

Chapter 4

Echinoderm Diversity in Panama: 144 Years of Research Across the Isthmus

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4.1 Introduction

The Republic of Panama is the southernmost country in Central America between 07°00'–10°00' north and 77°00'–83°00' west and is located between Costa Rica to the north and Colombia to the south. The country runs from east to west with a length of 772 km and a width that varies from 60 to 177 km (Meditz and Hanratty 1987). Panama has both Caribbean and Pacific coastlines that total some 2,857 km and which incorporate a vast diversity of marine habitats and ecosystems. The 80 km Panama Canal bisects the country and although this is theoretically a freshwater barrier, it provides a link between the Atlantic and Pacific Oceans. Approximately one hundred and fifty rivers flow into the Caribbean, while over three hundred rivers flow into the eastern Pacific.

Panama's weather is governed by the Inter-Tropical Convergence Zone which dictates the seasonal patterns of wind and rainfall in the region. The dry season (mid-December to mid-April) is characterised by low precipitation but strong winds as a result of the northeast trade winds (Forsbergh 1969; Amador et al. 2006). The rainy season (May to November) has light winds with heavy rainfall

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which varies regionally from less than 1.3 m to more than 3 m per year, with rainfall on the Caribbean side typically being heavier than on the Pacific side of the continental divide (Meditz and Hanratty 1987).

The formation of the Isthmus of Panama is considered to be one of the most important geologic events of the past 60 million years as it had an enormous impact on Earth's climate and environment. It occurred due to the gradual collision of the Pacific, Cocos, Nazca and Caribbean plates which led to uplift of the sea floor and the formation of volcanic islands. Over the next 12 million years vast quantities of sediment from North and South America were deposited in between the newly emerging islands, with final closure of the straits occurring in the late Pliocene, 2.8 million years ago (mya) (Coates et al. 2005). This formation blocked the North Equatorial Current which had previously flowed westward through the Central American Seaway and forced the current northwards forming the Gulf Stream of today (Berggren and Hollister 1974; Burton et al. 1997). With the Pacific and Atlantic no longer mixing, there were significant changes in temperature, salinity and primary productivity. This resulted in both species extinctions and species radiations as environments changed (Jackson et al. 1993). Sister species that were isolated on either side of the isthmus and that subsequently diverged are referred to as geminates (Jordan 1908). These represent initially similar genomes that were isolated and diverged over the last 3 million years (Lessios 2008) and provide insights into evolutionary adaptations in response to the changing environments.

Today the Caribbean coast of Panama incorporates coral reefs, seagrass beds, rocky shores, mud-flats and mangroves and has a narrow continental shelf. It continues to be influenced by the Atlantic North Equatorial Current which flows through the Lesser Antilles (Kinder et al. 1985). The coast of the south-western Caribbean including Panama is also affected by a cyclonic gyre that develops from this current (Gordon 1967; Kinder et al. 1985; Gómez et al. 2005). For an in-depth review of the Caribbean habitats of Panama, see Gómez et al. (2005). The Caribbean experiences very small tidal ranges (less than 0.5 m) and has relatively stable conditions. Its waters are clear and nutrient poor (D'Croz and Robertson 1997; D'Croz et al. 2005; Collin et al. 2009) and unlike the north coast of Colombia there is no upwelling. These conditions are suitable for growth of extensive coral reefs which date back to the early Pleistocene (Glynn 1982; Cortés 1993). Surface waters of the Caribbean have an upper 200 m layer of warm water heated by solar radiation, which has a correspondingly high salinity. Surface water temperatures vary from 27 °C in the dry season to 30 °C in the rainy season, while salinity varies from 36 psu in the dry season to 32 psu in the rainy season (D'Croz and Robertson 1997). Two archipelagos are present off the Caribbean coast of Panama, the San Blas (Kuna Yala) Archipelago which has a very narrow continental shelf and is subject to strong ocean influence with an oligotrophic coastal area (D'Croz and Robertson 1997) and the Bocas del Toro Archipelago, with a larger continental shelf, and greater influence from continental run-off (D'Croz et al. 2005). Five national parks have been created along the Caribbean coast of

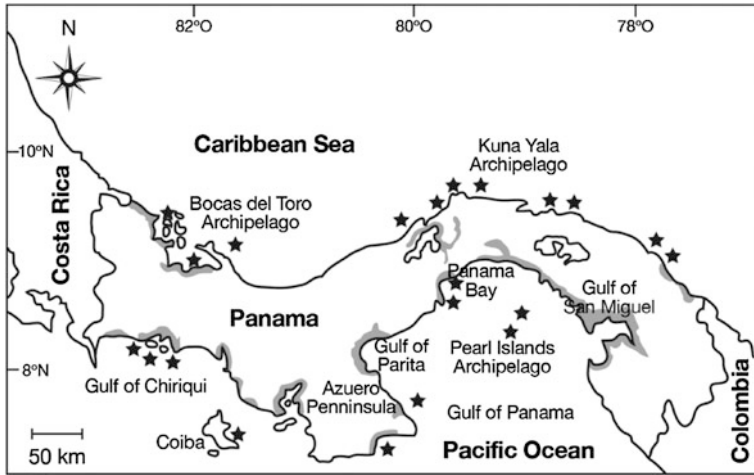


Fig. 4.1 Distribution of coral reefs and mangrove forests along the coasts of Panama (adapted from Gómez et al. 2005). *Black stars*: coral reefs; *grey shading*: mangroves

Panama: Bastimentos Island National Marine Park, Portobelo, Soberania, Galeta, Chagres, and the wetlands of San San Pond Sank (Gómez et al. 2005).

The Pacific coast of Panama is comprised of two gulfs; the Gulf of Chiriquí and the Gulf of Panama which are separated by the Azuero Peninsula (Fig. 4.1). These regions experience broad semi-diurnal tides with a range of up to 6 m (Glynn 1972). Despite their close proximity, they experience very different hydrological conditions. The Gulf of Panama includes the Gulf of San Miguel, the Gulf of Parita and Panama Bay, as well as the Pearl Islands Archipelago which is a Marine Special Management Zone (Guzman et al. 2008). The gulf is broad and shallow, with much of it being less than 40 m deep due to the extension of the continental shelf. The coastal environments consist of muddy and sandy beaches with extensive mangrove forests, which receive large amounts of freshwater runoff from rivers such as the Rio Chepo and Rio Chico as well as the discharge from the Panama Canal. Coral reefs are only moderately developed and are associated with the Pearl Islands Archipelago and the inshore island of Taboga. Throughout the rainy season the surface water temperature ranges from 26–28 °C, while salinity is typically below 30 psu (D’Croz et al. 1991). During the dry season (December to April) the Gulf of Panama experiences wind-driven, seasonal upwelling of colder, more saline, nutrient-rich water (Forsberg 1963; Forsbergh 1969; D’Croz et al. 1991; D’Croz and Robertson 1997; Gómez et al. 2005; Pennington et al. 2006), which results in significantly increased primary productivity. This occurs due to the displacement of the surface water by northern winds and can result in a surface water temperature decrease of 12 °C within 24 h (Glynn 1972). The Gulf of Panama is also subjected to the effects of the El Niño-Southern Oscillation (ENSO) every two to seven years (Guzman and Cortes 2007) resulting in the warming of the water up to 31 °C (Glynn 1985a).



Fig. 4.2 *Pocillopora* spp. framework on Uva Reef, Gulf of Chiriquí, 2010

In contrast, the Gulf of Chiriquí has a narrower continental shelf and less freshwater input from continental runoff. It contains Chiriquí National Park and Coiba Nacional Park which has World Heritage Site status. Several island complexes are present, including the islands of Boca Brava, Los Ladrones, Islas Secas, Parilla, Isla Palenque, Montuosa, and Isla Jicaron, with Isla Jicarita being the island furthest south of the Panama mainland. In the northwest of the gulf, water depth gradually increases down the continental shelf. However, in the east, water depth sharply drops to 160 m before plunging down the continental slope and reaching a depth of 1,000 m less than a 1 km south of the Azuero Peninsula. The Gulf of Chiriquí is shielded from the trade winds out of the North by the Central Cordillera and therefore experiences no seasonal upwelling. The Gulf of Chiriquí contains some of the most developed coral reefs on the continental shelf in the eastern Pacific. These are predominantly formed of a loose *Pocillopora* spp. framework (Fig. 4.2) that originated in the Holocene (Glynn 1976; Cortés 1993).

4.2 Research

The first records of the echinoderm fauna of Panama date back to the late 19th and early 20th century and are the result of the expeditions of the U.S. Fish Commission Steamer *Albatross*. Addison Emery Verrill (Fig. 4.3a) wrote the first paper in 1867 that included echinoderms from Panama. It contained descriptions of many new genera and species. In 1891 Alexander Agassiz (Fig. 4.3b), onboard the *Albatross* collected specimens from the intermediate depths of the eastern Pacific and the Caribbean Sea to study the relationship between forms of marine life on either side

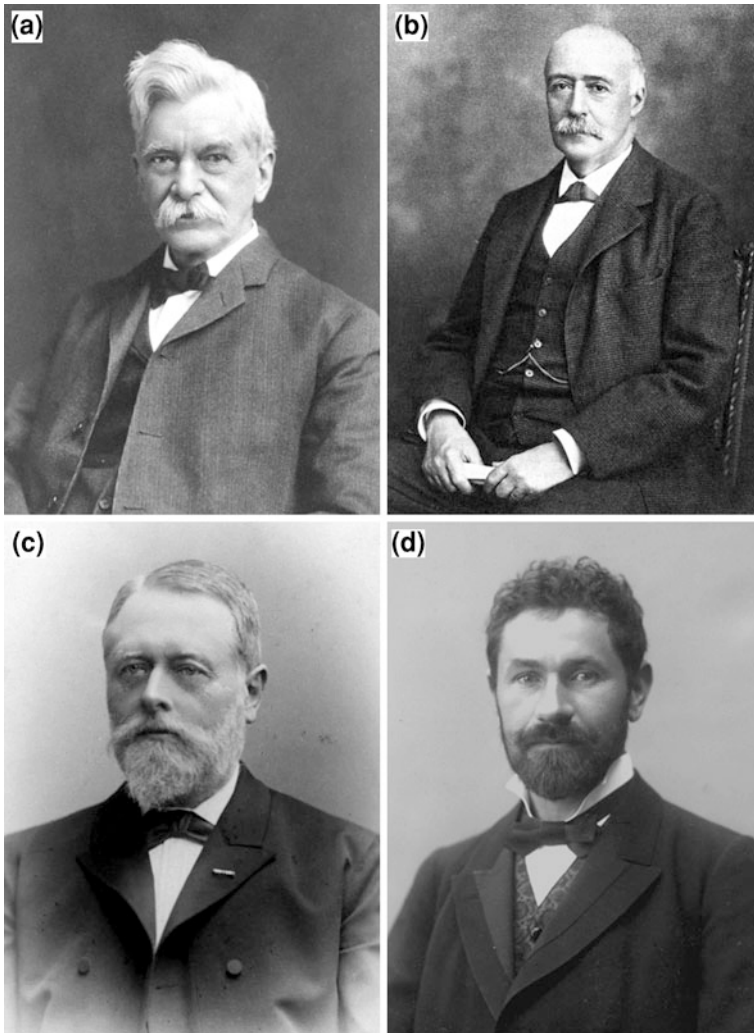


Fig. 4.3 **a** Addison Emery Verrill, **b** Alexander Agassiz, **c** Christian Frederik Lütken, **d** Theodore Mortensen (photos courtesy of the Smithsonian National Museum of Natural History)

of the Isthmus of Panama. The collections from this expedition were used by many authors to describe new echinoderm species (e.g. Agassiz 1892, 1898, 1904; Ludwig 1894, 1905; Lütken and Mortensen 1899, (Fig. 4.3c, d), Clark 1917).

