts could not possibly succeed with echinoids, because the echinoid fossil record is not extensive enough for this purpose (Kier, 1977). Attempts to determine past echinoid abundance from fossils have been made, but they have produced results that can only be described as mixed (Simenstad *et al.*, 1978; Greenstein, 1989; Donovan, 2005). Information about population fluctuations of echinoids in times that precede global change is, thus, sorely needed. We would like to have such information for two reasons: (1) in the absence of information on past fluctuations, it will be difficult to determine whether any future ones are due to «natural» or to anthropogenic causes; (2) the ecological effects observed in past changes of echinoid abundance can guide the predictions of what may happen when they occur in response to global change. It is, therefore, useful to look at changes in echinoid populations documented in the literature in order to establish a baseline of what can happen before ocean temperatures rise and pH falls.

The available data can be placed in two general categories: direct observations of population fluctuations, and reconstructions of recent or more distant past demographic history by indirect means. Neither set of data is perfect for our purposes. Published direct observations have only been possible in the «anthropocene», the period of time in which humans have already started affecting marine environments. There will, thus, always be doubts as to whether their causes are natural, or have resulted from overfishing, pollution, or some other effect caused by humans. Indirect reconstructions, such as the ones, derived from old documents (Jackson, 1997), museum specimens (Levitan, 1992), or genetic markers (Lessios *et al.*, 2001a), suffer from biases (different in each case). They are also not suitable for determining the cascade of effects that changes in population density of sea urchins have had on the ecosystem. Nevertheless, it is worth putting all this information together and attempt to use it in speculating about the future.

## POPULATION FLUCTUATIONS

Uthicke *et al.*, (2009) called echinoderms a «boom-bust» phylum because of large population fluctuations undergone by some of its species. They reviewed evidence of population crashes or break-outs of 28 echinoderm species, eight of them belonging to the Echinoidea: *Arbacia lixula*, *Diadema antillarum*, *Echinometra mathaei*, *Echinocardium cordatum*, *Paracentrotus lividus*, *Strongylocentrotus droebachiensis*, *S. purpuratus*, and *S. franciscanus*. To these, one should add the range expansion of *Centrostephanus rodgersii* into Tasmanian waters (Ling, 2008; Ling and Johnson, 2009) and the frequent population increases and unusual population fluctuations of the Caribbean and western Atlantic *Lytechinus variegatus* (Beddingfield and McClintock, 1994; Macia and Lirman, 1999; Rose *et al.*, 1999). Lawrence (1996) has reviewed mass mortalities of echinoderms due to abiotic factors. Mortalities due to such physical factors are generally localized, ephemeral, and infrequent, so they may not hold any lessons regarding the possible effects of global change. This chapter is intentionally unbalanced: contributions by other authors to the same compendium cover the population fluctuations of *Strongylocentrotus droebachiensis* on the East coast of North America (Scheibling, this volume), *Paracentrotus lividus* and *Arbacia lixula* in the Mediterranean (Hereu, this volume), *Centrostephanus rodgersii* in Tasmania (Ling, this volume) and *Diadema africanum* (Hernández, this volume). The present chapter will, therefore, concentrate on species that are not the main focus of other contributions. Additional imbalance comes from the variable amount of published information regarding each of these case studies. Finally, documentation of such population fluctuations is not independent of the geographical distribution of research centers in Europe, North America, Australia, and the Caribbean.

## STABLE POPULATION DENSITIES

Densities of every natural population go up or down through time. To determine what constitutes boom-bust population fluctuations, one first needs to decide what changes occur under «normal» circumstances. Unfortunately, data on long-term population monitoring of echinoid populations are scarce (Uthicke *et al.*, 2009), so one has to generalize from a few examples. Pearse and Hines (1987) studied populations of *Strongylocentrotus franciscanus* and of *S. purpuratus*, at irregular intervals ranging from 1 to 8 months, in a reserve on the coast of California from 1972 to 1981. During the nine years of this study, population densities of *Strongylocentrotus franciscanus* stayed uniformly low. *S. purpuratus*, on the other hand, experienced a single event of high recruitment that temporarily increased its density from 0.2 to 5 individuals per m<sup>2</sup>. Most of these recruits had disappeared a year later. This species, like its congener *S. droebachiensis* on the East coast of North America, is involved in «urchin barrens», where kelp is almost entirely removed (Dayton *et al.*, 1992). Hereu *et al.* (2012) monitored populations

