Chapter 18

Diadema

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1. INTRODUCTION

1.1. Species and Evolution of *Diadema*

Six species of *Diadema* (Gray, 1825) are recognized: *Diadema antillarum* (Phillipi, 1845); *Diadema mexicanum* (A. Agassiz, 1863); *Diadema savignyi* (Michelin, 1845); *Diadema setosum* (Leske, 1778); *Diadema palmeri* (Baker, 1967) and *Diadema paucispinum* (A. Agassiz, 1863) (Pearse, 1998). Long black spines characterize the genus, and individual species are sometimes difficult to identify in the field except for *D. palmeri*, which has a distinctive red coloration. The sympatric species *D. savignyi* and *D. setosum* may occur in single species groups or in mixed groups and may be distinguished by test color pattern, spine morphology and pedicellarie shape. Most populations of *D. setosum* in Kenya have an orange ring around the anus and five bright (rarely pale) white spots on the aboral ends of the interambulacrals (Muthiga, 2003). *Diadema savignyi*, on the other hand, has iridescent blue or green lines along the interambulacrals and around the periproct and sometimes five very pale white spots on the aboral ends of the interambulacrals (Pearse and Arch, 1969).

These characteristics are apparently common for other populations of these species throughout the Indo-Pacific (H. L. Clark 1921, 1946; Mortensen, 1940; Pearse and Arch, 1969; Lessios and Pearse, 1996). However, individuals with intermediate characteristics are sometimes encountered, and populations of *D. setosum* in the Red Sea show more variability in the color pattern (A. M. Clark, 1966; Pearse, 1970). Mortensen (1940) suggested that the intermediate characteristics are due to hybridization. Lessios and Pearse (1996) confirmed that hybridization and introgression occurs between *D. savignyi* and *D. setosum*, which could result in intermediate characteristics. According to Lessios and Pearse (1996), individuals of *D. paucispinum* are characterized by having no orange ring, no white spots and no iridescent blue dots. Coppard and Campbell (2004) describe spine morphology of *Diadema* species and show that the spines of *D. paucispinum* are visibly more robust than the other species and this is reflected in the internal structure of the spine with large closely packed solid wedges, small axial cavity and strengthening structures such as spokes and trabeculae. The spines of *D. setosum* are also distinct, especially in relation to the length relative to test size.

In terms of phylogenetic relationships between the species, a detailed comparison of 28 morphological features of the test showed that the apical system, markings on the genital plates, features of the median areas of the interambulacra and distribution of the iridophores (Coppard and Campbell, 2006a) and pedicellariae (Coppard and Campbell, 2006b) were particularly useful for distinguishing species and phylogenetic relationships in the genus. Four species, *D. antillarum, D. mexicanum*, *D. savignyi* and *D. paucispinum*, were found to have closely associated morphological features. The outlying species in the genus *D. setosum* and *D. palmeri* had very narrow tridentate pedicellariae, which is one of the first morphological features thought to diverge evolutionarily. The most unique species in the genus was *D. palmeri*, which had both the narrow and broad forms of pedicellaria and was the only species with a monocyclic apical system. The pedicellariae of *D. antillarum* and *D. mexicanum* were found to be the most similar within the genus.

1.2. Biogeography and large-scale distribution

Sea urchins of the genus *Diadema* are some of the most widespread, abundant and ecologically important sea urchins in tropical regions (reviews in Lawrence and Sammarco, 1982; Lessios, 1988; Birkeland, 1989; Carpenter, 1997; Tuya et al., 2005). *Diadema* populations occur in all tropical seas to a depth of up to 70 m (Mortensen, 1940). Lessios et al. (2001a) summarize the geographical distributions of the different species of *Diadema* as follows: *D. antillarum* primarily occurs in the tropical Atlantic, from Florida

and Bermuda to Brazil and from Madeira (but contrary to Mortensen, 1940, not in Azores; Wirtz and Martins, 1993) to the Gulf of Guinea; *D. mexicanum* occurs in the tropical eastern Pacific from the Sea of Cortez to Ecuador, including the Islands of Revillagigedo, Clipperton, Isla del Coco and Galapagos (Maluf, 1988); *D. palmeri* is only known from the north coast of New Zealand (Baker, 1967) and from the south coast of Australia (Rowe and Gates, 1995); *Diadema paucispinum* is thought to be primarily a Hawaiian species, occurring in the South Pacific and Hawaiian islands (A. M. Clark and Rowe, 1971), but Pearse (1998) indicates that it may occur in other parts of the tropical Indo-Pacific. A. M. Clark and Rowe (1971) reported that both sympatric species *D. savignyi* and *D. setosum* occur in the Mascarene Islands, East Africa and Madagascar, south east Arabia, Ceylon, East Indies, North Australia, Philippine Islands, China and south Japan and the South Pacific Islands. In addition, only *D. setosum* was reported in the Red Sea, Persian Gulf and Bay of Bengal, while *D. savignyi* was reported in the islands of the western Indian Ocean.

Because some confusion existed as to the true distributions of *D. savignyi* and *D. setosum*, Pearse (1998) examined populations across the tropical Pacific from Honshu Island, Japan to Moorea, French Polynesia, and found the distribution of these species occurred along an inshore/landmass to offshore/oceanic gradient, suggesting that *D. setosum* is more tightly associated with land masses in the tropical Pacific, while *D. savignyi* is more widely spread throughout this region. In East Africa, *D. setosum* populations are more tightly associated with islands, while both *D. savignyi* and *D. setosum* are found along the mainland coast (McClanahan, unpub.). Genetic studies of the mDNA of *Diadema* (Lessios et al., 1996, 2001b) indicated that *D. setosum* is the outgroup among species of this genus. These findings are consistent with the test morphology analysis conducted by Coppard and Campbell (2006a), which also confirmed *D. palmeri* as an outlier in the genus. The mDNA analysis also showed that *D. antillarum* and *D. savignyi* are nearly indistinguishable genetically (Lessios et al., 2001a). Hence the *D. antillarum*/*D. savignyi* clade is pantropical in distribution, with the exception of the Red Sea, while *D. setosum* is more restricted to continental shelves and adjacent islands of the Indian and west Pacific oceans. *Diadema savignyi* is the most widely distributed species in the genus (Lessios et al., 2001a).

1.3.   Local distribution and abundance patterns

Several factors have been shown to control the distribution of *Diadema*, including depth, wave exposure, sediment type and size, physical relief and benthic composition. *Diadema* species are ubiquitous and common throughout their range and are found primarily on shallow rocky and reef habitats on sand, rubble or coral (Bauer, 1980), although *D. savignyi* and *D. setosum* also occur in the channels of mangroves and in estuaries and creeks along the Kenyan coast (Muthiga, pers. obs.). *Diadema* distribution is patchy, although some Indo-Pacific populations occur in large aggregations (Fox, 1926; T. Stephenson et al., 1931; Onada, 1936; Pearse and Arch, 1969; McClanahan, 1988), whereas in the Red Sea the animals are cryptic and hide in crevices and under ledges during the day (Magnus, 1967; Pearse, 1970). Aggregations have also been observed for *D. antillarum* in the Caribbean (Randall et al., 1964; Kier and Grant, 1965) and *D. mexicanum* in the Eastern Tropical Pacific (Pearse, 1968a).

The upper limit of *D. setosum* is restricted by desiccation, and Indo-Pacific species of *Diadema* are reported to depths of 10 m (Pearse, 1998), while *D. antillarum* has been reported to depths of 70 m (The Nature Conservancy, 2004). The distribution of *D. setosum* correlated with sediment size, and their densities increased with increased sediment size (Dumas et al., 2007). Hernández et al. (2008) also showed that sediment type, relief and wave exposure played a role in the distribution of *D. antillarum* in the Canary Islands. Higher densities were recorded in areas of high relief, high wave exposure and sediments containing >20% sand. Benthic composition was also shown to affect the distribution of *D. antillarum* in the Canary Islands, where rocky habitats with high sea urchin numbers ('barrens') had much less erect algae than areas without high numbers (Tuya et al., 2006; Clemente et al., 2007). The availability of refuges did not affect their densities within the barrens as sea urchins had a lower density within crevices (~6 ind·m^{-2}) than in exposed areas (~11 ind·m^{-2}; Clemente et al., 2007), suggesting that aggregation may have conferred an adaptation against predation. Abundances were also shown to be significantly lower within MPAs than in highly fished sites (10 and 0.4 ind·m^{-2}, respectively; Clemente et al., 2009) and increased with depth (Tuya et al., 2007). Wave exposure and its possible influence on predators was also important in structuring *D. antillarum* populations in Cuba, since their densities were significantly higher in reef crests than in reef front habitats (Martin-Blanco et al., 2010).