In the 1930's and 1940's expeditions to the eastern Pacific were undertaken by the New York Zoological Society onboard the *Arcturus* 1925 and *Zaca* 1937–1938, and by the Allan Hancock Foundation onboard the *Velero III* 1937–1941. As a result of these expeditions, a significant amount of echinoderm research was published (e.g. Clark 1939; Clark 1940, 1948; Ziesenhenné 1940,

1942, 1955; Deichmann 1941, 1958). In 1915 Mortensen spent several months collecting echinoderms and other invertebrates in the Gulf of Panama, including from St. Elmo in the Pearl Islands Archipelago and the islands of Taboga and Taboguilla in Panama Bay. His findings were later included in a broader work on larval development (Mortensen 1921) and as part of his monumental monograph on echinoids (Mortensen 1928, 1935, 1940, 1943a, b, 1948a, b, 1950, 1951). Other researchers in the 1920's, 30's and 40's made collection trips to specific regions in Panama (e.g. Boone 1928, Clark 1946) focusing more on specific taxa. In later years echinoderms were collected from the Caribbean Sea off Panama as part of general benthic sampling expeditions undertaken by the RV *Oregon* in 1962, the RV *Pelican* in 1963, the RV *Oregon II* in 1970, the RV *Pillsbury* in 1971 and the RV *Alpha Helix* in 1977.

The Smithsonian Tropical Research Institute (STRI) established its first field station on Barro Colorado Island in the Panama Canal Zone in 1923. The marine program at STRI began fifty-one years ago, in 1961. Today STRI runs two field stations on the Caribbean Coast (Galeta Marine Laboratory in Colón and Bocas del Toro Research Station) and two in the Pacific (Naos Island Laboratories complex and a Field Station on Ranchería Island, Coibita). The first research vessel was acquired by STRI in 1970, the 65-ft RV *Tethys* (1970–1972), followed by the 45-foot RV *Stenella* in 1972 (1972–1978) and the 63-foot RV *Benjamin* in 1978 (1978–1994). These research vessels allowed STRI scientists to collect and document the shallow water echinoderm fauna. In 1994 STRI purchased the 96-foot RV *Urraca* (1994–2008) that had an A-frame and oceanographic winch which finally provided the means to trawl and dredge to depths of 250 m. In 1995 the submersible DSRV *Johnson Sea Link* was used to collect samples from the Gulf of Chiriquí at depths over 1,000 m, providing a further insight into the deep water species present off Panama's Pacific coast. STRI researchers who worked on echinoderms in the 70's and 80's included Peter Glynn, Gordon Hendler and Harilaos Lessios. For just over 30 years Lessios has worked at STRI on the life histories and evolution of echinoderms in Panama. His research has focused primarily on echinoids, including work on speciation, molecular biogeography and the evolution of reproductive isolation. Lessios (2005a) published a review of the echinoids of the Pacific waters of Panama, providing information on the species and new records of their distributions.

4.3 Ecology

Ecological research in Panama has included work on all classes of echinoderms, but with fewer studies on crinoids. Eleven species of echinoderms were recorded in the seagrass meadows of *Thalassia testudinum* Banks and Sol. ex K.D. Koenig (1805) in the Canal Zone off the Caribbean coast of Panama (Heck 1977). Species richness of echinoderms correlated with proximity to well developed reefs and was found to be stable throughout the study period (July 1974 to May 1975), without any major decrease in population numbers during periods of reduced salinity.

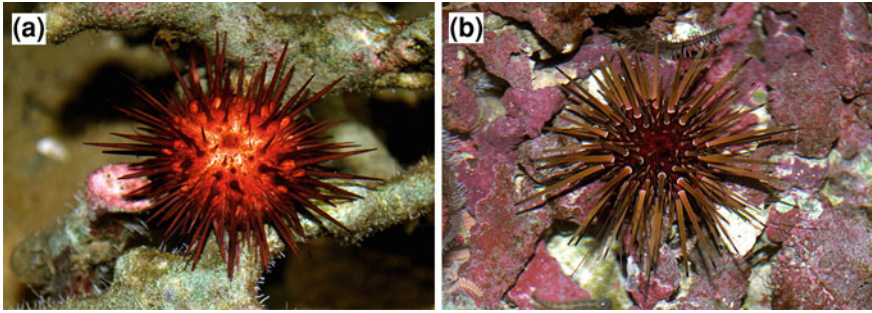


Fig. 4.4 a *Echinometra lucunter*, b *Echinometra viridis* at Galeta Point Panama

Mortality of sea urchins on the fringing reef-flat off Galeta Island has been reported to occur twice yearly as the result of physical stress generated by extended aerial exposure of the reef platform (Glynn 1968; Hendler 1977; Cubit et al. 1986). *Tripneustes ventricosus* (Lamarck, 1816), *Lytechinus variegatus* (Lamarck, 1816) and *Diadema antillarum* Philippi, 1845 were found to be less tolerant to high temperature than either *Echinometra lucunter* (Linnaeus, 1758) (Fig. 4.4a) or *Echinometra viridis* Agassiz, 1863 (Fig. 4.4b), and are therefore more likely to die during the periods of exposure.

In the Caribbean *D. antillarum* has been shown to be the dominant herbivore on coral reefs that have been subjected to heavy human fishing pressure, while herbivorous fishes dominate in more pristine conditions where urchin populations are kept in check by fish predators (Hay et al. 1983; Harborne et al. 2009). Off Galeta Island, where human fishing pressure is reported to be low (Hay 1984), almost all grazing on bioassays of *T. testudinum* was attributed to herbivorous fishes (Hay 1984). Off the San Blas Islands of Panama, the grazing activity of *D. antillarum* has been shown to be the primary determinant of fleshy algal biomass on shallow reefs (<3 m) (Foster 1987a). At the time of Foster's study (pre-mass mortality of *D. antillarum*, see Sect. 4.6) this was particularly true in the back reef environment, where *D. antillarum* occurred at densities three times higher ($\sim 6 \text{ ind m}^{-2}$) than in Elkhorn coral habitats ($< 2 \text{ ind m}^{-2}$) (Foster 1987a).

Chemical defence by coral reef macroalgae has been shown to have an import role in deterring grazers (Hay et al. 1987). Extracted terpenoid compounds (naturally occurring in macroalgal species of *Dictyota*, *Dilophus*, *Laurencia* and *Styopodium*) were applied to assays of *T. testudinum* and shown to deter grazing by herbivorous fishes and *D. antillarum* at Galeta (Hay et al. 1987). However, Cymopol, a terpenoid bromohydroquinone from the green alga *Cymopolia barbata* (Linnaeus) Lamouroux, 1816, significantly reduced feeding by reef fishes but significantly stimulated feeding in *D. antillarum*.

The ability of the damselfish *Stegastes dorsopunicans* (Poey, 1868) to exclude and therefore reduce the grazing impacts of *D. antillarum* from their territories was studied by Foster (1987b) in San Blas. Despite the major negative impact of

D. antillarum on the algal biomass in damselfish territories, this damselfish species was found to rarely defend its feeding areas against *D. antillarum* and therefore had little effect on its distribution.

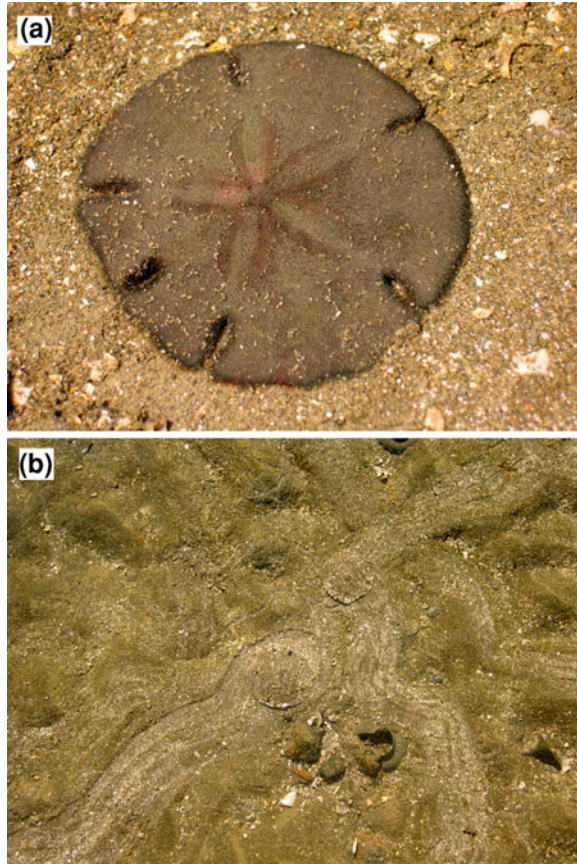
On the Pacific coast of Panama grazing by *D. mexicanum* results in the bioerosion of the predominantly *Pocillopora* spp. coral reefs (Glynn 1988). This species contributes 78 % of the overall bioerosion $13 \text{ kg m}^{-2} \text{ y}^{-1}$ produced by benthic eroders (Glynn 1988; Eakin 1991). Analysis of faecal pellets has revealed that the diet of *D. mexicanum* consists of 75.2 ± 11.03 % coral and only 23.0 ± 11.4 % of crustose coralline algae (CCA). In contrast the diet of *Toxopneustes roseus* (A. Agassiz, 1863) is composed of approximately 20 % coral and 80 % of CCA (Glynn 1988). This highlights the potential damage *D. mexicanum* poses to reef structures, particularly when present in large numbers. Such a threat was realised following the 1982–83 El Niño Southern Oscillation event (ENSO). This resulted in mass coral bleaching and a 50 % reduction of live coral cover on Uva Reef (Glynn 1985a), which was followed by a dramatic increase in the population size of *D. mexicanum* from 2–5 ind m^{-2} pre 1983 to 60–100 ind m^{-2} post 1982–83 ENSO (Glynn 1988, 1990; Eakin 1991, 1992). Such large numbers of *D. mexicanum* resulted in high rates of reef framework erosion, shifting the reef environment into a state of near accretionary stasis (Eakin 1992; Glynn 1997). Low predation pressure (with the removal of potentially important fish predators as a result of over-fishing), increased habitat availability, and the increased abundance of benthic algae as a result of the newly dead coral substratum allowed *D. mexicanum* to attain high population densities (Glynn 1988). However, such a large population of *D. mexicanum* could not be sustained and in the year 2000 the population of *D. mexicanum* dropped to near 1974 levels (>10 ind m^{-2}) (Eakin 2001).