of *Paracentrotus lividus* from 1991 to 2010 and of *Arbacia lixula* from 1995 to 2010 in annual censuses in North-West Mediterranean. They found that annual density differences in *P. lividus* living in boulders could be as high as eightfold, whereas densities of the same species living in vertical walls were not significantly different between years. Similar inter-annual variation was seen in *A. lixula*. Increases were due to pulses of recruitment, but the overall densities were smoothed within a year by mortality. Wing (2009) monitored populations of *Evechinus chloroticus* in the Fiordland of the South Island of New Zealand from 1998 to 2007 at intervals ranging from one to three years. Fjords in this area are characterized by dense kelp growth at the entrances, replaced by broken blades and debris in the innermost areas, and by fresh water lenses overlaying layers of normal salinity. Sea urchin populations at the fjord entrances were composed of large individuals and a stable size structure, indicating steady recruitment, whereas at the inner areas there was evidence of high turnover, caused by severe mortality followed by high recruitment.

In summary, the few available sets of data from long-term monitoring, all of them from species in the temperate zone, suggest that fluctuations in population density of sea urchins do occur, but there are also stabilizing mechanisms of recruitment followed by mortality, and of mortality followed by recruitment that, in a decadal scale, tend to maintain fairly steady levels. Ability of sea urchin species to recolonize areas in which physical factors have caused localized mortalities (e.g., Andrew, 1991; Lawrence, 1996; Junqueira *et al.*, 1997; Beddingfield and McClintock, 2000; Lawrence and Agatsuma, 2007) also suggest that if sufficient numbers of individuals of a species survive in areas close enough for larvae to reach and reseed bare patches, overall populations will remain relatively stable.

There is, of course, some circularity in designating as «normal» situations that appear to be stable, but the object here is to provide a baseline with which to compare phenomena of instability. Large echinoid population fluctuations, appearing to drive marine ecosystems into alternate stable states have also been noted. Such deviations from «normal» fluctuations in echinoid population density have generally been noticed and studied after they have occurred. Population expansions as a rule manifest themselves as sea urchin barrens due to overgrazing. Population constrictions are sometimes obvious from the accumulation of dead tests. In either case, interpretation of causes and quantification of the magnitude of the event are hampered by the lack of data as to the state of the populations before the change occurred.

#### POPULATION EXPANSIONS

Unusual increases in population densities of particular species of echinoids have been documented in several parts of the world. As a rule, they have dramatic consequences on the benthic communities by removing algae and leaving bare substrate in their path.

One of the earliest reported major positive changes in sea urchin abundance was the increases of *Strongylocentrotus purpuratus* and *S. franciscanus* off the coast of southern California (North and Pearse, 1970). The increase has been ascribed to the removal of predators, such as sea otters (Estes *et al.*, 1989) and lobsters (Lafferty, 2004), and of competitors, such as abalone (Dayton *et al.*, 1998). The ecological effect was devastation of kelp forests during sea urchin population increases, followed by recovery when sea urchins were removed by disease or overfishing (Dayton *et al.*, 1992).

The best documented case of the ecological effects of sea urchin population density increases is that of *Strongylocentrotus droebachiensis* off the coast of Nova Scotia, studied over the last thirty years by Robert Scheibling and colleagues. As this topic is covered in another chapter (Scheibling, this volume), there is little that needs to be added here. The same species also caused barrens in laminarian kelp forests in northern Norway in the early 1980s (Hagen, 1983).

The case of echinoid population expansion most likely to be the product of global change is that of *Centrostephanus rodgersii* in Tasmania, first observed in 1978 (Andrew and Byrne, 2001; Johnson *et al.*, 2005; Ling, 2008). This case is also covered in another chapter (Ling, this volume), so it will only be briefly mentioned here. *C. rodgersii* off New South Wales has increased its populations in recent times to a density that has created sea urchin barrens. The increase is attributed to the reduction of its predators through overfishing (Andrew and Byrne, 2001). Although it was originally absent from Tasmania, *C. rodgersii* recently invaded this island with the same ecological impact as in its historic range. This range expansion, reflected by a number of other species (Poloczanska *et al.* 2007), was most likely the result of pole-ward intrusions by the East Australian Current (Johnson *et al.* 2005). To the extent that echinoid species ranges are controlled by temperature, such spreading of species towards lower latitudes are expected as the planet warms and ocean current circulation patterns are altered.

Although the expansion has not been documented for lack of previous data, there appears to have been an increase of population density of *Diadema africanum* (Rodríguez *et al.* 2013) in the Canaries due to overfishing of its predators (Tuya *et al.*, 2004). This increase has manifested itself in the formation of barrens devoid of macroalgae. Hernández *et al.* (2008) monitored populations of *Diadema* at multiple islands in the Canaries in irregular intervals between 2001 and 2006. As a rule, the population densities fluctuated by a factor of two, but there was an outbreak in 2006. By December 2006 populations in three islands appeared to be on their way to returning to their previous levels.