Prior to 1983, *D. antillarum* was the most dominant herbivore in tropical western Atlantic reef habitats (Ogden, 1977; Sammarco, 1980; Hawkins and Lewis, 1982). Bauer (1980) surveyed *D. antillarum* at 30 sites across the western North Atlantic and reported densities ranging from 0.04 to 25.8 ind·m^{-2}. In general, the highest densities were found in shallow, intertidal communities with relatively high water movement. Other factors controlling this variability included seasonal changes in salinity and turbidity, sewage outfalls (that generally increased densities) and silty conditions (that decreased densities). The Indo-Pacific species of *Diadema* along the east coast of Africa , Madagascar and Zanzibar occur at densities ranging from 0.02 to 58 ind 10m^{-2} for *D. savignyi* (biomass of 2.7 and 7305 kg wet weight ha^{-1}, respectively) and 0.01 to 37 ind 10·m^{-2} for *D. setosum* (biomass of 1.27 and 4868, respectively) (Table 18.1). Both species were found at the highest densities on shallow Kenyan reef lagoons. *Diadema savignyi* was more abundant than *D. setosum* in Kenya (McClanahan and Shafir, 1990; McClanahan, 1998; McClanahan, unpub. data) and Tanzania (McClanahan et al., 2009), whereas *D. setosum* was more abundant in Madagascar, Mozambique and Zanzibar.

Table 18.1 Range in population density (ind 10 m⁻²) and biomass (kg ha⁻¹) of *Diadema* species at reef sites along the east coast of Africa, Madagascar and Zanzibar Island.

	D. savignyi		D. setosum	
	Density (ind 10 m⁻²)	Biomass (kg ha⁻¹)	Density (ind 10 m⁻²)	Biomass (kg ha⁻¹)
Kenya	0.02 – 58	2.7 – 7305	0.01 – 32	1.27 – 4868
Madagascar	0.56 – 1.78	69 – 222	7.6 – 37	1133 – 5583
Mozambique	0.22 – 10.9	27 – 1361	0.94 – 22	141 – 3250
Tanzania	0.11 – 27.2	14 – 3309	0.19 – 4.4	28 – 634
Zanzibar	0.1 – 1.7	6.7 – 176	16 – 34	1557 – 3032

Density estimates are compiled from McClanahan et al. (1998; 2009) and McClanahan (unpublished). Kenya (n=19 sites), Madagascar (n=4 sites), Mozambique (n=5 sites), Tanzania (n=12 sites) and Zanzibar (n=3 sites). Ten quadrats were sampled at each reef site.

2. Population biology and ecology

2.1. Reproductive biology and ecology

Diadema are gonochoric with separate sexes and hermaphroditism is rare (Pearse and Cameron, 1991). Bak et al. (1984) reported blastulae in the gonads of two individuals of *D. antillarum* and suggested that this was due to parthenogenesis. However, Pearse and Cameron (1991) suggested that the blastulae more likely resulted from self-fertilization within hermaphroditic gonads, as reported for other species of sea urchins. Although some sea urchins show some external sexual differences including differences in the size of genital papillae, no external sexual characteristics have been reported in *Diadema*. It is expected that *Diadema* populations mainly have 1:1 sex ratios, but few data are available to verify this. *Diadema savignyi* and *D. setosum* populations at Kanamai, Kenya had a 1:1 sex ratio (Muthiga, unpub.), whereas Hori et al. (1987) found more male than female *D. setosum* (1.0:0.7) out of a total of 487 individuals in Singapore. On the other hand, sex ratios were highly skewed towards females in *D. setosum* and *D. savignyi* in Fiji (Coppard and Campbell, 2005), which was attributed to high concentrations of tributyltin from antifouling paint at the sites sampled.

The developmental stages of the gametogenic cycle in *Diadema* are similar to those in most echinoids. They consist of a regular sequence of changes in the gametogenic cells and nutritive phagocytes, and differ only in the timing of the different stages amongst species (Pearse and Cameron, 1991). The morphology of nutritive phagocytes also varies with stage, position in the gonad and species. Nutritive phagocytes appear particularly distinct among diadematoids, including *Centrostephanus* and *Diadema* (Pearse, 1970; Pearse and Cameron, 1991). The cells are flat or squat in shape and line the gamete-filled lumen of the gonadal tubules after gamete production has terminated (Pearse, 1970). The sequence of events during the gametogenic cycle is described in detail for *D. setosum* in the Gulf of Suez (Pearse, 1970), *D. savignyi* in South Africa (Drummond, 1995) and for both species in Kenya (Muthiga, 2003).

The process of spermatogenesis from production of spermatocytes to accumulation of numerous sperm is completed in one to two months in *D. setosum* in the Gulf of Suez (Pearse, 1970) and one month in *D. setosum* and *D. savignyi* in Kenya (Muthiga, 2003). Oogenesis also follows a regular sequence of events and is completed in one month in both *D. savignyi* and *D. setosum* (Muthiga, 2003). The length of the vitellogenetic stage varies among different species and has been estimated to be less than a month in *D. setosum* (Iliffe and Pearse, 1982) and in *D. setosum* and *D. savignyi* (Muthiga, 2003). Ova range in size between 67 to 73 μm in *D. antillarum*, 67 μm in *D. mexicanum* and 92 μm in *D. setosum* (Emlet et al. 1987). Lessios (1987) showed that there was great variability in egg size and found differences between individuals of the same species, within a sample, between days, months, years and habitats, and with no apparent correlation with time, body or gonad size or fecundity in 13 echinoid species in Panama. *Diadema antillarum* showed significant daily variation in egg size whereas *D. mexicanum* showed no differences in egg volume between days.

2.2. Reproductive cycles

The reproductive cycles of *Diadema* species can be continuous or restricted and vary from one geographic location to another (Table 18.2), indicating that several factors influence reproduction. For example, *D. antillarum* reproduces continuously throughout the year in the Virgin Islands and Curacao (Randall et al., 1964), on the Caribbean side of Panama (Lessios, 1981), in Puerto Rico (S. M. Williams et al., 2009) and the Canary Islands (Hernández et al., 2011). Spawning was seasonal in Bermuda (Iliffe and Pearse, 1982), Barbados (Lewis, 1966) and south Florida (Bauer, 1976). In addition, *D. savignyi* and *D. setosum* reproduce throughout the year at the same localities along the Kenyan coast but with peaks at different times of the year (Muthiga, 2003). Coppard and Campbell (2005) also showed that peak spawning was offset in these species and occurred from November to December in *D. setosum* and December to March in *D. savignyi* in Fiji.

Table 18.2 Seasonal and lunar spawning cycles of *Diadema*.

Species	Location	Spawning season	Lunar period	References
D. antillarum	USA, California	Annual	New moon	Kennedy and Pearse (1975)[a]
	Bermuda	Apr – Oct	New moon	Iliffe and Pearse (1982)
	South Florida	Oct – Dec	New moon	Bauer (1976)
	Virgin Islands	Continuous	New moon	Randall et al. (1964)
	Barbados	Jan – Apr		Lewis (1966)
	Curacao	Continuous (peak Jan – Mar)		Randall et al. (1964)
	Panama (Caribbean)	Continuous		Lessios (1981)
D. mexicanum	Panama		New moon	Lessios (1984)
	Panama (Pacific)	Sep – Nov		Lessios (1981)
	Panama		Full moon	Lessios (1984)
D. savignyi	Kenya	Continuous (peak Feb – May)	After full moon (days 17–18)	Muthiga (2003)
D. setosum	South Africa	Dec – Apr	After full moon	Drummond (1995)
	N.E Australia	No synchrony	Irregular	Stephenson (1934)
	Egypt	No synchrony	Irregular	Mortensen (1937)
	Japan		Full moon	Yoshida (1952)
	Philippines	Continuous	Full moon	Tuason and Gomez (1979)
	Singapore	Continuous		Hori et al. (1987)
	NW Red Sea	Jun – Sep		Pearse (1970)
	Mozambique	No synchrony	Irregular	MacNae and Kalk (1958)[b]
	Japan	Monthly	Full & new moon	Kobayashi and Nakamura (1976)
	Japan		Full moon	Yoshida (1952)
	Guam, Madang, Moorea, Samoa		After full moon	Pearse, personal communication
	Kenya	Continuous (peak Feb –May)	Lunar days 8–10	Muthiga (2003)
	Canary Islands	July		Hernandez et al. (2006a)[c]

[a]Kennedy, B. A., and Pearse, J. S. (1975). Lunar synchronization of the monthly reproductive rhythm in the sea urchin *Centrostephanus coronatus* Verrill. *J. Exp. Mar. Biol. Ecol.* 17, 323–331.
[b]MacNae, W. & M. Kalk (eds) (1958). A natural history of Inhaca Island, Mozambique. Witwatersrand Univ. Press, Johannesburg. I-iv, 163 pp.
[c]Hernández JC, Brito A, García N, Gil-Rodríguez MC, Herrera G, Cruz-Reyes A, Falcón JM (2006) Spatial and seasonal variation of the gonad index of *Diadema antillarum* (Echinodermata: Echinoidea) in the Canary Islands. Scientia Marina 70:689–698.