The ability of damselfish in the eastern Pacific to exclude *Diadema* from their territories appears to be a very different situation to that reported in the Caribbean. The territorial action of *Stegastes acapulcoensis* (Fowler, 1944) on Uva Reef results in few sea urchins being present in their territories (Glynn 1990), with consequently lower levels of erosion (6.3 mm y^{-1}) than elsewhere on the reef (21.8 mm y^{-1}) (Eakin 1992).

Ecological studies on irregular echinoids in Panama have focused on sand dollars. Seilacher (1979) studied the distribution of *Mellita quinquesperforata* (Leske, 1778) (as *Mellita lata* Clark, 1940), a subjective junior synonym of *M. quinquesperforata*) at María Chiquita on the Caribbean coast of Panama. This species lives partially buried in the sand (with some of the apical surface exposed) and is restricted to a 4 m wide region of the surf-zone that runs parallel to the beach (Seilacher 1979). This species was observed feeding along this zone, but migrated to deeper water when the intensity of the wave action increased.

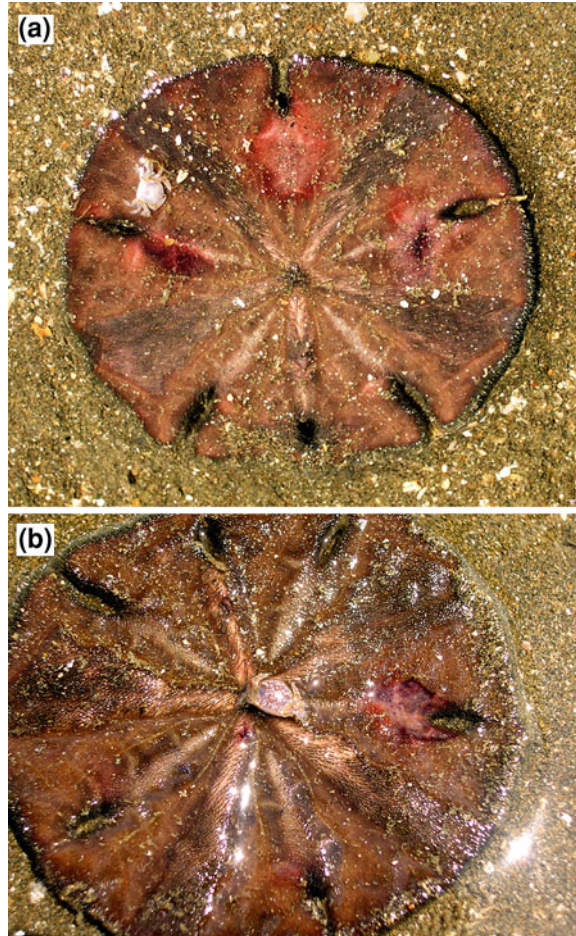
The behavioural ecology of a population of *Mellitella stokesii* (L. Agassiz, 1841) (as *Encope stokesi* L. Agassiz, 1841 [sic]) was studied over a year at Venado Beach, on the eastern Pacific coast of Panama by Dexter (1977). Densities of this species were reported to vary from a low of 19 ind m^{-2} in the rainy season to a

Fig. 4.5 *Mellitella stokesii* at Venado beach, **a** aboral view, **b** feeding during low tide



high of 65 ind m^{-2} in the dry season, with numbers concentrated in the mid-intertidal zone where the median sediment grain size was between 170 and 200 μm . No sand dollars were found in the muddy sand bar which had a high silt and clay fraction. Migrations towards the substrate surface were observed at low tide which correlated with the appearance of an organic film on the substrate, composed of a combination of diatoms and fine detrital material. Observations by one of the authors (SEC) at Venado Beach (see Fig. 4.5a, b) agree with Dexter's findings. During high tide this species typically remains buried in the substrate, perhaps to avoid predation, and only migrates to the surface at low tide, where it moves through the upper sediment layer in the shallow tide pools ingesting small particulate mater (Fig. 4.3b). Water temperatures in these pools regularly gets in excess of 40 °C (Coppard unpublished data), demonstrating that *M. stokesii* has a tolerance for high water temperatures. Dexter (1977) reports that this species has a high growth rate, in conjunction with a small maximum size (she recorded a maximum horizontal diameter of 57 mm) and a short life expectancy of typically

Fig. 4.6 *Mellitella stokesii* (oral views) on Venado beach with *Dissodactylus* spp., **a** multiple wounds, **b** a single wound



less than 1 year. Recruitment of the population was reported to occur throughout the year, but with a peak in settlement during February, in the middle of the Panamanian dry season. This is the season of increased food availability for planktotrophic larvae, due to the upwelling of nutrients and subsequent increase in phytoplankton (Martin et al. 1970).

Two species of pinnotherid crab (pea crab), *Dissodactylus nitidis* Smith, 1870 and *Dissodactylus xantusi* Glassell, 1936 were found associated with *M. stokesii* (Dexter 1977). These species remove the spines near the lunules or marginal slits on the oral surface, creating a wound in which they live (see Fig. 4.6a, b). Dexter questioned whether this relationship is really commensal, as she found that these crabs in aquaria removed larger numbers of spines on the oral surface, which decreased the ability of the sand dollar to feed and move, ultimately resulting in the death of the host.

Telford (1982) described the feeding habits of four species of *Dissodactylus* and found that all of them feed extensively upon their sand dollar hosts, with 50–100 % of their food intake coming from their host's tissues. This is supported by the fact that some *M. stokesii* often have multiple wounds with only a single crab present (Fig. 4.6a).

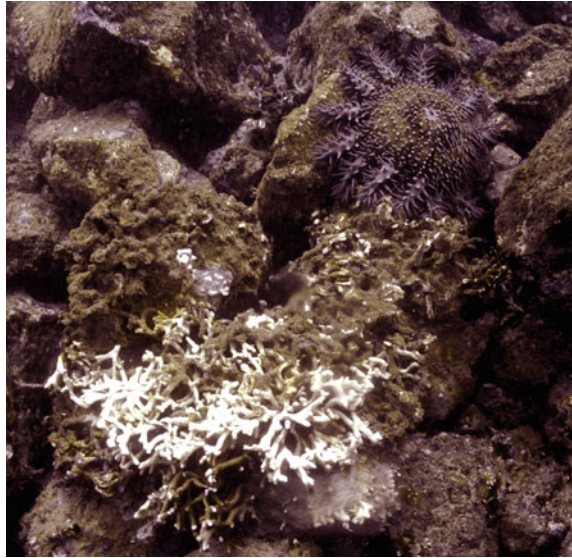
Ecological work on ophiuroids in Panama is primarily the result of research by Gordon Hendler. Hendler and Meyer (1982) reported the presence of the polychaete *Branchiosyllis exilis* (Gravier, 1900) associated with *Ophiocoma echinata* (Lamarck, 1816) on the Caribbean coast of Panama. This association has only been reported from Panama, despite the fact that both species' distributions are overlapping and widespread. The polychaete displays active recognition of its host and seeks out *O. echinata* in preference to other species of the same genus. They consistently found one polychaete per host, indicating that *B. exilis* is aggressive to member of its own species, and concluded that *B. exilis* is parasitic on *O. echinata*.

An interesting association between juvenile and adult *Ophiocoma aethiops* Lütken, 1859, from Punta Paitilla in Panama was documented by Hendler et al. (1999). Juveniles were found in the bursae (respiratory structures that in brooding and viviparous ophiuroids also serve as brood chambers) of adults that live intertidally at Punta Paitilla but not those that live subtidally at Isla Taboguilla. They proposed this association helped protect juveniles against desiccation and predators. No similar association was found in other species of *Ophiocoma* form either the Pacific (*O. alexandri* Lyman, 1860) or from the Caribbean (*O. echinata*, *O. wendtii* Müller and Troschel, 1842) of Panama.

Much of the ecological work on starfish in Panama has focused on *Acanthaster planci* (Linnaeus, 1758) (e.g. Glynn 1973, 1974, 1976, 1977, 1981–1985a,b, 1990). Glynn (1973) assessed the possible effect of *A. planci* on the coral species on Uva Reef in the Gulf of Chiriquí. He reported an average density of 25–36 ind ha⁻¹, with a disc diameter of 17–19 cm and a size frequency that had a unimodal distribution. Population densities of *A. planci* remained fairly stable on Uva Reef from 1970 to 1980, ranging from 7 to 30 ind ha⁻¹ (Glynn 1981). At that time these densities were comparable to population sizes in the Indo-Pacific that were not considered to have a serious impact on coral communities (Glynn 1974). However, prey preference data (Glynn 1974) indicate that *A. planci* selectively eats rarer non-branching corals (e.g. species of *Pavona*, *Gardineroseris*, *Porites*, *Millepora*, Fig. 4.7), which are replaced by faster-growing species (e.g. *Pocillopora* spp.), resulting in *A. planci* having a negative effect on species diversity (Glynn 1976). Such a preference can partly be explained by the presence of crustacean symbionts (*Trapezia* sp. and *Alpheus* sp.) in large branching pocilloporid colonies which repulse *A. planci* by nipping at its vulnerable oral surface (particularly the sensory tube feet) as it attempts to mount the coral to feed (Glynn 1976).

Between 1982 and 1983 a strong El Niño-Southern Oscillation had a dramatic impact on the coral reefs of the Eastern Tropical Pacific, causing a die off of between 70–95 % of coral on Pacific Panamanian reefs (Glynn 1985a, b). However, population densities of *A. planci* before and after the 1983 event were not statistically different (Glynn 1990), with *A. planci* continuing to feed on the

Fig. 4.7 *Acanthaster planci* feeding on *Millepora intricata* Milne-Edwards and Haime, 1860, Coiba National Park, Gulf of Chiriquí (photo courtesy of Angel Chiriboga)



dispersed, surviving coral. As the reefs recovered the relative effect of predation by *A. planci* intensified due to the loss of the crustacean guards (*Trapezia* and *Alpheus*), therefore reducing local coral species diversity (Glynn 1985b).