*Echinometra mathaei* in heavily exploited reefs off the coast of Kenya showed a ten-fold increase in population density between 1970 and 1985 (McClanahan and Muthiga, 1988). Large differences between protected and unprotected areas indicated that the increased abundance of *Echinometra* was due to the removal of its predators (McClanahan and Shafir, 1990).

An extreme case of local echinoid population density increase was documented in the Outer Bay of Florida (Macia and Lirman, 1999; Rose *et al.*, 1999).

Between 1996 and 1997 average density of *Lytechinus variegatus* in the Outer Florida Bay was 0.2 individuals per m<sup>2</sup>. In September 1997 a large aggregation of this species reached densities of 364 sea urchins per m<sup>2</sup>. It formed a large 2-3 km grazing front that denuded approximately 0.81 km<sup>2</sup> of the *Syringodium filiforme* sea grass bed. By the time of the last observations in April 1998, densities had dropped to approximately 18.5 sea urchins per m<sup>2</sup>. Such a grazing front by *L. variegatus* in the northeast Gulf of Mexico had also been reported previously (Camp *et al.*, 1973), though without data of population densities in normal times.

Thus, echinoids appear capable of expanding their populations when predators are removed, or when conditions become favorable for recruitment. Interestingly, population regulation does not appear to be exercised through food limitation. Even after they have created barrens, sea urchins were able to maintain high population densities until another factor, such as disease caused drastic reductions (Lang and Mann, 1976; Andrew, 1991; Dayton *et al.*, 1992; Lauzon-Guay and Scheibling, 2007).

#### POPULATION CRASHES

Whereas populations of *Centrostephanus rogersii* in Tasmania appear to remain stable or still increase, population expansions of *Strongylocentrotus* in three parts of the world are checked by mass mortalities, so that kelp ecosystems fluctuate in alternate stable states. At both coasts of North America, as well as in Scandinavia, barren-causing sea urchin populations are confronted by pathogens or parasites, sometimes in combination with other factors, such as storms. In California one population of *S. purpuratus* was decimated by disease, allowing kelp to recruit to the site (Dayton *et al.*, 1992). At Norway populations of *S. droebachiensis* that had overgrazed algae were infested by *Echinomermella matsi*, a nematode parasite of sea urchins, which is presumed to have reduced their density, so that kelp could recover (Hagen, 1987, 1992, 1995). The only case in which the pathogen was unambiguously identified and studied in detail was that of *S. droebachiensis* off the coast of Nova Scotia. The causative agent, proven by Koch's postulates, is an amoebozoan, *Paramoeba invadiens* (Jones *et al.*, 1985; Jones and Scheibling, 1985). Infection by *Paramoeba* only flares up when sea water temperatures exceed 10° C, so that high mortality occurs seasonally in the summer and early fall, and is also correlated with hurricane activity (Feehan *et al.*, 2012). At the Canaries, moribund *Diadema africanum* were found to contain trophozoites of *Neoparamoeba branchiphila*, a close relative of *Paramoeba invadiens* (Dykova *et al.*, 2011). Thus, events of unusual population increases may, in some cases, be followed by events of unusual mortality. To some, this may indicate the resilience of an ecosystem to perturbations, whereas to others it is an indication of alternate stable states (Simenstad *et al.*, 1978; Scheibling, 1984).

Two cases in which population crashes do not appear to be due to self-correction are the fairly gradual decline of *Paracentrotus lividus* populations



at Lough Hyne in Ireland and the mass mortality of *Diadema antillarum* in the Caribbean and the western Atlantic. *Paracentrotus lividus* population fluctuations due to recurrent recruitment and mortality in the North Western Mediterranean have been mentioned in this chapter as an example of a stable population. This has not been the case at the oldest marine reserve in Europe, Lough Hyne, a semi-enclosed lagoon. *P. lividus* at Lough Hyne was present at high densities from 1964 to 1984 but has undergone a steady decline between 1984 and 2000 (Barnes *et al.*, 2001; Barnes and Crook, 2001) eventually completely disappearing in 2002 (Barnes *et al.*, 2002). The actual causes of the decline remain unclear. Given the apparent stability of the Irish populations over twenty years and their eventual demise over the next twenty, one could argue that the Mediterranean populations of the same species, followed by Hereu *et al.*, (2012) for ten years, might meet the same fate if one were to monitor their density long enough. If so, my having designated them as stable is premature. Only time will address this point.

