

Peter Vine

Abstract

In this chapter the author reflects on five strands of marine biological research in which he was involved in the Red Sea and reviews subsequent progress in their respective fields. He presents his own findings and those of other biologists on: (1) Crown of Thorns starfish (*Acanthaster planci*) outbreaks; (2) Corals-v-algae and the influence of herbivorous fish on the outcome; (3) Corals-v-sponges and the ecological impact of the battle for dominance; (4) General reef ecology and conservation; and finally, (5) Taxonomy of Red Sea marine life. There have been substantial scientific developments in all the fields covered. Whilst we know much more than we did in the 1960s and 1970s, when much of the coral-reef research effort in the Red Sea was in its early stages, there are many questions still unanswered. Research continues, taking advantage of modern technologies, revealing the rich complexity and dynamic nature of the Red Sea's coral reefs.

Introduction

The Red Sea is like a living laboratory for tropical marine research, offering a wide range of environments, from sheltered muddy inlets to vertiginous coral drop-offs. Its remarkably clear waters and rich assemblages of fish and invertebrates attracted attention of European scientists as far back as Danish naturalist Peter Forsskål (1732–1763), who died during the 'Arabia Felix' expedition in Yemen. His collection, or surviving remnants of it, eventually arrived in Copenhagen and formed the starting point for many subsequent studies (Vine and Schmid 1987).

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Arriving in Port Sudan in 1970 in order to join the Cambridge Coral Starfish Research Group (CCSRG), the author had previously spent a year on Tarawa atoll in Kiribati (then known as the Gilbert and Ellice Islands) and a year based at James Cook University in Townsville, Australia. Tarawa provided a unique introduction to SCUBA diving among coral reefs that was consolidated during a Rotary Fellowship year (1969) on Australia's Great Barrier Reef, together with the oceanic islands of Melanesia, Micronesia and Polynesia. Port Sudan's marine life had already been popularised by the exploits of Dr. Hans Hass and his wife Lotte, together with Cmd. Jacques Cousteau and the crew of Calypso. The latter had built an underwater house on nearby Shaab Rumi ('Roman Reef') and their books and television films had inspired a young generation of underwater explorers.

CCSRG was a loose affiliation of young British biologists and diving enthusiasts that was led by its chairman, Dr. Christopher Roads and Scientific Director, Rupert Ormond. The present author fulfilled the role of deputy director for two years, prior to becoming director of a new marine laboratory established by Khartoum University at the ancient, deserted city of Suakin. What Sudan offered was easy access to some of the world's most prolific coral reefs: Sanganeb, Shaab Rumi, Wingate, Towartit and the islands of the Suakin Archipelago. CCSR's *raison d'être* was to investigate the ecological triggers resulting in large aggregations of *Acanthaster planci* (Crown of Thorns starfish: COTS) that were being reported in 'plague' numbers on coral reefs right across the Indo-Pacific.

In order to understand the population dynamics of COTS it is necessary to gain an appreciation of coral reef ecology in general, especially the various forces at play governing the recruitment and survival of corals, crustose coralline algae (CCA), invertebrates such as COTS and their predators (at all stages of their life-cycle). In 1970, when I started my work in the Red Sea, there were huge gaps in our knowledge of these criteria and 'scientific' conclusions often took the form of unsubstantiated hypotheses rather than data-driven factual analysis.

During the course of my Red Sea research we raised COTS larvae from the eggs; studied the starfish's larval responses to a range of physical and chemical factors; studied fish predators of COTS; investigated the ecological impact of aggressive behaviour by damselfish; demonstrated the ecological significance of CCA; collected serpulid tube worms, naming a new genus and four new species (Vine 1972); studied competition between corals, sponges and algae; monitored growth rates of coral colonies on Cousteau's garage at Shaab Rumi (Vine and Head 1977); and tested systems for raising Tilapia (*Sarotherodon niloticus*)—normally a freshwater fish—in the saline waters of the Red Sea.

This research was facilitated by a number of supportive organisations including CCSRG (partially funded by the UK Government's Overseas Development Administration—ODA); Khartoum University's Suakin Marine Biology Laboratory and the joint Saudi-British Fisheries Development Project, based in Jeddah.