Fong and Glynn (1998) modelled the impacts of predation by *A. planci* and that of the El Niño-Southern Oscillation (ENSO) on the structure of a population of the massive coral *Gardineroseris planulata* (Dana, 1846) on Uva Reef. The results of the simulations suggested that predation was far more important than the ENSO in controlling the size structure of the coral *G. planulata* in the eastern Pacific.

Although *A. planci* has few predators, it has been observed in Panama being attacked by the Harlequin shrimp *Hymenocera picta* Dana, 1852 and by the polychaete *Pherecardia striata* (Kingberg, 1857) (Glynn 1981). The shrimp attacks the aboral surface of the starfish, eventually amputating the arms and using its chelae to expose and feed on the internal soft parts. However, the harlequin shrimp typically prefers other starfish species such as *Phataria unifacialis* (Gray, 1840), *Pharia pyramidatus* (Gray, 1840) and *Nidorellia armata* (Gray, 1840) (Glynn 1977). The wounds created by the harlequin shrimp are used also by the polychaete *P. striata* to enter *A. planci* and feed on the internal tissues. Glynn (1981) calculated that 5–6 % of the *A. planci* population is under attack by *H. picta* and about half of these starfish are killed over a 3-week period.

Guzman and Guevara (2002a) studied the spatial distribution, abundance, and size structure of *Oreaster reticulatus* (Linnaeus, 1758) (Fig. 4.8) in the Bocas del Toro Archipelago. They found a mean density of 149.7 ind ha⁻¹ and estimated the population size to be over seven million. Approximately 45 % of the population was found at a density of 308.3 ± 50.9 ind ha⁻¹, in areas dominated by the

Fig. 4.8 *Oreaster reticulatus* in the *Thalassia testudinum* seagrass bed, Bocas del Toro (photo courtesy of Edgardo Ochoa)



seagrass *T. testudinum*, with a substratum that consisted of coarse, calcareous sand. The lowest density (5.6 ind ha^{-1}) was observed in coral reef habitats.

Feeding patterns of *O. reticulatus* off the San Blas Islands were studied by Wulff (1995). She found that 61.4 % of the starfish were eating sponges; however, this depended on their availability. *Oreaster reticulatus* fed upon sixteen of twenty species that normally grow only on the reefs, but surprisingly only one of fourteen species that live in the seagrass meadows and rubble flats surrounding the reefs. Therefore *O. reticulatus* actively searches for and consumes edible sponges that wash into the seagrass beds from reefs, or off mangrove roots (Wulff 1995, 2006).

Meyer (1973) described the feeding behaviour, microgeographic distribution, population size, bathymetric distribution and adaptive skeletal morphology of eight species of Caribbean crinoids from four main study areas, including San Blas and Galeta, in Panama. Based on his findings he divided the species into two categories: 1) those forming a filtration fan (*Nemaster grandis* Clark, 1909, *Tropiometra carinata* (Lamarck, 1816), *Comactinia echinoptera* (Müller, 1840), *Analcidometra caribbea* (A. H. Clark, 1908) and *Neocomatella pulchella* (Pourtalès, 1878)) and 2) those with a radian posture (*Davidaster rubiginosus* (Pourtalès, 1869), *Davidaster discoidea* (Carpenter, 1888) and *Ctenantedon kinziei* Meyer, 1972). Species diversity and population size of shallow-water comatulids was found to be greatest in Panama (seven species). Meyer (1973) proposed that the diversity and abundance of comatulid crinoids can be correlated to increased primary productivity which occurs close to continental land masses.

Ecological studies on holothuroids in Panama have been carried out by Guzman and Guevara (2002b). They studied the population structure, distribution and abundance of the sea cucumbers *Isostichopus badionotus* (Selenka, 1867), *Holothuria (Halodeima) mexicana* Ludwig, 1875 and *Astichopus multifidus* (Sluter, 1910) in the Bocas del Toro Archipelago. *Holothuria (Halodeima) mexicana* was found to be more abundant in seagrass, *I. badiodotus* occurred at higher densities in interspersed areas, while *A. multifidus* showed no specific habitat preference. For the Bocas del Toro Archipelago Guzman and Guevara

(2002b) estimated populations of 7,630,164 individuals for *H. (H.) mexicana*, 5,536,349 for *I. badionotus*, and 231,074 for *A. multifidus*. However, the densities of these sea cucumbers in Panama were 50 times lower than those measured at other Caribbean sites (Guzman and Guevara 2002b).

4.3.1 Physiology

Lawrence and Glynn (1984) studied the diet of the sea urchin *Euclidaris thourarsii* (Valenciennes, 1846) through the absorption of nutrients from the predation on the coral *Pocillopora damicornis* (Linnaeus, 1758) in the Gulf of Panama. The absorption efficiency was determined to be 44.7 % for carbohydrates, 85.3 % for protein and 69.3 % for lipids. The urchin absorbs 0.402 mg carbohydrate, 2.814 mg protein and 1.108 mg lipid for each gram of *P. damicornis* ingested; 0.201 mg carbohydrate, 1.407 mg protein and 0.554 mg lipid per individual per day; and absorbs 0.824×10^{-3} kcal carbohydrate, 7.950×10^{-3} kcal protein and 235×10^{-3} kcal lipid per individual per day. The authors concluded that despite the high efficiency of digestive absorption of organic constituents of the coral ingested, *E. thourarsii* needs to consume large quantities to meet its nutritional requirements.

Work by Hendler and Byrne (1987) on *Ophiocoma wendtii* collected in Galeta, Panama Caribbean, Belize and Florida, resulted in the identification and description of three structures in the dorsal arm plate (DAP) that comprise a photoreceptor system. The upper surface of the DAP bears transparent microscopic structures which are expanded peripheral trabeculae of the calcite stereom. These structures are part of the photoreceptor system and can facilitate light transmission through the DAP by decreasing light refraction, reflection and absorption that occur at stereom/stroma interfaces. Bundles of nerve fibres located below the expanded peripheral trabeculae function as primary photoreceptors. The third elements of the system are the chromatophores that regulate the intensity of light impinging on the sensory tissue are regulated by the diurnal activity cycle. During the day the chromatophores cover the expanded peripheral trabeculae and thereby shade the nerve fibres. At night they retract into inter-trabecular channels, uncovering the expanded peripheral trabeculae and thereby exposing the nerve fibres to transmitted light. Thus, the transparent stereom may play a role in photoreception, in addition to its generally recognized skeletal function. Although ciliated cells that may be sensory are present in the epidermis of *O. wendtii*, they do not appear to be photoreceptors (Hendler and Byrne 1987).

4.3.2 Reproduction

Reproductive cycles of echinoids on both sides of the Panama Isthmus have been studied by Lessios (1981a, 1984, 1985a, 1991). Populations of *D. mexicanum* and *E. vanbrunti* from Punta Paitilla, Isla Urabá and Culebra Island in the seasonal Gulf of Panama have well-defined, synchronous, reproductive cycles (Lessios 1981a). The majority of individuals reached a peak gonad size in September, with spawning predicted to occur from September to October. This would allow the newly metamorphosed sea urchins, rather than the larvae, to benefit from the increased food production as a result of the dry season upwelling (Lessios 1981a). Populations of *D. antillarum* and *E. lucunter* from Maria Chiquita and Fort Randolph in the less seasonal Caribbean demonstrated only slight, if any synchrony between individuals. However, *E. viridis* which is rarer at these locations had a well defined, population wide cycle. Based on these data Lessios (1981a) proposed that in a constant environment the intensity of selection for synchrony between individual gametogenic cycles may be inversely proportional to population density. Later work by Lessios (1985a) on Caribbean echinoids did not directly support this hypothesis. However, Lessios (1985a) suggested that population density may be one of the factors determining the degree of synchronicity. This study (1985a) revealed that *E. viridis*, *L. williamsi*, *Clypeaster rosaceus* (Linnaeus, 1758) and *Leodia sexiesperforata* (Leske, 1778) are reproductively active during Panama's rainy season from May to November, but quiescent during the dry season (Lessios 1985a), while *L. variegatus*, *T. ventricosus*, and *Clypeaster subdepressus* (Gray, 1825) have ripe gonads throughout the year. Only *E. lucunter* showed non-periodic fluctuations in readiness to spawn.

Lessios (1984, 1991) also worked on lunar spawning periodicity in Panamanian echinoids. *Diadema mexicanum* was found to spawn on the third quarter of the lunar cycle, with a peak three to four days after full moon, while its allopatric congener *D. antillarum*, spawned during the first lunar quarter, one to two days after new moon. Lessios (1984) wrote that it is therefore possible that geminate species of *Diadema* have acquired a prezygotic isolating mechanism while in allopatry and therefore reproductive isolation need not be the product of natural selection against hybridization, thus casting doubt on the speciation by reinforcement theory.

Lunar spawning rhythms were not found in *T. ventricosus*, *E. viridis*, *L. sexiesperforata*, *C. rosaceus* or *L. williamsi* (Lessios 1991). *Euclidaris tribuloides* and *D. antillarum* were found to have a distinct lunar rhythm spawning at different lunar phases, while *L. variegatus* has a semilunar rhythm spawning every new and full moon (Lessios 1991). Such spawning rhythms are unlikely to be cued by tides as the Atlantic coast experiences only small tidal ranges (<0.5 m) where water level is determined as much by meteorological conditions as by tides. Lunar periodicity was therefore shown to not be a lineage specific trait inherited from a common ancestor, but has evolved independently in different echinoid taxa (Lessios 1991).

Temporal and spatial variation in egg size of thirteen Panamanian echinoids was studied by Lessios (1987). His results showed that mean egg size from different females collected from the same locality on the same day were significantly different in all species studied. However, daily (within-month) variation in egg size was only significant in *E. tribuloides*, *D. antillarum*, and *L. variegatus*, while no significant differences were found in the daily means of egg volume in *D. mexicanum* and *E. viridis*. Monthly means of egg volume were different in *L. variegatus*, *L. williamsi*, *T. ventricosus*, *E. viridis*, *E. vanbrunti*, *C. rosaceus* and *C. subdepressus*. Between-years variation was also significant in all of these species except *L. variegatus*. All Caribbean species showed a decline in egg size after September, however, this could not be explained by any obvious environmental fluctuation. *Echinometra lucunter* showed no significant variation between months of the same year but exhibited differences between years. No significant monthly or annual variation was observed in *E. tribuloides*, *E. thousarii* (Valenciennes, 1846), *D. antillarum*, *D. mexicanum* or *Leodia sexiesperforata*. Correlations between size of eggs collected at a particular time and the intensity of spawning by the population at that time was not significant, suggesting that size of mature eggs is not determined by the reproductive state of the parental population (Lessios 1987).