The *Diadema antillarum* die off in the Caribbean and the American Atlantic coast is the most severe and most extensive case of mass mortality in a marine organism documented to date. It was first noticed on the coast of Panama in January 1983. In a little more than a year it had spread to the entire Caribbean, Florida and Bermuda (Lessios *et al.*, 1984a). The mass mortality did not reach the eastern Atlantic (Hernández *et al.*, 2008) either because currents did not carry the pathogen across, or because *Diadema africanum* is actually a different species (Lessios, 2001; Lessios *et al.*, 2001b; Rodríguez *et al.* 2013). Pre-mortality population density data were available in eight areas in the Caribbean. The average population reduction at these sites ranged between 87 and 100 % (Lessios, 1988a). The cause of the mortality was never identified, but indirect evidence points to a species-specific pathogen (Lessios *et al.*, 1984a,b; Lessios, 1988a). The immediate result of the removal of *Diadema* from the reefs was increase by macroalgal cover, which, in time, prevented recruitment of corals and even overtopped adult colonies (de Ruyter van Steveninck and Bak, 1986; Hughes *et al.*, 1987; Hughes, 1994). Populations of other echinoids on the reefs were not affected either negatively by the pathogen, or positively by possible release from competition (Lessios, 1988b). Herbivorous fishes, on the other hand, did benefit. By 1990, populations of the surgeon fishes *Acanthurus coeruleus* and *A. chirurgus* in the San Blas area of Panama had increased their population density by more than 160%, whereas those of *A. bahianus*, which feeds in areas where *Diadema* was never present, remained constant (Robertson, 1991). Genetic diversity of *D. antillarum*, measured by isozymes before and after the mass mortality, did not change (Lessios, 1985). This species also maintained much higher molecular diversity in mitochondrial DNA in the Caribbean than *D. africanum* did in the eastern Atlantic and *D. mexicanum* in the eastern Pacific (Lessios *et al.* 2001a).

Despite some early signs that population recovery of *Diadema antillarum* would commence soon after mass mortality (Lessios *et al.*, 1984b; Hunte and Younglao, 1988), it proved to be very slow. A number of studies started monitoring

populations after the mass mortality and found some increases, but at locations without pre-mortality data it is not possible to determine the extent of recovery. Subjective impressions of the species being plentiful once again can be misleading, because *Diadema* tends to aggregate in shallow areas, so that patches with high spot densities can be misjudged as indications of high overall abundance. The only objective determinations can come from locations in which there were pre-mortality data. Twenty years after mass mortality, population density in Panama was at 6.5% of their pre-1983 values (Lessios, 2005a). Eighteen years after January 1984, when mass mortality reached the US Virgin Islands, populations at St. Croix were at 5.2% of pre-mortality levels (Miller *et al.*, 2003). Nineteen years after die offs in Curacao, populations of *D. antillarum* on the leeward side of the island were at 1.9-9.6 % of what they used to be (Debrot and Nagelkerken, 2006), and continued to be low three years later despite evidence of renewed recruitment (Vermeij *et al.*, 2010). In Discovery Bay, Jamaica, increases in population density of *Diadema* were accompanied by higher incidence of coral recruits (Edmunds and Carpenter, 2001). A correlation between *Diadema* and coral recruit abundance was also found in six other sites of the Caribbean (Carpenter and Edmunds, 2006).

Was the mass mortality of *Diadema antillarum* a natural correction in a species that had overpopulated its environment due to anthropogenic causes? Hay (1984), through comparisons between areas in the Caribbean with different fishing pressures, had suggested that the removal of fish predators and competitors of the sea urchin had been responsible for high pre-mortality densities. Levitan (1992), in a study of the relative size of test and jaw dimensions of museum specimens in space and time (a proxy for food limitation), concluded that fishing had an effect on *Diadema* population density, but that this effect was minor. Jackson (1997), on the basis of anecdotal accounts in 16<sup>th</sup> century Spanish manuscripts, argued that *Diadema* was abundant in the Caribbean before fishing pressure increased. Donovan (2005), on the basis of a very patchy and fragmentary fossil record of *D. antillarum* ossicles in sediments, concluded that the species had been abundant long before prehistoric times.