Although gametogenesis is well described for *Diadema* and echinoids in general, the factors that regulate its timing and that of spawning are still poorly understood. Studies that have compared conspecific populations of *Diadema* from different latitudes (Pearse, 1968b, 1970) show that reproductive cycles tend to become more synchronized with increased distance from the equator and seasonality presumably becomes more pronounced. Pearse (1974) compiled information on *D. setosum* and suggested that reproduction is controlled by temperature, since populations in northern Japan and Suez spawned during the boreal summer while populations in Australia spawned in the austral summer. Pearse (1974) concluded that gametogenesis proceeds when temperatures are above ~25°C in this species.

Correlative evidence of the influence of temperature has also been shown at localities with similar latitudes but with different degrees of seasonality. For example, *D. mexicanum* from the seasonal environment of the Bay of Panama displayed a synchronous, well-defined reproductive cycle, whereas *D. antillarum* from the less seasonal Caribbean shore of Panama showed less synchrony (Lessios, 1981). Moreover, information from populations of *D. setosum* that occur near the equator supports this suggestion, since populations in the Philippines (Tuason and Gomez, 1979), Singapore (Hori et al., 1987) and Kenya (Muthiga, 2003) reproduce throughout the year. Many of the studies that report the influence of temperature are correlative, and the exact mechanism of how temperature influences gametogenesis remains unclear. For example, Pearse (1974) failed to induce gametogenesis in *D. setosum* individuals that were moved from the temperate Gulf of Suez and maintained at warmer summer temperatures, suggesting that temperature was not the cue for the onset of gametogenesis in this species. Pearse and Cameron (1991) and Drummond (1995) also questioned the role of water temperature in the reproduction of *Diadema* species. Temperature may have an indirect influence, for example by affecting feeding rate or food availability, which could affect reproductive cycles (Coppard and Campbell, 2005).

Most species of *Diadema,* like most diadematoids, have monthly reproductive rhythms. Spawning mainly occurs around the full moon in *D. mexicanum* and *D. setosum,* while *D. antillarum* and *D. savignyi* spawn around the new moon (Table 18.2). Interestingly, comparisons of coexisting populations of *D. savignyi* and *D. setosum* along the Kenyan coast showed a contrasting cycle, with *D. savignyi* spawning after the full moon (between lunar days 17 and 18) and *D. setosum* spawning before the full moon (lunar days 8 to 10). Temporal separation of reproductive cycles has also been reported in coexisting populations of *D. savignyi* and *D. setosum* in Fiji (Coppard and Campbell, 2005) and populations of *D. mexicanum* separated by the isthmus of Panama (Lessios, 1984).

The factors affecting the spawning behavior of *Diadema* are not always very clear. For example, *D. setosum* has been reported to spawn at different phases of the moon including full moon (Yoshida, 1952; Pearse, 1972; Tuason and Gomez, 1979), new moon (Coppard and Campbell, 2005), both full and new moon (Fox, 1924; Kobayashi and Nakumura, 1967) and in some cases show no lunar periodicity (A. Stephenson, 1934; Mortensen, 1937; Pearse, 1968b, 1970). Monthly cycles may be controlled by moonlight. However, the lack of synchrony among different populations of *D. setosum* in the Red Sea (Pearse, 1972) suggests that synchrony within populations is either not under worldwide lunar control, or that it can be adjusted by local environmental conditions. Pearse (1972) suggested that spawning in *D. setosum* and *Centrostephanus coronatus* could also be explained by tidal rhythms.

Other factors influencing gametogenesis include the age and size of individuals. These influence the age and size at sexual maturity as well as the quantity of gametes produced. Lawrence (1987) reported that the gonads of extremely large *D. setosum* show little reproductive activity. Food availability can also affect gonad growth, and poorly fed individuals have small or no gonads (Levitan, 1988a). However, there is little evidence that nutrition has a role in regulating the onset of gametogenesis (Pearse and Cameron, 1991).

2.3. Larval supply, recruitment and settlement

The factors that control larval supply, settlement and recruitment in *Diadema* and the influence of these life history traits on adult populations have been investigated in several studies in *D. antillarum*. Larval supply measured with plankton tows was shown to coincide with monthly spawning in *D. antillarum* in Puerto Rico, and their plutei were recorded during most months of the year (S. M. Williams et al., 2009). However, plutei densities peaked from April through July at the peak of reproductive activity. Larval abundances were variable between months and across years. The study also showed that the early larval stages were confined within the inner shelf fore reefs by local currents, suggesting the influence of oceanographic factors in larval distribution. Variability in larval supply is common in organisms that disperse pelagic larvae (Ebert, 1983; Muthiga, 1996; S. M. Williams and Garcia-Sais, 2010).

Larval settlement was also reported to be variable among sites and months in the Florida Keys (M. W. Miller et al., 2009). In addition, monthly rates of larval settlement were much lower in the Florida Keys (maximum < 2 settlers m^{-2}) than at comparable sites in Puerto Rico (16 settlers m^{-2}) that had moderate *D. antillarum* recovery after the 1982–1983 die-off. Moreover, larval settlement rates in both these locations were much lower than historical reports prior to the die-off reports in Curaçao (Bak, 1985). The study suggested that low larval supply was limiting *D. antillarum* recovery in the Florida Keys. Nevertheless, the results did not indicate a correspondence between adult density and larval settlement. This was not consistent with a previous study, which found positive density-dependent recruitment for *D. antillarum* (R. J. Miller et al., 2007). Consequently, other factors must have been constraining the recovery of *D. antillarum* in the Florida Keys. S. M. Williams et al. (2011) also showed high spatial variability in larval settlement measured on settlement plates in Puerto Rico. Higher settlement was recorded at depths of 9 m and on shelf-edges than on inshore and mid-shelf reefs, suggesting that the latter reefs had lower larval supply and higher settler mortality.

Recruitment studies have also shown high variability and a lack of density-dependent recruitment of *D. antillarum* in Puerto Rico (S. M. Williams et al., 2010). In this study, the lowest recruitment rates were recorded on inshore reefs, which also had the highest densities of adults. This suggests that the high recruitment in the shelf-edge reefs did not result in high population densities in this area, unless the recruits migrated to shallow water. Additionally, Vermeij et al. (2010) reported that although recruitment in 2005 was 56 times higher in Curaçao than before the die-off, the increase in adult densities was moderate, suggesting that high post-settlement mortality was constraining *D. antillarum* recovery in this location. In Jamaica, very few sites had small juveniles of *D. antillarum* three years after the die-off (Hughes et al., 1987), which suggested that low supply of larvae could be one of the factors constraining recruitment and ultimately the recovery of this species.

The role of other factors that influence recruitment and settlement of *D. antillarum,* including reproductive output (measured as the gonad index), temperature and primary water-column productivity (measured as pyhtoplankton concentration), were compared over a seven-year period in the Canary Islands (Hernández et al., 2010). As shown in other studies, there was great temporal and spatial variability in settlement and a positive relationship between settlement and recruitment. Settlement also coincided with reproductive activity but was negatively correlated with phytoplankton concentrations. The strongest relationship recorded in the study was between temperature and settlement, which was highest during warm years. Clemente et al. (2009) also showed a lack of density-dependent recruitment effects for *D. antillarum* for a comparison of settlement, recruitment and predation in these same Canary Islands sites. No difference was found between recruitment and settlement in fished and unfished sites, although there was a significant difference in adult densities, which were significantly higher in fished than unfished sites. This suggested that top-down processes, occurring sometime after early recruitment, were more important in structuring these populations of *D. antillarum* than density-dependent or self-regulating population processes.

2.4. Feeding ecology

Species of *Diadema* are mainly omnivorous grazers and detritus feeders, ingesting substrate and scraping algae off hard substratum (Mortensen, 1940; Randall et al., 1964; Lewis, 1964; Pearse, 1970). *Diadema antillarum* preys on live coral as well as coral spat (Bak and van Eys, 1975; Carpenter, 1981; Sammarco, 1980, 1982b) and seagrass (Ogden, et al., 1973). Feeding activity in *Diadema*

varies with species and environment. Lewis (1964) reported that the feeding activity of *D. antillarum* is greatest in the afternoon and early evening, and Tuya et al. (2004a) found nocturnal activity that peaked at midnight in *D. antillarum* in the eastern Atlantic. Lawrence and Hughes-Games (1972) also reported a nocturnal activity rhythm in *D. setosum* at Eilat, Red Sea, with feeding occurring only at night. The foraging behavior of *D. antillarum* maintains 'halos', a common feature associated with patch reefs in the Caribbean, that consist of a band of bare sand between the base of the reef and the adjacent *Thalassia* and *Syringodium* beds (Ogden et al., 1973).