Lessios (1990) looked at adaptation and phylogeny as determinants of egg size in twenty-two species of echinoids and two species of asteroids from the Caribbean and Pacific coasts of Panama. Lessios (1990) identified four trends: (1) species have eggs that are significantly different from those of other congeneric species; (2) species evolving for three million years in separate environments have accumulated differences in their egg sizes and the direction of these differences is not random; (3) egg size of congeneric species is similar where developmental modes are similar (n.b. the volume of *Clypeaster rosaceus* eggs is eight times greater than that of its congener *C. subdepressus*, an adaptation that reflects developmental mode as the larvae of *C. rosaceus* are facultative planktotrophs, while those of *C. subdepressus* are obligate planktotrophs); (4) there is no similarity between the egg sizes of species belonging to the same family or higher taxonomic category, even if these species inhabit the same ocean. He concluded that because the phenomena of smaller eggs in the Pacific (a pattern attributed to higher levels of primary productivity in the eastern Pacific) holds for lineages that have not shared a common ancestor for a long time, it is likely that independent adaptation by the members of each pair has occurred due to the environments of the two oceans during the last three million years.

McAlister (2008) studied the plasticity of larval feeding arms for geminate species pairs to determine how food availability can influence growth and the arm length of the larvae. No plasticity in arm length was found in either Caribbean or Pacific species, however, arm length was significantly longer in Caribbean species (including in *D. antillarum*). McAlister (2008) suggests that historical changes in food levels led to the development of longer feeding arms in Caribbean species, while plasticity may be limited by egg size or the timing of reproduction.

The evolution of gametic incompatibility in neotropical *Echinometra* was investigated by Lessios and Cunningham (1993). They used fertilization

experiments to determine the degree of reproductive isolation both between the sympatric *E. lucunter* and *E. viridis*, in the Caribbean, and with the allopatric *E. vanbrunti* from the eastern Pacific. They reported that, contrary to the predictions of the ‘speciation by reinforcement hypothesis’, the degree of incompatibility between the allopatric *E. lucunter* and *E. vanbrunti* is higher than between the sympatric *E. lucunter* and *E. viridis*. Crosses between *E. viridis* and *E. vanbrunti* produced rates of fertilization almost equal to those of homogamic crosses, while sperm of *E. lucunter* were found to be able to fertilize eggs of the other two species. However, few *E. lucunter* eggs are fertilized by heterospecific sperm (Lessios and Cunningham 1993). In the wild *E. lucunter* and *E. viridis* maintain their genetic integrities despite having this unidirectional gamete isolation. Allozyme data placed the speciation event of the sympatric species after the rise of the isthmus. Thus there is no correlation between genetic divergence and strength of reproductive isolation (Lessios and Cunningham 1993).

Later work by McCartney and Lessios (2002) confirmed these findings and demonstrated a much stronger block to cross-species fertilization of *E. lucunter* eggs than was previously shown. They reported that gamete incompatibility in these species is weaker in sympatry than in allopatry, and based on the mtDNA data in McCartney et al. (2000), such gamete incompatibility in these species arose in the last 1.5 million years.

Zigler et al. (2008) looked at egg energetics, fertilization kinetics, and population structure in echinoids with facultatively feeding larvae. This work included *C. rosaceus*, one of only two echinoid species known to have facultatively planktotrophic larvae. The eggs of *C. rosaceus* resemble those of echinoid species with obligately feeding larvae in egg energetic density, egg buoyancy and fertilization kinetics, but resemble non feeding larvae in time to metamorphosis, the early formation of the coelom and the reduced allocation to larval feeding structures (Zigler et al. 2008).

Cross-fertilization experiments between *C. rosaceus* and *C. subdepressus* by Zigler et al. (2008) revealed that bidirectional gametic incompatibility has evolved between the two species. These species are commonly found together or within close proximity to one another in the shallow waters of the Caribbean in Panama (both species live in the sand, but *C. rosaceus* is typically more common in turtle grass beds). These species have no temporal reproductive isolation, as both have ripe gonads for much of the year, but with peaks from July to October (Lessios 1984). The results of Zigler et al. (2008) indicate that the small eggs of *C. subdepressus* are particularly resistant to fertilization by *C. rosaceus* sperm, while the larger *C. rosaceus* eggs are slightly more vulnerable to fertilization by *C. subdepressus* sperm, but at levels that are unlikely to result in conspecific fertilizations in nature.

Research on the sea urchin sperm protein bindin in sea urchin species found off the coasts of Panama has been conducted by Zigler and Lessios (2003a, b, 2004), McCartney and Lessios (2004), Zigler et al. (2005), and Geyer and Lessios (2009). Bindin is a sea urchin sperm protein that mediates sperm-egg attachment and membrane fusion. Across echinoid genera, its divergence has been shown to be correlated with heterospecific incompatibility in fertilization (Zigler et al. 2005).

In sympatric species, a region of the bindin molecule reportedly evolves at high rates under strong positive selection (Metz and Palumbi 1996), whereas in allopatric species (e.g. *T. ventricosus* in the Caribbean and *T. depressus* in the eastern Pacific), bindin variation was reported to be low, with no evidence of positive selection. However, this does not appear to be the case for all sea urchin species. *Lytechinus williamsi* and *L. variegatus*, which have overlapping distributions in the Caribbean, show no clear evidence of selection (Zigler and Lessios 2004). While in spatially overlapping *E. lucunter* and *E. viridis*, positive selection was only found to have accumulated along the bindin lineage of *E. lucunter* (McCartney and Lessios 2004). Further, Geyer and Lessios (2009) found no evidence to suggest that the source of selection on bindin in *E. lucunter* is reinforcement, as bindin showed no evidence of stronger selection in areas of sympatry relative to areas of allopatry. Geyer and Lessios (2009) propose that the evolution of this molecule is a result of the processes acting within species, such as sexual selection and sperm competition.

The reproductive cycle of the starfish *O. reticulatus* in Isla Solarte, Bocas del Toro Archipelago, was studied from February 2000 to February 2001 by Guzman and Guevara (2002a). Males and females with ripe gonads were observed almost every month, however, the gonad index revealed peaks in reproductive activity, during July, November, and January. Gonad maturation was not triggered by changes in water temperature (these ranged from 27 °C to 30 °C), but may have responded to chemical cues in the water (e.g. nutrients, salinity) (Guzman and Guevara 2002a).

Guzman et al. (2003) assessed the reproductive status of two commercial species of sea cucumber, *I. badionotus* and *H. (H.) mexicana* in the Caribbean of Panama. They reported that for both species the minimum reproductive length was 13–20 cm with a weight of 150 g. Both species were gonochoric with a 1:1 sex ratio. Gametogenesis and spawning occurred throughout the year; however there were periods of peak reproductive activity, between July and November for *I. badionotus* and from February to July for *H. (H.) mexicana* (Guzman et al. 2003).

4.3.3 Evolution

Molecular work on echinoids in Panama started with Lessios (1979), who used geminate species of Panama (*E. tribuloides* and *E. thouarsii*, *D. antillarum* and *D. mexicanum*, *E. viridis*, *E. lucunter* and *E. vanbrunti*) to test the molecular clock hypothesis. This hypothesis predicts that each protein changes at a constant rate, so that the degree of divergence between two species is linearly related to the time for which their lineages have remained separate (Wilson et al. 1977). Lessios (1979) found that this does not hold for Panamanian echinoids, as very different rates of divergence were found in the enzymatic proteins between geminates in the different genera. *Eucidaris* and *Echinometra* exhibited transisthmian distances

sixteen and thirty-seven times greater than intraspecific ones respectively, while the trans-isthmian distance in *Diadema* was twenty times smaller than for the *Echinometra*. Lessios (1979) proposed that the most plausible explanation was that the molecules used in this investigation were evolving under the influence of natural selection.

In 1981(b) Lessios combined this molecular work with morphometric data using twenty morphological measurements. The morphometric data showed that differentiation between members of each geminate pair are not significantly different from local variation within each species. However, the ratio of inter to intraspecific Mahalanobis distance was congruent with the molecular data, being lowest in *Diadema*, intermediate in *Eucidaris*, and highest in *Echinometra*. Morphological rates of divergence were found to be more rapid in sympatric species, possibly due to habitat separation between congeners (Lessios 1981b).

Bermingham and Lessios (1993) used mitochondrial DNA (mtDNA) and isozymes in these sea urchin species to measure the degree of divergence. Trans-isthmian isozyme divergence in the geminate pairs differed by an order of magnitude, while mtDNA divergence was equivalent in all pairs demonstrating that mtDNA can provide accurate estimates of time since separation (Bermingham and Lessios 1993).

After the mass mortality of *D. antillarum* in the Caribbean (see Sect. 4.6. Threats to echinoderms), Lessios (1985b) looked at the genetic consequences of the restriction in the genetic structure of populations. His results showed no loss of genetic variability to that recorded in the same populations of *D. antillarum* in 1977. Lessios suggested that organisms with planktonic larvae are likely to recover from local extinction events without significant losses of their genetic variability, as larval exchange allows re-seeding of affected areas by recruits not exposed to the bottleneck.

A phylogenetic survey of sea urchin retroviral-like (SURL) retrotransposable elements in 33 species of echinoid (regular sea urchins, sand dollars, and heart urchins) was conducted by Gonzalez and Lessios (1999). High ratios of synonymous to nonsynonymous substitutions suggest that the reverse transcriptase of the elements is under strong purifying selection (Gonzalez and Lessios 1999). They report that despite the predominance of vertical transmission, sequence similarity of 83–94 % for SURL elements from hosts that have been separated for 200 Myr suggests four cases of apparent horizontal transfer between the ancestors of the extant echinoid species. In three additional cases, elements with identical RT sequences were found in sea urchin species separated for a minimum of 3 Myr. Thus, horizontal transfer plays a role in the evolution of this retrotransposon family (Gonzalez and Lessios 1999).

Cytochrome oxidase I (COI) divergence was assessed in Atlantic and eastern Pacific *Echinometra* by McCartney et al. (2000), using the closure of the Isthmus of Panama to date cladogenic events. They reported that the Atlantic species *E. lucunter* and *E. viridis* diverged 1.27–1.62 mya at a time in the Pleistocene when sea levels fell and Caribbean coral speciation and extinction rates were high. The fact that these species split so recently, yet do not hybridize, demonstrates that

reproductive barriers between marine species can occur in less than 1.6 million years (McCartney et al. 2000).