One way to answer the question of population size in past ages is the study of DNA. Diversity of selectively neutral genetic markers depends only on the rate of substitution of the marker in question and on effective population size. Thus, if the former is known, the latter can be modeled. Lessios *et al.* (2001a) sequenced two genes of mitochondrial DNA in 110 individuals of *D. antillarum* from seven localities around the Caribbean. They estimated rate of substitution from divergence between *D. antillarum* and *D. mexicanum*, separated 2-3 million years ago by the rise of the Isthmus of Panama. They were thus able to estimate the trajectory of female effective population expansion through time, and found that it began between 400 and 100 millennia ago. The conclusion is that human activity may have had some effect upon *Diadema* population densities, but the large increase of the population occurred too far back in time to have been caused by humans.

In summary, sea urchin populations appear to remain stable for undetermined periods of time, but some species at certain times may undergo break out increases that alter the ecosystem through their grazing, and some species experience die offs from which they can recover rapidly if the mortality is localized, but take decades to be repaired if the majority of individuals throughout the species range have died.

#### WHY SHOULD THE ECHINOIDEA SHOW BOOM-BUST FLUCTUATIONS?

Uthicke *et al.* (2009), in examining severe population fluctuations in 28 species of echinoderms, concluded that anthropogenic disturbance, including climate change and disease outbreaks, were the most common causes. They also suggested that boom-bust cycles are linked to two life history traits, common among all the examples mentioned above: broadcast spawning and planktotrophic larvae. External fertilization depends on the proximity of sperm and eggs during spawning, the probability of which decreases rapidly with increased distance of individuals of the two sexes (Pennington, 1985; Levitan, 1991; Lauzon-Guay and Scheibling, 2007). This leads to an Allee effect, a feedback loop of disproportional effects of adult population rarity upon the abundance of juveniles in the next generation. According to Uthicke *et al.* (2009), planktotrophic larvae decouple factors that regulate resources for the early life stages from adult resources, so that rate of recruitment is dependent on the rate of larval production and on the vagaries of survival in the plankton, rather than being limited by adult densities. An additional mechanism that forms self-reinforcing loops and would accentuate the magnitude of positive and negative fluctuations has been documented for several species of sea urchins. This is the positive feedback resulting from the negative correlation between algal abundance and sea urchin recruitment. Adult sea urchins, by grazing algae, provide suitable substrate (possibly due to the absence of micropredators) for the settlement of larvae. This may well be the case in *Centrostephanus rogersii* (Ling and Johnson, 2009), *Strongylocentrotus droebachiensis* (Lang and Mann, 1976), *S. purpuratus*, *S. franciscanus* (Tegner and Dayton, 1981) and *Diadema antillarum* (Bak, 1985). A yet additional feedback mechanism in some of the same species is the protection afforded to juveniles by adult spine canopies, as it happens in *S. purpuratus* (review in Rogers-Bennett, 2007), and apparently also in *Diadema antillarum* (Miller *et al.*, 2007). Thus, increases in adult echinoid population densities in each generation lead to new disproportional increases in the next; decreases in adults lead to disproportional reductions in recruitment and survivorship of juveniles.

DO DATA FROM THE PAST  
HELP PREDICT THE FUTURE?

Predictions based on scant data are always dangerous, but certain points can be made on the basis of cases I have summarized. If echinoids are, in fact, subject to boom-bust trends, global warming may affect their populations disproportionately relative to those of other organisms. Guessing which species will be affected and to what degree is not possible by the present data, but some may succumb to disease, whereas others may experience large population increases that would wreck havoc with the ecosystems they occupy. Given the association of outbreaks of *Paramoeba invadiens* in *Strongylocentrotus droebachiensis* with higher temperatures and hurricanes, it seems very likely that mass mortalities in this species will continue or, more likely, increase with global warming. Similarly, the coincidence between bald sea urchin disease in *Paracentrotus lividus* with high temperatures at the Canaries (Girard *et al.*, 2012) does not auger well for the prospects of temperate sea urchins as the seas become warmer. Temperature, however, is not always the trigger for echinoid disease. Even though the *Diadema* mortality occurred in an El Niño year, the initiation of its outbreak in Panama preceded the increase of temperatures in the Caribbean by several months (Lessios *et al.* 1984b).

To the extent that higher temperatures may not always cause disease, echinoids (other than species living close to the poles, which have no escape towards lower latitudes) may be affected much more severely by overfishing and pollution than by global warming and ocean acidification. Sea urchins in the tropical eastern Pacific survive well, despite the low pH values in this ocean (Manzello *et al.*, 2008). They also survive with no apparent ill effects high temperatures during El Niño events that cause extensive coral bleaching and mortality (Lessios, 2005b). If anything, species like *Diadema mexicanum* and *Eucidaris thouarsi* benefit from coral mortality, because it opens new areas for algal colonization. This, by no means, indicates that echinoids will be immune to global change. They might, however, become even more prominent components of benthic ecosystems.

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