Intestinal contents of *Diadema* species usually reflect the type of food most available. For example, *D. antillarum* collected from seagrass beds have gut contents that largely contain the seagrasss *Thalassia* with smaller amounts of fine silt. In contrast, the guts of individuals collected from reef areas usually contain algae and detritus (Randall et al., 1964). On Kenyan reefs, *D. savignyi* and *D. setosum* had gut contents composed of coral sediment (48 to 52%), algae (~28%), seagrass (20%) and invertebrates (2%) (McClanahan, 1988). Tuya et al. (2001) showed that preference for algae in *D. antillarum* in the Canary Islands varied: *Halopteris, Lobophora* and *Dictyota* were preferred; *Padina* was intermediate and *Cystoseira* was least preferred. Solandt and Campbell (2001) found *D. antillarum* in Jamaica were attracted towards water passing over heavily calcified *Halimeda opuntia* and less-calcified algae such as *Lobophora variegata*. They were not attracted to *Sargassum* sp. or *Galaxaura* sp. Despite this difference in attraction to algae, there was no preference when a variety of algae were provided for consumption.

Defense chemicals produced by marine algae mediate the rate of herbivory by *Diadema*. *Laurencia obstusa, Stypopodium zonale* and various species of *Dictyota* are consumed at relatively low rates by herbivores, including *Diadema* in Caribbean reefs (Littler et al., 1983; Hay, 1984; Hay and Paul, 1986), which suggests secondary metabolites in these seaweeds are defenses against herbivory. Hay et al. (1987) extracted secondary metabolites from tropical marine algae and found that stypotriol from *Stypopodium zonale,* pachydictyol-A from *Dictyota* and other algae, elatol from *Laurencia obstusa* and isolaurinterol from species of *Laurencia* reduced the amount of *Thalassia* eaten by *D. antillarum*. Cymopol from the green alga *Cymopolia barbata* stimulated feeding by *Diadema*. Gut contents analysis, *in situ* feeding observations and grazing preferences trials in aquaria of *D. savignyi* and *D. setosum* conducted in Fiji showed that the preferred algae were generally non-calcareous with reported low concentrations of tannins, phenols and bioactive compounds (Coppard and Campbell, 2007). Both species preferred *Codium geppiorum* followed by *Hydroclathrus clathrus.*

Food passes through the guts of *D. antillarum* in 8 to 12 hours. Enzymes that digest carbohydrates, proteins and lipids are present in the gut (Lewis, 1964). In *D. setosum* from Eilat, food is present in the stomach only at night when feeding occurs and is retained in the intestine throughout, indicating that digestion mainly occurs in the intestine (Lawrence and Hughes-Games, 1972). Lewis (1964) describes the morphology of the gut of *D. antillarum* and suggests that digestive enzymes are mainly produced in the caecum and foregut while absorption occurs in the hindgut.

Although seasonal changes have been reported in the size of the gut of some sea urchins related to changes in food availability (Lawrence et al., 1965), no seasonal changes have been reported in *D. setosum* in the Red Sea or on Kenyan reefs (Pearse, 1970; Muthiga, 2003). On the Kenyan coast, the relative size of the gut of *D. savignyi* increased when gonad size decreased, suggesting that a seasonal feeding pattern may occur in this species (Muthiga, 2003). Some species of *Diadema* have also been shown to regulate body size when food is limited, increasing the size of the jaw and decreasing the size of the test in *D. setosum* (Ebert, 1980) and *D. antillarum* (Levitan, 1989). The increase in jaw size is primarily due to a decrease in size of the test (Levitan, 1991). A larger jaw under conditions of food limitation is an adaptive response, as it increases the efficiency of food collection.

2.5. Growth and longevity

Estimates of growth in *Diadema* (Table 18.3) have been reported mainly from laboratory-reared animals, size frequency measurements in natural populations and observations of individuals held in aquaria or cages (Randall et al., 1964; Lewis, 1966; Bauer, 1976, 1982; Ebert, 1982; Drummond, 1994). Tagging using monofilament line was not successful on *D. antillarum* (Randall et al., 1964). Ebert (1982) found tetracycline was unreliable with *D. setosum*, possibly due to the low levels of incorporation of tetracycline or reworking of calcite in the skeletal elements. Ebert (1982) reported a growth parameter K of 0.008 for a few individuals of *D. setosum* in Zanzibar and Eilat. These estimates were based on the Richards function, and an extrapolation (T. Ebert, pers. comm.) generated a K value of 0.42. These estimates are lower than growth estimates reported for the conspecific *D. savignyi* in South Africa (K=0.79, Drummond, 1994) or for *D. antillarum* in the Virgin Islands (Randall et al., 1964). Ebert (1982) reported maximum test diameters of 52.19 and 83.6 mm for *D. setosum* at Zanzibar and Eilat, respectively. These estimates are within the range of the largest *D. setosum* (88.5 mm) and *D. savignyi* (90 mm) measured at Kanamai, Kenya (N. Muthiga, unpub.). *Diadema setosum* has a slow initial growth rate in contrast to its conspecific *D. savignyi* that shows rapid growth and a short life span of three to five years (Drummond, 1994).

Growth studies of Caribbean *Diadema* have mainly been on caged or laboratory-reared individuals. Randall et al. (1964) recorded growth rates of the test diameter of 3.5 to 6.7 mm per month in caged *D. antillarum* with test diameters of 4 to 25 mm from the Virgin Islands. Lewis (1966) recorded similar rates of growth in laboratory-reared individuals in Barbados. Sea urchins with test diameters between 10 mm and 30 mm grew at a rate of 3.2 mm per month. This was faster than for larger individuals with test

Table 18.3 The growth parameter (K), maximum length (Li$_{nf}$) and mortality estimates (Z) for species of *Diadema*.

Species	Location	N	K	L$_{inf}$(mm)	Z	Reference
D. antillarum	Virgin Islands	44	1.18	75.6	1.3/yr	Randall et al. (1964)
	Florida Keys				1.4/yr	Lewis (1966)
D. setosum	Zanzibar, Tanzania	55	0.42*	52.19*	0.29/yr	Ebert (1982)
	Eilat, Israel	7	0.42*	83.57	0.64/yr	Ebert (1982)
D. savignyi	Isipingo Beach, South Africa		0.79			Drummond (1994)
D. paucispinum	Kealakekua Bay, Hawaii				1.9/yr	Ebert (1982)

*The values K, L$_{inf}$ and Z for *D. setosum* from Zanzibar and Eilat have been revised for comparison (Ebert, personal communication).

diameters of 30 to 50 mm, which grew at a rate of 1.8 mm per month. Bauer (1976, 1982) recorded similar growth rates for *D. antillarum*. These growth rates are considerably lower than reported for other Caribbean sea urchins (Lewis, 1958; Moore et al., 1963).

2.6. Pelagic larval dynamics

Mortensen (1931, 1937) described the structure of the planktotrophic larvae of *D. antillarum* and *D. setosum*. *Diadema* species similar to other members of the order Diadematoida have larval forms that are characterized by long fenestrated postoral arms that are seven times the length of the body, or more than 1.5 mm long (Pearse and Cameron, 1991). The significance of these long arms in *Diadema* has not been investigated, although shape and size of feeding larvae may have significance for larval development. Longer arms, for example, may provide a more effective defense against some predators. They may increase the efficiency of feeding since longer arms will have a larger ciliated surface area that may result in increased clearing rates for feeding larvae (Strathmann et al., 1992).

McAlister (2008) experimentally explored the question of whether changes in food resources would have evolutionary significance for larval arm length by comparing larvae of different species of echinoids, including *Diadema,* on different sides of the Isthmus of Panama. Caribbean species that lived in low food level environments had longer arms, compared to Pacific species that lived in high and seasonally variable food environments. This suggested that changes in food levels led to the evolution of constant rather than plastic differences in larval form between the Caribbean and Pacific species. The causal factors and evolutionary consequences of different larval forms were also studied by Uthicke et al. (2009). They compared larval forms of species, including *Diadema,* which showed boom (outbreaks) and bust (die-offs) population fluctuations and showed a predominance of planktotrophic larval forms. Species with this larval form showed a high-risk-high-gain life history strategy that was attributed to a high dependence on adult densities, a low potential for compensatory feedback, and an uncoupling of larval and adult ecology (Uthicke et al., 2009).