A global molecular phylogeny of *Diadema* (including *D. antillarum* and *D. mexicanum* from Panama) was published by Lessios (2001) and Lessios et al. (2001). This molecular study showed that *Diadema* is composed of reciprocally monophyletic mtDNA clades, and that the eastern Atlantic *D. antillarum* (*D. antillarum*-b) from Madeira, Canary Islands, Cape Verde and Sao Tome is genetically distinct from the western Atlantic *D. antillarum*. These species are separated by the long stretch of deep water separating the eastern from the western Atlantic. *Diadema antillarum ascensionis* Mortensen, 1909 from the central Atlantic islands of Ascension and St. Helena was found to be genetically isolated, but nested within the Brazilian clade of the western Atlantic *D. antillarum*. Lessios suggests that the biogeographic barrier between the Caribbean and Brazil may be caused by the outflow from the Amazon and Orinoco Rivers. High levels of gene flow were reported among populations of *D. mexicanum* in the eastern Pacific, with *D. mexicanum* from the Galapagos and Cocos Island belonging to the same population as sea urchins from Panama and Mexico (Lessios et al. 2001).

A study of the phylogeography of the pantropical sea urchin *Tripneustes* by Lessios et al. (2003) showed that based on morphology, COI, and bindin data, *T. depressus* A. Agassiz, 1863 from the eastern Pacific is in fact the same species as *T. gratilla* (Linnaeus, 1758) from the western Pacific. The formation of the Isthmus of Panama, the deep water separating the eastern and western Atlantic, and the freshwater plume of the Orinoco and Amazon rivers between the Caribbean and the coast of Brazil were shown to be important barriers to the evolution of *Tripneustes*. However, the Eastern Pacific Barrier (5,000 km of deep water) between the central and eastern Pacific was unimportant in the subdivision in the genus.

A phylogeographic study of the genus *Lytechinus* by Zigler and Lessios (2004) using mitochondrial COI, and the entire molecule of nuclear bindin shows that the genus *Lytechinus* is paraphyletic (using *Toxopneustes* and *Tripneustes* as out-groups), with *Sphaerechinus granularis* (Lamarck, 1816) coming out as the sister species to *L. euerces* Clark, 1912. The authors propose that *L. euerces* should be moved into the monotypic *Sphaerechinus*, rather than placing *Sphaerechinus* in *Lytechinus* which would increase the range of the genus to the temperate eastern Atlantic and Mediterranean (Mortensen 1943a). *Lytechinus semituberculatus* (Valenciennes in L. Agassiz, 1846) and *L. panamensis* formed a clade with no distinction between the two species, while *L. anamesus* and *L. pictus* were also phylogenetically indistinguishable. A well supported Atlantic clade was formed of *L. williamsi* and the three subspecies of *L. variegatus* (*L. variegatus variegatus*, *L. variegatus atlanticus*, *L. variegatus carolinus*). *Lytechinus williamsi* from the Caribbean was found to share mtDNA haplotypes with *L. variegatus variegatus*, however, their bindin was shown to be distinct and to coalesce within each morphospecies. A small private clade of mtDNA was found in some *L. williamsi* from Panama and Belize. Zigler and Lessios (2004) suggest that this may be

indicative of former differentiation in the process of being swamped by introgression, or of recent speciation.

Molecular work on the starfish *A. planci*, including specimens from Panama, revealed that it is not in fact a single species, but a pan-Indo-Pacific species complex consisting of four deeply diverged clades (Pacific, Red Sea, Northern Indian Ocean, and Southern Indian Ocean) (Vogler et al. 2008). These clades reportedly diverged between 1.95 and 3.65 mya (Pliocene to early Pleistocene) and have genetic distances (8.8–10.6 %) equivalent to the distances between other sibling species of starfish (Waters et al. 2004). Vogler et al. (2008) propose that this speciation process was driven by sea level changes (Pillans et al. 1998) that isolated populations.

Zulliger and Lessios (2010) published a global phylogeny of the genus *Astropecten* based on 117 specimens belonging to 40 species. This genus is one of the most species-rich genera among starfish containing over 150 described species with six species recorded from Panama: *A. armatus* Gray, 1840, *A. articulatus* (Say, 1825), *A. cingulatus* Sladen, 1883, *A. exiguus* Ludwig, 1905, *A. fragilis* Verrill, 1870 and *A. regalis* Gray, 1840. Such diversity is remarkable, because most species of *Astropecten* have a long-lived planktotrophic larval stage. Consequently one would expect this to lead to a low speciation rate (Zulliger and Lessios 2010). Zulliger and Lessios (2010) compared their molecular phylogeny to Döderlein's (1917) morphological phylogeny. They found high levels of congruence on the whole, but many discrepancies on a local scale. Phylogenetic inference from their data reveals that that morphological and ecological convergence has taken place in *Astropecten*, resulting in allopatric non-sister taxa with similar morphologies and habitat preferences. Varieties of several species were also shown to exhibit genetic distances large enough to justify recognizing them as separate species.

Reviews on speciation in organisms separated by the Isthmus of Panama have been written by Lessios (1998, 2008). Lessios (1998) wrote a chapter in “Endless Forms: Species and Speciation” on the first stage of speciation as seen in organisms separated by the Isthmus of Panama. Lessios points out that although geminate species have had a long history of contributing evidence relevant to speciation, they remain an underutilised tool for understanding vicariant speciation. Lessios's (2008) review showed that a total of 38 regions of DNA have been sequenced in nine clades of echinoids, 38 clades of crustaceans, 42 clades of fishes, and 26 clades of molluscs with amphi-isthmian subclades. Of these, 34 clades are likely to have been separated at the final stages of Isthmus completion, 73 clades split earlier and eight clades maintained post-closure genetic contact (e.g. via a circumglobal route or through the Panama Canal). As no vicariant event is better dated than that of the Isthmus of Panama, molecular divergence between species pairs remains to be of great interest, particularly as adaptive divergence can be seen in species life history parameters.

4.4 Diversity and Distribution of Echinoderms

Chesher (1972) published a list of Pacific and Caribbean echinoids and identified potential geminate species pairs. Maluf (1988) synthesised and tabulated the composition and distribution of central eastern Pacific echinoderms from the literature, which has proved to be a valuable resource for researchers. Lessios (2005a) updated the records of echinoids found in the Pacific waters of Panama, and distinguished species that have been documented for Panama from those that have collection records that straddle Panama, but with no published records of actual presence in Panama. In the latter category Lessios (2005a) lists *Kamptosoma asterias* (Agassiz, 1881), *Plesiodiadema horridum* (Agassiz, 1898), *Cystocrepis setigera* (Agassiz, 1898), *Pourtalesia tanneri* Agassiz, 1898, *Homolampas fulva* Agassiz, 1879, *Echinometra oblonga* (Blainville, 1825) and *Encope perspectiva* Agassiz, 1841. The inclusion of *E. perspectiva* in this category is a mistake as it was collected in Panama from Playa Grande, on San Jose Island, Pearl Islands Archipelago by Clark (1946) and more recently by Coppard (2010) from the same location. *Plesiodiadema horridum* is listed in the Smithsonian, National Museum of Natural History collections as collected off Panama (USNM 21050). However, the coordinates of the collection site (3°09.00'N, 82°08.00'W) indicate that it was collected off Colombia. Lessios (2005a) gives details of why the subtropical *Centrostephanus coronatus* (Verrill, 1867) and central and western Pacific species *E. oblonga* are unlikely to occur in Panama, and that the record of *Caenocentrotus gibbosus* (Agassiz, in Agassiz and Desor, 1846) in Panama is a mistake in the literature.

Alvarado et al. (2008) assessed the diversity of echinoderms in the Caribbean of Central America and gave faunal lists for each country. Panama had the greatest species richness, with 154 species listed, comprised of 15 species of crinoids, 23 species of asteroids, 56 species of ophiuroids, 30 species of echinoids and 30 species of holothuroids. Among the crinoids they included both *Davidaster insolitus* Clark 1917 and *Davidaster discoideus* (Carpenter, 1888). The number of species of crinoids should be reduced to 14 because *D. insolitus* is currently considered a junior synonym of *D. discoideus* (Messing 2010). Among the asteroids, two species are missing from their list for Panama. These are *Echinaster (Othilia) echinophorus* (Lamarck, 1816) collected from Limon Bay (Smithsonian National Museum of Natural History, USNM 38235) and Fort Randolph (USNM E 26417, USNM E 26418), and *Persephonaster patagiatus* (Sladen, 1889) collected from the Gulf of Mosquitos (USNM E 31501). The number of ophiuroid species is incorrect as *Amphiodia riisei* (Lütken, 1869) [sic] is a junior synonym of *Ophiophragmus riisei* (Lütken in: Lyman 1860) (Stöhr 2010). Among the holothuroids they list *Thyone deichmannae* Madsen, 1941 and *Thyone inermis* Heller, 1868 which are junior synonyms of *Havelockia inermis* (Heller, 1868) (Hansson 2011). Although Alvarado et al. (2008) state that there are 30 echinoid species recorded from off the Caribbean coast of Panama they only list 29 species which agrees with more recent work by Coppard (2010).

Table 4.1 Number of echinoderm species recorded from Panamanian waters

| | Pacific | Caribbean | Both pacific and caribbean | Total |
|---------------|---------|-----------|----------------------------|-------|
| Crinoidea | 7 | 14 | 0 | 21 |
| Ophiuroidea | 75 | 51 | 4 | 130 |
| Asteroidea | 56 | 25 | 2 | 83 |
| Echinoidea | 49 | 27 | 2 | 78 |
| Holothuroidea | 73 | 27 | 2 | 102 |
| Total | 260 | 144 | 10 | 414 |

Alvarado et al. (2010) documented the echinoderm diversity in the Pacific coast of Central America, again providing faunal lists for each country. Although Alvarado et al. (2010) included the paper by Lessios (2005a) in their bibliography they unfortunately ignored Lessios's comments and tables. These indicate echinoid species that have distributions in the eastern Pacific that straddle Panama (but have not been recorded from Panama), those unlikely to occur in Panama, and errors in the literature. Alvarado et al. (2010) also incorrectly listed *Encope grandis* Agassiz, 1841 in Guatemala, El Salvador, Honduras, Nicaragua and Panama. This species is endemic to the Gulf of Mexico; *Encope michelini* Agassiz, 1841 in Costa Rica (this is an Atlantic species that occurs off Florida), *Dendraster excentricus* (Eschscholtz, 1829) in Panama (this temperate species has a distribution range from Alaska to Baja California), as well as including many junior and senior synonyms as separate taxa (e.g. *Ophionereis annulata* (Le Conte, 1851) and *Ophionereis dictyota* Ziesenhene 1940; *Sclerasterias alexandri* (Ludwig 1905) and *Hydrasterias diomediae* Ludwig 1905; *Lissothuria ornata* Verrill 1867 and *Thyonepsolus beebii* Deichmann, 1937). Alvarado et al. (2010) list 253 species of echinoderms from Panama, the country with the highest species richness in Central America. This is explained by the long coastline (1,690 km) of Panama which incorporates high levels of coastal heterogeneity and reflects the greater echinoderm research effort than in other Central America countries (Alvarado et al. 2010).

A web-based project by Coppard (2010) ("The Echinoderms of Panama") has documented 414 species of echinoderms that occur off the Caribbean and Pacific coasts of Panama (Table 4.1 and Appendix). This work was carried out in conjunction with the Encyclopaedia of Life and contains images (including type material), diagnostic descriptions and references with links to nomenclators, GenBank, Barcode of Life, and depth, distribution and specimen data. All species names were checked with the World Register of Marine Species and lists of junior synonyms are given. Where physical specimens were not found in museum collections, records from the literature were used.

Since the final closure of the Panama Isthmus unequal rates of speciation, extinction and migration have occurred in the Caribbean and Pacific, resulting in very different levels of biodiversity seen on either side of the isthmus today (Vermeij 1978; Jackson et al. 1996; Budd 2000). Among invertebrates, greater levels of diversity have been reported in the Caribbean than in the Pacific for

Fig. 4.9 *Nemaster grandis* with arms spread for feeding, Bocas del Toro, Caribbean Sea (photo courtesy of Edgardo Ochoa)



corals (Glynn 1982), sponges (Van Soest 1994), benthic foraminiferans (Collins 1999), cheilostome bryozoans (Cheetham et al. 2001) and cupuladriid bryozoans (O’Dea et al. 2004). With the exception of crinoids, the diversity of echinoderms off Panama shows a very different trend, with a far greater diversity in the Pacific (270 species) than in the Caribbean (154 species). The high diversity of crinoids in the Caribbean is most likely a consequence of greater coral reef development, which provides a broad range of suitable habitats for species such as *Nemaster grandis* (Fig. 4.9).

For the other classes of echinoderms, the greater number of species in the Pacific of Panama can partially be explained by a number of species having crossed the Eastern Pacific Barrier (e.g. *Toxopneustes roseus*, *Tripneustes depressus*, *Acanthaster planci*) and thus have a West Pacific origin, with no sister species in the Caribbean. However, in many genera, particularly those that contain mud and sand dwelling species, a genus in the Caribbean often contain one or two species, while in the Pacific the same genus will often have more than double the number of species (e.g. in Panama the genus *Luidia* has three species recorded from the Caribbean, but nine species from the eastern Pacific; *Astropecten*, two species from the Caribbean, four species from the Pacific; *Encope*, one species from the Caribbean, five species from the Pacific). The different hydrological conditions in the Gulf of Chiriquí and the Gulf of Panama have created high levels of coastal heterogeneity providing a diverse range of habitats. However, such morphological variation that has given rise to authors erecting many species names in the Pacific may simply reflect ecophenotypic variation within a species.

Sampling the sharp drop down the continental slope to a depth over 1,000 m just south of the Azuero Peninsula has resulted in a number of deep water species being recorded from the Pacific of Panama, such as sea lilies (e.g. *Calamocrinus diomedae* Agassiz, 1890, depth 1,430 m), brittle stars (e.g. *Astrodia plana* (Lütken and Mortensen 1899), depth 3,058 m; *Asteronyx loveni* Müller and Troschel, 1842,

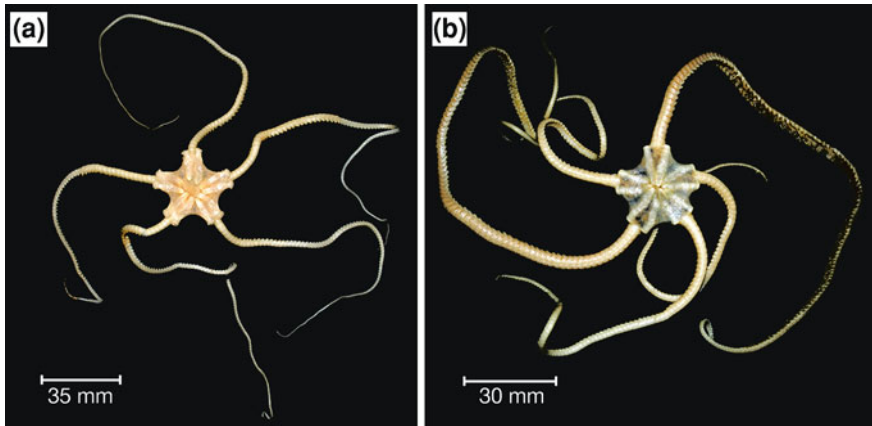


Fig. 4.10 Deep water ophiuroids, **a** *Astrodia plana* and **b** *Asteronyx loveni*

depth 1,866 m, Fig. 4.10), starfish (e.g. *Dytaster gilberti* Fisher, 1905, depth 2,690 m; *Pectinaster agassizi* Ludwig 1905, depth 2,323 m), sea urchins (e.g. *Salenocidaris miliaris* (Agassiz 1898), depth 3,058 m; *Caenopedina diomedea* Mortensen, 1939, depth 850 m; *Araeosoma leptaleum* Agassiz and Clark, 1909, 1,062 m) and sea cucumbers (e.g. *Molpadia spinosa* (Ludwig, 1893), depth 3,279 m; *Protankyra brychia* (Verrill, 1885), depth 4,000 m).

Ten species have collection records from both sides of the Panama Isthmus. These are the ophiuroid species *Hemipholis elongata* (Say, 1825), *Ophiactis savignyi* (Müller and Troschel, 1842), *Ophioderma panamensis* Lütken, 1859 and *Amphipholis squamata* (Delle Chiaje, 1828); the asteroid species *Linckia guildingii* Gray, 1840, *Ctenodiscus crispatus* (Retzius, 1805); the echinoid species *Moira atropos* (Lamarck, 1816) (the subspecies *Moira atropos clotho* Michelin, 1855 is recorded from the Pacific), *Meoma ventricosa* (Lamarck, 1816) (the subspecies *Meoma ventricosa grandis* Gray, 1851 is recorded from the Pacific); and the holothuroids *Holothuria* (*Thymiosycia*) *arenicola* Semper, 1868 and *Holothuria* (*Thymiosycia*) *impatiens* (Forskål, 1775). With the final closure of the isthmus (2.8 mya) there has been no gene flow between populations in the Pacific and Caribbean. However, the opening of the freshwater Panama Canal in 1914 provided a means for echinoderms to cross the isthmus, either as larvae in the ballast tanks of ships or associated with fouling organisms on the hulls of ships. Roy and Sponer (2002) found identical mtDNA haplotypes of *Ophiactis savignyi* in the Caribbean and Pacific. This led them to suggest that these sponge-dwelling brittle stars have been recently transported between oceans on the hulls of ships. Global phylogenies have also shown that genes of certain species have travelled around the world during the last 3 million years providing a connection between tropical species on the two sides of tropical America (Bowen et al. 2001, 2006; Lessios et al. 2001; Rocha et al. 2005).

Some echinoderm species have records in Panama that may represent transient populations. *Arbacia spatuligera* (Valenciennes, 1846) is recorded (specimen not examined) from the reef off French Fort (USNM 1017377), in Panama Bay. This may be a misidentification or represent a transient population of this species, with larvae carried up from Ecuador into the Gulf of Panama but with insufficient recruitment to establish a viable population. This species has therefore not been included in the Pacific data for Panama, since to the best of our knowledge it is the only record of this species in Panama. Records of *Lytechinus pictus* in Panama are probably erroneous. Mortensen (1921) described *L. panamensis* based on specimens he obtained from Taboga Island. Clark (1948) collected one specimen from Bahia Honda as well as one specimen from Gorgona Island, Colombia. However, Clark (1948) states that these may be specimens of *L. panamensis*, a view supported by Zigler and Lessios (2004) and Lessios (2005a). Lessios (2005a) reports that he has only seen two specimens of this species collected off Isla Saboga in the Perlas Archipelago (8°38'N, 79°03'W). Clark (1925) and Mortensen (1928–1951) speculated that *Lytechinus* from Peru and Ecuador may not be *L. semituberculatus* but *L. panamensis*, with the larvae of this species occasionally settling in the Gulf of Panama.

Panama is the type locality of 82 species of echinoderms (nine Caribbean, 73 eastern Pacific, one of these species occurs in both the Caribbean and Pacific). However, four of these species (starfish) are now considered subjective junior synonyms of other species. The majority of the Pacific species were established from Panamanian specimens in the late 1800s and early 1900s by authors such as Lütken and Mortensen (1899) and Ludwig (1894, 1905), as a result of the material collected on expeditions by the *Albatross*. The majority of new Caribbean species were discovered much later in the 1960s, 1970s and 1980s by authors such as Chesher (1968, 1970, 1972) and Hendler (1995, 2005), as a result of the laboratories of the Smithsonian Tropical Research Institute in Panama. In recognition of this, Hendler (2005) named the ophiuroid species *Ophiothrix stri* Hendler 2005.

4.5 Aquaculture and Fisheries

The sustainable aquaculture of echinoderms in Panama has not been developed. In 1997 the Panamanian government granted a permit for the harvesting and processing of bêche-de-mer (sea cucumbers) in Bocas del Toro. However, this exploitation was short lived, with the permit being revoked 30 days later. Nevertheless, in that short time period Guzman and Guevara (2002b) estimate that 750,000 sea cucumbers were harvested (based on 25 fishermen extracting an average of 1,000 and a maximum of up to 1,500 cucumbers day⁻¹). This consisted primarily of three species *Holothuria (Halodeima) mexicana*, *Isostichopus badionotus* and *Astichopus multifidus*. This quantity represents a biomass of ca. 180 tons (based on average body wet weight of 240 g). If such fishing pressure was permitted, Guzman and Guevara (2002b) estimate that stocks of the three

Fig. 4.11 *Astichopus multifidus* photographed in Bocas del Toro (photo courtesy of Juan Sanchez)



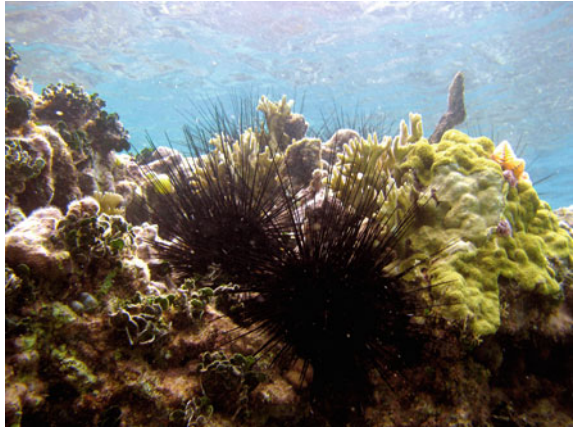
species of holothuroids would collapse within a very short period of time (305 days for *H. (H.) mexicana*, 221 days *I. badionotus* and only 9 days for *A. multifidus*), based on a catch effort of 25,000 ind day⁻¹ (Fig. 4.11)

Commercial bêche-de-mer fishing currently is banned in all Panamanian waters under Decree 157–2003. However, there are reports of illegal fishing activities, with five species being commercially exploited in Panama: *Actinopyga agassizi* (Selenka, 1867) *H. (H.) mexicana*, *A. multifidus*, *I. badionatus* (Caribbean) and *I. fuscus* (eastern Pacific) (Toral-Granda 2008). In Parque Nacional Marino Isla Bastimentos, *H. (H.) mexicana* showed a maximum density of 956 ind ha⁻¹ in 480 ha representing only 10 % of the shallow water protected area, while *I. badionotus* and *A. multifidus* were strikingly absent in 95 % of the protected insular area around Cayos Zapatillas. This indicates that that illegal fishing has taken place inside the park (Guzman and Guevara 2002b). Data from the statistics department in Hong Kong, revealed that 281 kg (dry weight) of bêche-de-mer were imported from Panama in 2004 and 408 kg (dry weight) in 2005 (Toral-Granda 2008).