The factors that influence the rate of larval development in sea urchins are mainly abiotic and include temperature, salinity and food availability (Pearse and Cameron, 1991). However, few studies have been done with *Diadema*. The larval period for *D. setosum* has been estimated to be ~40 days, which is about average for many echinoids (Emlet et al., 1987). In species that have planktotrophic (feeding) larvae, egg size may be an important factor controlling larval growth. The eggs of *Diadema* are some of the smallest (67 to 92 μm) reported for species with planktotrophic larvae (Emlet et al., 1987). *Diadema* reared at 26°C developed into blastulae within 6 hours and early plutei within 35 hours (Amy, 1983). This is a relatively fast rate compared to the cidaroid *Eucidaris tribuloides* (egg diameter = 95 μm). However, as noted by Lessios (1987), egg size is very variable and is not a good predictor of larval success.

2.7. Benthic population dynamics

The single most significant event that has affected *D. antillarum* populations was the 1983–84 mass mortality, the most extensive die-off of a marine animal ever reported. Lessios (1988) describes the advance of the disease that was first reported in Panama. It spread 2000 km east to Tobago and 4000 km west along the coastlines of Central America, through the Gulf of Mexico to Bermuda. It generally followed the surface currents, indicating that the agent that caused the mass mortality was water borne. The disease, however, also spread from Florida to the Lesser Antilles against the major offshore currents. The disease caused the death of more than 93% of *D. antillarum* individuals over a 13-month period. Interestingly, despite the first records of the die-off occurring at the mouth of the Panama Canal, the disease did not infect the Panamanian populations of *D. mexicanum* (Lessios et al., 1984).

In general, populations that initially had high densities of *D. antillarum*, such as Barbados, experienced less mortality (Hunte and Younglao, 1988). The causal agent of the mass mortality remains unknown. Bauer and Ageter (1987) cultured two species of bacteria (*Clostridium*) from infected individuals that caused mortality in healthy individuals but cautioned that the evidence is not sufficient to conclude that these bacteria caused the mass mortality. In addition, although the die-off coincided with the 1983 El Niño that caused some mortality of corals in the Caribbean, there was no direct link between the El Niño and the die-off (Lessios, 1988).

A similar mortality event occurred in the Florida Keys in 1991 (Forcucci, 1994), reducing densities of *D. antillarum* by 97% in the offshore reefs off Key West and by 83% at a patch reef offshore from Long Key. The cause of this decline is unknown (Forcucci, 1994). Although no large-scale die-off of *Diadema* has been reported in the recent past, a disease with similar characteristics as the mass die-off in the 1980s was reported in Bahias de Huatulco, Mexico in 2009 (Benitez-Villalobos et al., 2009).

Although many reefs experienced recruitment a few months after the mass die-off, *D. antillarum* populations continued to decline in Panama (Lessios, 1988), Jamaica (Hughes et al., 1985) and Curaçao (Bak, 1985) a few years after the die-off as a result of recruitment failure (Karlson and Levitan, 1990). A compilation of more than 200 density estimates of *D. antillarum* (Fig. 18.1) collected before and after the mass mortality from more than 15 countries shows that recovery of *D. antillarum* populations has been low to moderate throughout most of its range (Lessios, 1988; Carpenter, 1990a; Karlson and Levitan, 1990; Edmunds and Carpenter, 2001; Lessios, 2005; Weil et al., 2005; Carpenter and Edmunds, 2006; Noriega et al., 2006; Steiner and Williams, 2006; Furman and Heck, 2009; Martin-Blanco et al., 2010; Cortes et al., 2010; Idjadi et al., 2010; Ruiz-Ramos et al., 2011).

There was a high spatial and temporal variability in recovery, but the general trend indicated barely detectable recovery immediately after the die-off and slow increases in density a decade later. *Diadema antillarum* densities were below the levels before the die-off at sites in Dominica, Lesser Antilles (Steiner and Williams, 2006), Venezuela (Noriega et al., 2006), Curaçao (Debrot and Nagelkerkon, 2006), Costa Rica (Myhre and Acevedo-Gutierrez, 2007), the Florida Keys (Furman and Heck, 2009; Chiappone et al., 2008), Cuba (Martin-Blanco et al., 2010) and Puerto Rico (Weil et al., 2005; Ruiz-Ramos et al., 2011). The rate of recovery was highly variable. For example, some reefs in Barbados showed up to 57% recovery by 1985 (Hunte and Younglao, 1988), a relatively rapid increase, but many reefs in Barbados have not achieved full recovery. Long-term data from the San Blas Archipelago, Panama showed densities in 2002 that were 56 to 100% lower than in 1980 (Lessios, 2005). In contrast, their densities in Puerto Rico increased by ~28% in a 17-year period (Weil et al., 2005). In Discovery Bay, Jamaica, where some of the strongest recovery records are reported, recovery was very slow immediately after the die-off, but *D. antillarum* densities subsequently increased to approach those recorded in the early 1970s and 1980s (Edmunds and Carpenter, 2001; Haley and Solandt, 2001; Carpenter and Edmunds, 2006; Idjadi et al., 2010).

The factors that limit or enhance recovery were difficult to elucidate because of characteristics such as patchy distribution patterns, stochastic recruitment, variability in mortality of larvae and juveniles, habitat structural complexity, competition and predation. Whereas earlier studies suggested that larval supply, settlement and recruitment may influence recovery of *D. antillarum* populations (Hughes et al., 1987; Pearse and Cameron, 1991; Edmunds and Carpenter, 2001; Chiappone et al., 2002; R. J. Miller et al., 2003; Knowlton, 2004; Lessios, 2005), later studies showed no correlation between these factors and the subsequent increase in *D. antillarum* populations (Clemente et al., 2009; S. M. Willians et al., 2009; Vermeij et al., 2010). Recovery is context specific and dependent on many factors, including previous densities of *D. antillarum,* previous herbivore assemblages, predation, nutrients and reef relief amongst others (Lee, 2006; Edmunds and Carpenter, 2001; Bechtel et al., 2006; Maciá et al., 2007; Alvarez-Filip et al., 2009; Harborne et al., 2009; Idjadi et al., 2010).
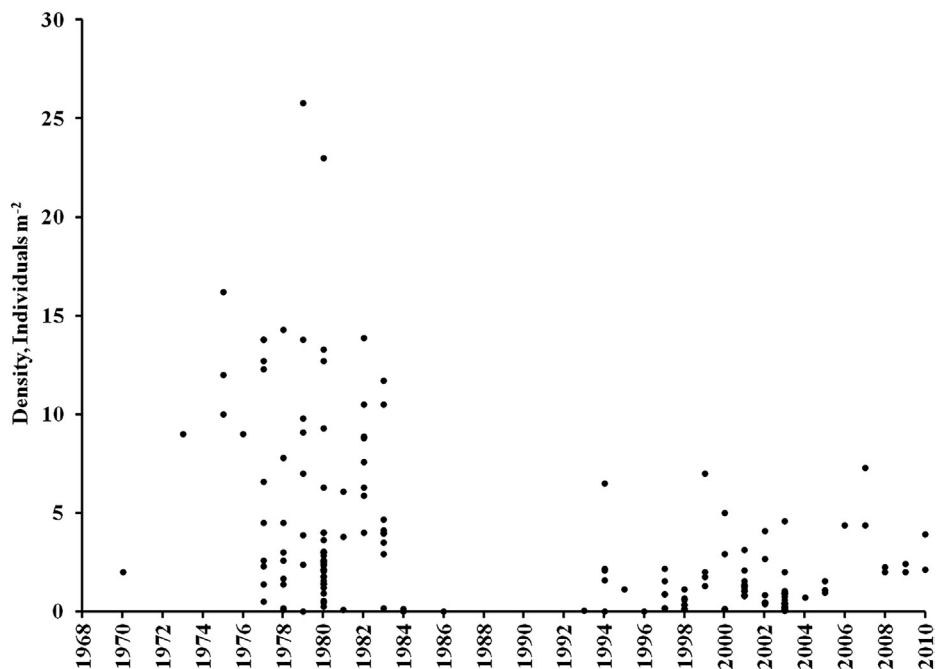

Fig. 18.1. The density of *Diadema antillarum* at 200 sites in the Caribbean. Data are average densities (ind·m^{-2}) at each site from 1970 to 2012.