4.6 Threats to Echinoderms

Between 1983 and 1984, *D. antillarum* suffered one of the most extensive and severe mass mortality events ever recorded for a marine animal. This was probably caused by a waterborne pathogen transported by ocean currents, since plots of surface currents in the Caribbean Sea coincided with the spread of the die-off (Lessios 1988; Miller et al. 2003). The mass mortality of *D. antillarum* has been a major factor leading to a shift from coral-dominated to algae-dominated communities on many Caribbean reefs during the past 20 years (Lessios 1988). The die-off was first observed in January 1983 at Galeta Point, near the entrance of the Panama Canal. In approximately three months it had extended to the San Blas Archipelago, before reaching the Panama-Colombia border by the end of June. By

Fig. 4.12 *Diadema antillarum* on a reef in San Blas, depth 2 m, June 2010



January 1984 the die-off had spread throughout the rest of the Caribbean with population densities in Panama reduced to 5.8 % of their previous levels (Lessios et al. 1984a). The first symptom of the presumed disease was accumulation of sediment on the spines and sloughing off of the spine ectoderm. This was followed by loss of pigmentation in the skin covering the spine muscles, the peristome, and in the periproctal cone. Spines became brittle and broke, while others fell off completely, exposing areoles and tubercles. Tube feet became flaccid, no longer retracted fully upon stimulation, and were unable to cling to the substrate. Many individuals at this stage were found on their sides or being moved to and fro by the surge. In advanced stages large patches of skin peeled off the test, the peristome and the anal cone lost practically all pigmentation, and the spines could be pulled off with little force (Lessios et al. 1984b).

Before the mass mortality, mean densities of *D. antillarum* on reefs at Punta Galeta and San Blas were 1.82 and 1.91 ind m⁻², respectively (Lessios et al. 1984b). After the mass mortality the densities dropped to an average of 0.05 ind m⁻² in San Blas, and to 0.004 ind m⁻² in Punta Galeta. This density reduction was not observed in other species of echinoids (*E. lucunter*, *E. viridis*, *Echinoneus cyclostomus* (Leske, 1758), *E. tribuloides*, *L. variegatus* and *T. ventricosus* (Lamarck 1816)) on the same reefs. In San Blas, the mean sizes were reduced from 48.6 mm to 25.0 mm (Lessios et al. 1984b). However, this mass reduction on the population did not have any consequence on its genetic variability (Lessios 1985b).

Five years after the event, Lessios (1988) did not observe any recovery of the populations on the San Blas reefs, with little influx of juveniles and no increase in population densities of other sea urchins species (*E. viridis*, *E. lucunter*, *E. tribuloides*, *T. ventricosus*, or *L. variegatus*). He reported no alteration in the reproductive behaviour of *D. antillarum*, proposing that the low recruitment success could be an effect of low populations densities and low adult numbers.

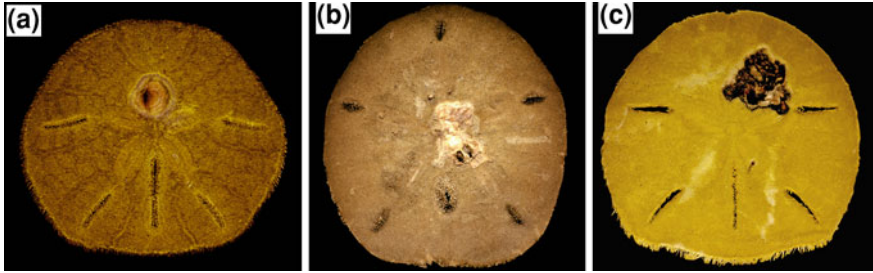


Fig. 4.13 Mellitid sand dollars showing varying degrees of predation and secondary infection, **a** *M. longifissa*, collected alive (sublethal predation), **b** *E. laevis* (lethal predation, no secondary infection), **c** *M. kanakoffi*, found dead (probable death from secondary infection due to the large amount of necrotised tissue)

Ten years after the mass mortality densities remained at less than 3.5 % of their pre-mortality levels, with *D. antillarum* being absent in its preferred habits in San Blas (Lessios 1995). Moreover, the mean size of individuals remained low (17.3–35.2 mm). This was thought to be a direct result of the disease, as food availability was not a limiting factor (Lessios 1995).

Twenty years after the mass mortality populations remained at less than 6.5 % of their pre-mortality levels in San Blas (Lessios 2005b). Some successful recruitment events have been observed on a few reefs. However, these have not been sustained over time (Lessios 2005b). The lack of apparent recruitment could have been caused by too few adults in upstream areas to reproduce at a rate that would overcome the normal sources of mortality (the Allee effect) or by the continuing presence of the pathogen that devastated the populations in 1983–1984. Recent observations (2010) on some San Blas reefs indicate a slight recovery (Fig. 4.12), however, it remains to be seen if these populations will be sustained.

On 27 April 1986 more than 8 million liters of crude oil spilled into a complex region of mangroves, seagrasses, and coral reefs east of the Caribbean entrance to the Panama Canal (Jackson et al. 1989). At the seaward edge, numbers of the most abundant sea urchin *E. lucunter* was reduced by 80 % within a few days of the spill, and the reef flat was littered with its skeletons (Jackson et al. 1989). However, further inshore no such mortality of *E. lucunter* was reported (Jackson et al. 1989).

During 2008–2009 Coppard (unpub. obs.) found large numbers of dead and dying sand dollars of the genera *Encope* and *Mellita* washed up on beaches from Punta Abreojos, Baja California Sur, Mexico, to Santa Elena Bay, La Libertad in Ecuador in the eastern Pacific and off Costa Rica and Belize in the Caribbean. In Panama dead mellitid sand dollars were found at Playa Las Lajas in the Gulf of Chiriqui, but not on beaches in the Gulf of Panama. These dead sand dollars were unusual in that they appeared to have an infection that originated at one or more circular denuded regions on the aboral surface of the test (Fig. 4.13a). The cause of such scars is most likely the result of attacks by gastropods from species such as

Northia pristis (Deshayes in Lamarck, 1844) and *Polinicies* sp. in the Pacific and *Cassia tuberosa* (Linneaus, 1758) in the Caribbean which have been reported to attack, and bore into the tests of mellitid sand dollars (McClintock and Marion 1993; Sonnenholzner and Lawrence 1998). Attacks always occurred on the aboral surface, and in the majority of cases centred over one or more petals. When the gastropods managed to bore through the test into the coelom (Fig. 4.13b), death of the sand dollar resulted. However, the presence of multiple scars of varying size indicates that such attacks are not always lethal. Following such attacks bacteria infected the majority of wounds which became dark green or black as a result of necrosis (Fig. 4.13c).

In many instances where the coelom had not been penetrated, the bacteria in the wound spread and caused the death of the sand dollar. Such pathogenic bacteria may be similar to that reported in *Meoma ventricosa* in Curaçao by Nagelkerken et al. (1999). In this instance a tetratoxin-producing bacterial strain of the genus *Pseudoalteromonas* was found in the sediment and was ingested by *M. ventricosa*. The density of such strains of bacteria may have increased as a result of the outflow of polluted water from the harbour.

In Bocas del Toro, only 2.8 % of the shallow habitats in the archipelago are within the protected area (Guzman and Guevara 2002a). Since 1997, coastal environments in Bocas del Toro have changed, as infrastructure such as roads, marinas, and hotels have developed. Destruction of these seagrass habitats is resulting in an increase in runoff and sedimentation in the coastal zone (Guzman and Guevara 1998). This has already started to affect the coral reefs (Guzman and Guevara 2001), and could potentially modify the function of the remaining coastal ecosystems.

The illegal harvesting of sea cucumbers continues to put pressure on the remaining populations particularly on the Caribbean coast of Panama, along the coastal perimeter of Laguna de Chiriquí, from the point of Península Valiente through the southern section of Isla Popa and Cayo Agua (Cruz 2000; Guzman and Guevara 2002a).

4.7 Conclusions and Recommendations

Echinoderm diversity in Panama is reported to be greater on both the Caribbean (Alvarado et al. 2008) and eastern Pacific coasts (Alvarado et al. 2010) than in other Central American countries. The length of coastline, with high levels of coastal heterogeneity may explain high levels of species richness. However, this diversity relative to other Central American countries is probably more of a reflection of the research effort that has taken place in Panama. The first phase of echinoderm research in Panama began in the late 1800's with the collections made by the U.S. Fish Commission Steamer *Albatross* in the eastern Pacific. This period of exploration resulted in many new species being described. The second phase of echinoderm research in Panama in the 1930's and 1940's continued to explore the

diversity of species and was the result of expedition by the New York Zoological Society and the Allan Hancock Foundation. These expeditions resulted in the collection of a vast number of specimens (some 28,835 echinoids alone from eastern Pacific of the Americas) with the description of many new species. The third phase of echinoderm research in Panama began with the inception of the marine program at STRI in 1961. This has resulted in extensive ecological and evolutionary echinoderm research, which has increased knowledge of echinoderms not only in Panama, but in many countries in tropical America, and other regions in the Atlantic and Pacific. Most of this knowledge concerns the ecology, reproduction and evolution in echinoids and certain species of asteroids (e.g. *A. planci* and *O. reticulatus*). However, less is known about holothuroids, ophiuroids and crinoids, particularly on a molecular and ecological level, highlighting a need for more research in these classes of echinoderm.

The continued monitoring of populations of *Diadema antillarum* needs to be maintained to determine whether the recently observed population increase is sustained, while the monitoring of sea cucumber populations, particularly in Bocas del Toro is needed to protect against illegal fishing. Guzman and Guevara (2002b) have proposed that protected areas should be established allowing the monitoring of natural populations. These could be part of the Parque Nacional Marino Isla Bastimentos (PNMIB) or may be located close to fishing communities willing to protect the resource.

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