Population fluctuations and spatial and temporal variability were also reported for *D. mexicanum* populations. For example, on Cocos Island, Costa Rica, densities averaged 11.4 and 6.1 ind·m^{-2} in 1987 and 1990, respectively (Guzman and Cortes, 1992) and decreased to 0.45 ind·m^{-2} in 2009 (Alvarado et al., 2012). However, densities of *D. mexicanum* on Cano Island and Culebra Bay were much lower (0.09 to 2.19 ind·m^{-2} range) in 1980 and 1996, respectively, and did not change in the 13- to 19-year period (Alvarado et al., 2012). The high densities at Coco Island in 1987 could have resulted from an outbreak following high coral mortality after the 1982–1983 El Niño (Guzman and Cortes, 1992, 2007). Relatively low densities of *D. mexicanum* were also reported in Ecuador (Sonnenholzer and Lawrence, 2002), at shallow depths (0 to 6 m) in Mexico (Zamorano and Leytes-Morales, 2005; Benitez-Villalobos et al., 2008) and in Nicaragua (Alvarado et al., 2011). The abundance and distribution of *D. mexicanum* was influenced by depth, with densities being higher at depths from 6 to 12 m than from 0 to 4 m in Mexico (Zamorano and Leytes-Morales, 2005). However, densities increased in the shallow zone after the mass mortality of coral after the 1982–83 El Niño that opened up space in the shallow zone. Migration to shallow areas also occurred in Brazil after the die-off of coral after the 1997–98 El Niño (Attrill and Kelmo, 2007).

The Pacific species of *Diadema* have not received as much attention as *D. antillarum*, and few long-term population studies exist except on Kenyan reefs. McClanahan (1998) compared the abundance, distribution and diversity of nine species of sea urchins including *D. savignyi* and *D. setosum* at several locations over a seven-year period in Kenya. The abundance of these species showed marked variability in space and time. For example, *D. savignyi* populations showed an average overall increase in density of 37% across all sites except at Kanamai, where a decrease of 7% occurred over the seven-year period. *Diadema setosum* also showed a similar overall average increase of 36%. However, two sites showed decreases; a newly established MPA, the Mombasa Marine Park (4%), and Kanamai (3%). At Diani, a heavily fished reef, an increase of ~136% was reported for several sites. Continued annual surveys at these sites showed marked variability and a slight downward trend in density for *D. savignyi* (Fig. 18.2a) and a large increase after 2001 that was more evident for *D. setosum* at Kanamai and Vipingo (Fig. 18.2b) by 2006 (T. McClanahan, unpub. data). Changes in *D. setosum* densities over the 20-year period suggest a weak inverse density dependence influence that dampened population growth between years and possibly competition with *Echinometra mathaei* (McClanahan, 1998).

The major factor controlling the abundance of sea urchins was the level of predation, with protected sites having the highest abundance of predators and the highest estimates of predation showing the lowest densities of sea urchins (McClanahan and Shafir, 1990; McClanahan and Mutere, 1994; McClanahan, 1998, 2000). This relationship between sea urchin abundance and predation remained robust across geographical regions, as comparisons between reefs in Kenya and Tanzania showed similar responses (McClanahan et al., 1999). Although fringing reefs had more *Echinometra, Diadema* were common on the patch and island reefs of Tanzania where *Echinometra* were rare. Tuya et al. (2004b) also reported that fishing pressure in the Canary Islands resulted in increased density of *D. antillarum* dominated by small- to intermediate-sized individuals.

3. COMMUNITY ECOLOGY AND COEXISTENCE

3.1. Ecosystem effects

Diadema and its effects on coral reef and rocky ecosystems have been well studied, especially the mass die-off in the western Atlantic, which produced a phase shift from hard corals to macroalgal dominated reefs across much of the Caribbean (Sammarco et al., 1974, 1986; Ogden and Lobel, 1978; Carpenter, 1981; Sammarco, 1982a). In contrast, in the eastern Atlantic where the die-off did not occur, a hyper abundance of *D. antillarum* has created sea urchin barrens and the elimination of erect algae in heavily fished rocky bottom habitats (Tuya et al., 2005; Hernández et al., 2008). Field experiments of density manipulations in these eastern Atlantic habitats have shown a large effect of *D. antillarum* on algal biomass, diversity and productivity. Other examples include *Diadema* studies from Jamaica (Carpenter and Edmunds, 2006), the Florida Keys (Furman and Heck, 2009) and Costa Rica (Myhre and Acevedo-Gutierrez, 2007), where decreased erect algal biomass and increased coralline algae followed increased *D. antillarum* densities. Crustose coralline algae have been shown to induce growth, survivorship and recruitment of hard corals (Sellers et al., 2009; Idjadi et al., 2010). Transplantation and density manipulation experiments in the Canary Islands also showed changes in the algal assemblage; increasing the cover of turf and bush-like algae where sea urchins were removed (Ortega-Borges et al., 2009), whereas adding sea urchins reduced algal cover in Jamaican reefs (Maciá et al., 2007).

Studies in the Caribbean and eastern Atlantic also showed the ecosystem effects of fishing by reducing the predators of *Diadema*. In the Canarian Archipelago, Tuya et al. (2004c) reported an increase in density of *D. antillarum* due to fishing that resulted in a decrease in fleshy macroalgae. In the absence of fishing, brown algal assemblages were abundant and reached deeper waters (Tuya et al., 2005). In the Caribbean, the intensity of the effects of the die-off of *D. antillarum* was also greater in those areas subjected to intense fishing (Hay, 1984; Carpenter, 1990b; Robertson, 1991). Marine protected areas may enhance the intensity of predation, but the ability for top-down control of *Diadema* can only be achieved if the right predator assemblages occur, such as porgies and large diodontids and labrids, suggesting that fish species composition may also play a role in influencing predation effects (Clemente et al., 2011). The effects of predation are not always positive, however. For example, Harborne et al. (2009) reported higher densities
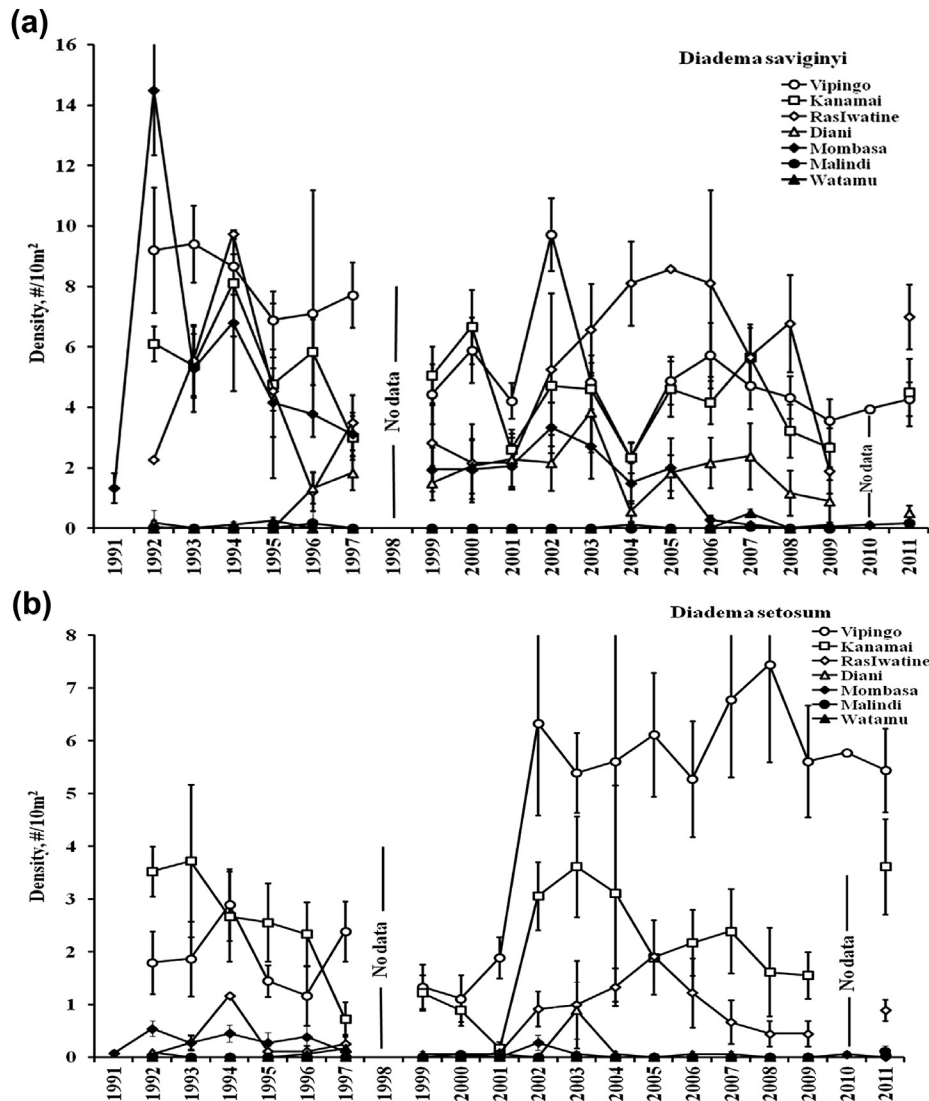
Fig. 18.2. Population densities of *Diadema savignyi* (a) and *D. setosum* (b) over a 20-year period on Kenyan reefs. Two reefs, Malindi and Watamu, have been closed to fishing since the mid 1970s and Mombasa was closed to fishing in 1991. The other reefs, Vipingo, Kanamai, Ras Iwatine and Diani, were open to fishing over the study period.

of *D. antillarum* outside reserves than inside reserves and suggested that predation was limiting recovery of *Diadema* in Bahamian marine reserves.

At intermediate densities, *D. antillarum* has a positive effect on coral recruitment by reducing competition for space with algae (Sammarco, 1980). Reefs that are showing recovery in Jamaica, for example, had an 11-fold increase in juvenile corals (Edmunds and Carpenter, 2001). Similar patterns have been reported on other Caribbean reefs (Carpenter and Edmunds, 2006). However, at very high densities – above seven adult individuals per m^2 – coral spat are preyed upon by *D. antillarum,* with negative effects on coral recruitment (Sammarco, 1980). O'Leary et al. (2012) have found that high numbers of sea urchins, of which *Diadema* were common, reduced coralline algae and coral recruitment in Kenya. This pattern was closely associated with the levels of fishery management.

Although *D. savignyi* and *D. setosum* are common, and often the most abundant sea urchins on reefs in the Indo-Pacific (Pearse, 1998; McClanahan et al., 1999), few detailed studies have been carried out on their ecological effect except in East Africa. McClanahan et al. (1996), in a sea urchin reduction experiment that included *D. savignyi* and *D. setosum,* reported large effects on the fish and algal biomass. The biomass of fish nearly tripled after reduction, with population densities increasing by 65% and species richness increasing by 30% compared to adjacent control plots. Algae and seagrass cover increased more in the reefs that were fished than in those that were not. Dart (1972) suggested grazing by sea urchins, including *D. setosum*, facilitated coral colonization in the Sudanese Red Sea. This may be dependent on density as suggested by the Kenyan studies (O'Leary and McClanahan, 2010; O'Leary et al., 2012). It is possible that there are both species and abundance effects of *Diadema* on crustose coralline algae and coral recruitment. These effects and population gradients have not been well studied.

3.2. Competitive interactions with other sea urchins

A comparison of differences in body morphology, distribution, diet and intra- and inter-competition between *D. savignyi*, *D. setosum* and *E. mathaei* showed that *E. mathaei* is the competitive dominant at reefs in Kanamai and Vipingo, Kenya (McClanahan, 1988). *Diadema savignyi* tended to occur in small crevices while *D. setosum* occurred in the open spaces between coral, usually in groups. Experimental manipulations showed that *E. mathaei,* though smaller, outcompeted both *Diadema* species for crevice space. Although interactions between *D. setosum* and *D. savignyi* always resulted in the larger individual winning, *D. savignyi* was the competitive dominant for crevice space due to the smaller spine length to test size ratio. This gives it a larger test size for the same crevice space requirement (McClanahan, 1988). Competitive interactions have also been reported between the Caribbean species of *Diadema* and *Echinometra,* with *D. antillarum* seemingly the superior competitor (A. H. Williams, 1977, 1980; Shulman, 1990). However, as pointed out by McClanahan and Muthiga (Chapter 23), this is unlikely as *Echinometra* usually takes refuge in its smaller burrows.

Diadema savignyi and *D. setosum* sometimes form large aggregations throughout their range (Fox, 1926; T. Stephenson et al., 1931; Onada, 1936; Dakin and Bennett, 1963). Similar formations have been reported for *D. antillarum* and *D. mexicanum* (Randall et al., 1964; Kier and Grant, 1965; Pearse, 1968a). Pearse and Arch (1969) suggest these aggregations function as protective social units, and form when population densities are so high that crevice space is limited. Levitan (1988b) reported aggregative behavior of *D. antillarum* was not related to reproduction and Pearse (1968a) and McClanahan (1988) suggested aggregation might be a predator-avoidance behavior.

Diadema savignyi and *D. setosum* also occur in large groups and coexist on the Kenyan coast because of a lunar spawning rhythm and seasonal reproductive cycle that reproductively isolates these sympatric species (Muthiga, 2003). *Diadema savignyi,* which is more abundant in East Africa (McClanahan et al., 1999), has a reproductive pattern that is highly synchronous during the lunar period and an annual reproductive output (measured as gonad index) that peaks at the time when primary productivity and temperature are highest, coinciding with the time most favorable for larval development. These two factors together could make *D. savignyi* more reproductively successful than *D. setosum.*

3.3. Competitive interactions with fish

Diadema directly compete with several species of fish, including damselfish and other herbivorous fish (Kaufman, 1977; A. H. Williams, 1977, 1978, 1980; Sammarco and Williams, 1982). The three-spot damselfish *Eupomacentrus planifrons* actively excludes *D. antillarum* from its algal lawns during the day at Discovery Bay, Jamaica, and influences the local distribution pattern and abundances of this sea urchin (Sammarco and Williams, 1982). Algal lawns encourage the growth of some species of coral, such as *Favia fragum,* but are also sites of high spat mortality of some coral species, such as *Agaricia* and *Porites* spp. Algal lawns may, however, have an overall net effect of increasing coral diversity within the reef community (Sammarco and Williams, 1982). Aggressive damselfish also exclude *Diadema* in algal lawns in the Gulf of Thailand (Kamura and Choonhabandit, 1986), Tahiti (Glynn and Colgan, 1988), Panama (Eakin, 1987; Glynn and Colgan, 1988) and the Galapagos (Glynn and Wellington, 1983).

The three-spot damselfish also plays a mediating role by altering the competitive interactions between *D. antillarum* and *E. viridis* in a back-reef environment in Jamaica (A. H. Williams, 1977, 1980). The more mobile but less abundant *D. antillarum* elicited a stronger territorial response from the damselfish than the more abundant *E. viridis,* which resulted in reduced competitive interactions between the two sea urchin species. Competitive interactions also occur between *D. mexicanum* and the Acapulco damselfish *Stegastes acapulcoensis* at Uva Island, Panama (Eakin, 1988). *Diadema mexicanum* was excluded from algal lawns by aggression and actively avoided algal lawns even when they were undefended at night. This suggests that, apart from the aggressive behavior of damselfish, algal lawns were not preferred either due to unpalatability or accessibility (Eakin, 1988). Since the algal lawns and underlying substratum were not grazed by *D. mexicanum,* this interaction is expected to influence the reef framework by reducing bioerosion of the substratum.

3.4. Predation and predators

Diadema remains have been identified in the guts of 15 species of finfish, including balistids, carangids, diodontids, labrids, ostraciids, pomadasyids, sparids and tetraodontids (mostly species with hard palates), two species of gastropods (*Cassis madagascariensis* and *C. tuberosa*) and the spiny lobster *Panulirus argus* (Randall et al., 1964; Levitan and Genovese, 1989). The toadfish *Amphichthys cryptocentrus* and *Sanopus barbatus* and the queen triggerfish, *Balistes vetula*, were reported to feed almost exclusively on *D. antillarum* before the die-off, but switched to small fishes and mobile benthic invertebrates afterwards (Robertson, 1987; Reinthal et al., 1984). Remains of *D. antillarum* have also been reported in the stomachs of small wrasses, including *Halichoeres bivittatus*, *Halichoeres poeyi* and *Thalassoma bifasciatum.* However, this is thought to be from the scavenging activities of these wrasses. The long-snouted

West Indian butterflyfish *Prognathodes aculeatus* and the Indo-Pacific butterflyfish (*Forcipiger*) feed on the tube feet of *D. antillarum.* The clingfish *Diademichthys lineatus* has also been reported to feed on *Diadema* tube feet and pedicellariae (Sakashita, 1992).

Direct observations of predation on *D. antillarum* on the rocky habitats of the Canary Islands (Clemente et al., 2010, 2011) showed 12 species of fish prey on this species. The predator assemblage depended on the intensity of fishing and the predator and prey sizes. While the balistids *Balistes capriscus* and *Canthidremis sufflamen* were the dominant predators at the marine protected area site, the sparid *Diplodus sargus* dominated in highly fished sites and fed predominantly on juvenile sea urchins. These observations were consistent with previous studies showing the top-down control of sea urchins by predatory fish in coral reefs and rocky shore habitats (Sala and Zabala, 1996; McClanahan, 1997; McClanahan et al., 2009). The seastar *Coscinasteras tenuispina* was also reported to prey on juvenile *D. antillarum* in the barren grounds of rocky habitats in the Canary Islands (Clemente et al., 2007).

No gut analysis or direct observation of predation on *D. savignyi* or *D. setosum* has been reported. McClanahan (1988) tethered both these species and found that predation rates were low compared to rates on tethered *E. mathaei,* the competitive dominant, at Kanamai and Vipingo reef lagoons in Kenya. He suggested that this leads to species coexistence. In addition, other than reports on predation on coral and coral spat by *D. antillarum* (Bak and van Eys, 1975; Carpenter, 1981; Sammarco, 1980, 1982b), few reports on predation by *Diadema* are available.

4. HERBIVORY AND GRAZING EFFECTS

4.1. Herbivory

Grazing by *D. antillarum* has an important ecological function on reefs and benthic algal communities throughout the Caribbean and western Atlantic (Ogden et al., 1973; Sammarco et al., 1974; Carpenter, 1981, 1986; Sammarco, 1982a; Lessios et al., 1984). It is estimated that, prior to the die-off, approximately 20% of the monthly net benthic primary production of the fringing reef in Barbados was consumed by *D. antillarum* (Hawkins and Lewis, 1982). This is considerably higher than the estimate of 7% for the sea urchin *Strongylocentrotus droebachiensis* in kelp beds, but lower than estimates of 47% for *Lytechinus variegatus* in seagrass habitats (Hawkins and Lewis, 1982). Tuya et al. (2004c) reported a similar important role for *D. antillarum* grazing on algal assemblages in the eastern Atlantic.

Sammarco (1982b) eliminated an entire population of *D. antillarum* on a reef at St. Croix, Virgin Islands. He found algal biomass increased by an order of magnitude, species composition was altered, shifts in dominance occurred (*Halimeda opuntia* the dominant algae was replaced in dominance by other species of algae, especially *Padina sanctae-crucis*), an increase in species numbers (at least five more algal species not found in grazed controls) and a decrease in equitability due mainly to the high dominance of *Padina sanctae-crucis*.

The well-documented mass mortality of *D. antillarum* of 1983–84 and the subsequent studies on the effects of the die-off emphasized the large-scale influence of grazing by this species. During this period, the population density of *D. antillarum* was reduced by 90 to 100% with dramatic increases of algal biomass (42 to 93%) and changes in community structure (Bak et al., 1984; Lessios et al., 1984; Carpenter, 1985b, 1990b; De Ruyter van Steveninck and Bak, 1986; Liddell and Ohlhorst, 1986; Hughes et al., 1985; 1987). In addition to the large increase in algal biomass, the trapping of sediments in algae increased and the abundance of corals and crustose coralline algae and coral recruitment decreased. This supports the hypothesis that grazing by *D. antillarum* was the primary determinant of algal distribution and biomass on shallow reefs throughout the Caribbean during the 1970s and early 1980s (Sammarco et al., 1974; Carpenter, 1986; Foster, 1987).

Herbivory by *D. antillarum* enhances the quality of algal turfs, increasing productivity by 2 to 10 times more per unit chlorophyll a than turfs that are not grazed (Carpenter, 1986). Further, ammonium excretion by *D. antillarum* supplies up to 19% of the total nitrogen requirement of these algal turfs (Williams and Carpenter, 1988). Because algal turfs account for the bulk of primary productivity in coral reefs, this enhanced productivity has a large effect on the community of reefs in the Caribbean.

Diadema are expected to compete for food with herbivorous fishes (Ogden, 1976; Wanders, 1977; A. H. Williams, 1981; Hay and Taylor, 1985). Therefore the die-off of *D. antillarum* led to substantial increases of algal biomass and had the potential to increase abundances of herbivorous fishes. Robertson (1991) showed that the numbers of surgeonfish (*Acanthurus coeruleus* and *Acanthurus chirurugus*), which feed almost exclusively in reefs where *D. antillarum* occur, increased by 250 and 160%, respectively, between 1979 and 1989. Nevertheless, no increase occurred in *Acanthurus bahianus,* a species that feeds in offshore habitats free from *D. antillarum*. These results are consistent with the suggestion that these two species compete for food with *D. antillarum* (Hay and Taylor, 1985) and that competition limited their population size (Carpenter, 1990b). Increases in herbivorous fish, including surgeonfish and parrotfish, were also reported in St. Croix after the die-off (Carpenter, 1990b). These findings are consistent with sea urchin reduction experiments reported from Kenya (McClanahan et al., 1996). However, at the highest algal biomass levels these herbivores may also be avoiding algal dominated areas with abundant morphologically and chemically defended algae (McClanahan et al., 2001).

4.2. Bioerosion

Prior to the die-off, the grazing activity of *D. antillarum* had a substantial effect on calcium carbonate budgets of reefs in the Caribbean (Ogden, 1977; Stearn and Scoffin, 1977; Stearn et al., 1977; Scoffin et al., 1980). It is estimated, for example, that at pre-mortality densities of 3 to 12 ind·m^{-2}, *D. antillarum* eroded the reef at rates of between 3.6–9.1 kg m^{-2} yr^{-1} (Ogden, 1977; Bak, 1994). Given that the average coral reef accretes at ~4 kg m^{-2} yr^{-1} (Bak, 1994), the populations of *D. antillarum* had a significant influence on calcium carbonate budgets of Caribbean reefs. In addition, at high densities, *D. antillarum* occasionally preys on coral spat and influences coral recruitment. Some grazing is beneficial for coral recruitment through reduction of algal growth, but coral recruitment is greatly depressed at high densities of sea urchins (Sammarco, 1980).

In the Indian Ocean, a study of bioerosion and herbivory on Kenyan reefs showed bioerosion to be greater than herbivory by sea urchins and was proportional to body size of the species (Carreiro-Silva and McClanahan, 2001). The larger *D. setosum* exhibited bioerosion rates of 1.8 ± 0.3 g CaCO$_3$ ind^{-1} d^{-1} and herbivory rates of 1.1 ± 0.2 g algal wet weight ind^{-1} d^{-1}, whereas the smaller *D. savignyi* exhibited bioerosion rates of 0.7 ± 0.2 CaCO$_3$ ind^{-1} d^{-1} and herbivory rates of 0.4 ± 0.1 g algal wet weight ind^{-1} d^{-1}. As the highest densities of sea urchins were recorded in fished reefs, rates of bioerosion (1180 ± 230 g CaCO$_3$ m^{-2} yr^{-1}) and herbivory (450 ± 77 g algal wet weight m^{-2} yr^{-1}) were highest on fished reefs (Carreiro-Silva and McClanahan, 2001). Reefs without fishing showed 20-fold lower rates of bioerosion and herbivory (50.3 ± 25.8 g CaCO$_3$ m^{-2} yr^{-1} and 20.7 ± 10.4 g algal wet weight m^{-2} yr^{-1}, respectively). The findings from this study suggest that sea urchins are important in the carbon cycle and reef development of Indian Ocean reefs and that fishing can influence these ecological processes.

Bioerosion by *Diadema* has also been reported to have minimal impact in some habitats. For example, Herrera-Escalante et al. (2005) reported relatively low rates of bioerosion by *D. mexicanum* in Bahias de Huatulco, Mexico. Bioerosion rates also varied with the species, test size and population density and did not have an impact on coral accretion on these reefs. These bioerosion rates were comparable to rates measured for *Diadema* sp. on Ningaloo reef, Australia (Johansson et al., 2010). Other factors that influenced bioerosion rates included habitat composition. *Diadema setosum* was reported to have higher bioerosion rates in areas without seagrass in the Philippines (Uy et al., 2001). Combined impacts of bioerosion and predation by the gastropod *Drupella* caused severe damage in a marine park in Hong Kong (Lam et al., 2007).

5. CONCLUSIONS

Sea urchins in the genus *Diadema* can be among the dominant grazers and forces of erosion of the substratum in shallow tropical reef environments. *Diadema* are likely to compete with other herbivores and also influence the interactions between algae and coral (McClanahan, 1992; Carpenter and Edmunds, 2006). Consequently, they can play an important role in the ecology of tropical reefs and the factors that influence their population dynamics and coexistence with others species are significant for reef ecology and fishery management (McClanahan et al., 1996, 1999). In some places and at some population densities, they are considered pests as they dominant benthic primary productivity and exclude other herbivores (Tuya et al., 2005). However, they can also be seen as important in maintaining and restoring coral populations (Carpenter and Edmunds, 2006) and, therefore, have been considered candidates for aquaculture and reef restoration. Consequently, the historical levels of their populations are of interest, as these may indicate the degree to which they are either required for the maintenance of coral reef ecology (Jackson et al., 2001; Lessios, 2001b) or pests that have been released from predation by overfishing (Hay, 1984; Levitan, 1992; Brown-Saracino et al., 2007; O'Leary and McClanahan, 2010). This is likely to differ with biogeographic region, evolutionary and fishing history and habitat. This will make it difficult to conclude what are the appropriate or historical levels of abundance. Modeling studies have shown, however, that at biomass of around 400 g wet weight m^2 (about four adults per m^2) *Diadema* dominate benthic primary productivity and exclude other herbivores (McClanahan, 1992, 1995). Consequently, for practical management purposes, at half these levels *Diadema* may keep algal biomass sufficiently low to allow for coral recruitment and create surplus benthic productivity available for other herbivores.

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