There have been numerous advances in the various strands of research that I pursued almost 50 years ago and I welcome the opportunity to revisit some topics of my early research and show where they have led since that time. I believe that there are lessons to be learnt from such an initiative, particularly in connection with the first topic of this chapter that deals with outbreaks of COTS, but also in relation to an appreciation of the physical and biological dynamics of a 'balanced' reef system. Little did I appreciate, when studying the aggressive behaviour of reef 'farmers' (such as *Stegastes nigricans*), that this would reveal how their activities impact on both the physical structure of shallow reefs (poorly cemented due to CCA exclusion) and their attractiveness (or lack of it) to larvae of both corals and COTS as settlement sites (owing to exclusion of CCA by 'farmed' filamentous algae).

Crown of Thorns Starfish (*Acanthaster planci*) Outbreaks

The Crown of Thorns starfish (*Acanthaster planci*) (COTS) (Fig. 13.1) was first mentioned by Rumphius in 1705 and described by Plancus and Gualtieri in 1743. The name *Acanthaster planci* was created by Linnaeus in 1758. The species rose in notoriety in the late 1950s and early 1960s when large numbers were recorded at popular tourist destinations such as Green Island off Cairns, in 1959, and other reports soon followed, describing widely distributed outbreaks right across the Indo-Pacific. Professor Thomas Goreau first reported on Red Sea aggregations in 1963.

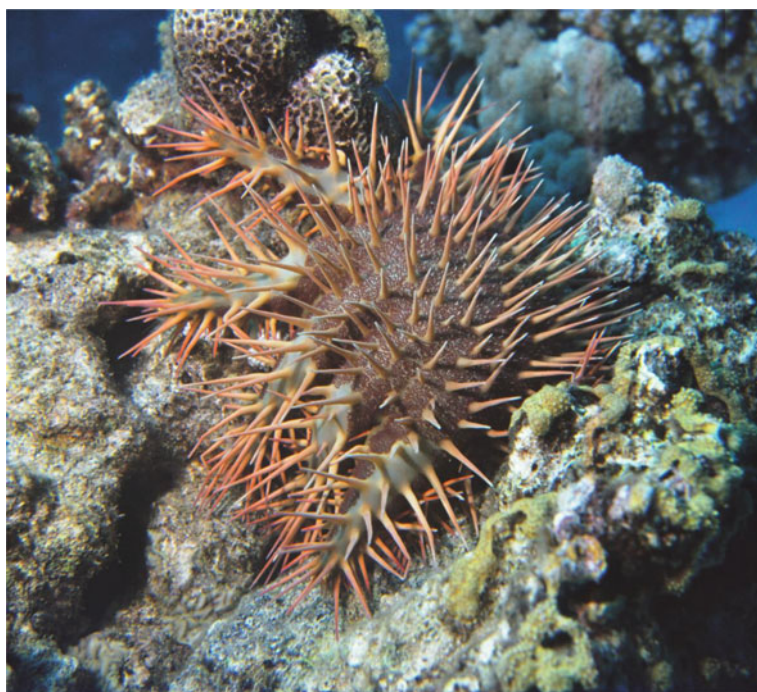
Our familiarity with life on coral reefs (and particularly COTS) can be traced back to the introduction to the general public of SCUBA (self-contained-underwater-breathing-

apparatus), starting in the mid-1950s when proponents could be counted in the hundreds rather than thousands or millions. Sixty years later, in 2016, there were approximately 6 million active SCUBA divers and 20 million snorkelers worldwide and marine watersports were among the fastest growing sectors of the leisure/tourism industry. There were several key events along the way with books and films playing a major role. Hans Hass's book *Diving to Adventure* was first published in German (*Drei Jäger auf dem Meeresgrund*) in 1939 and republished in English (translated by Barrows Mussey) in 1952 (Hass 1952a). It described Hans Hass's early adventures in the Caribbean and off Curaçao. In the same year his first account of diving in the Red Sea was published in English (Hass 1952b). Hass played a big role in popularizing diving during its early stages of development. The British Sub Aqua Club was founded in 1953 and wetsuits first became available to the public in 1956. In the United States, the National Association of Underwater Instructors (NAUI) was founded in 1959 whilst PADI (the Professional Association of Diving Instructors) was established in 1966. Cousteau's *Silent World* film, partially shot in the Red Sea, received an Academy Award for Best Documentary Feature and the Palme d'Or award at the Cannes Film Festival in 1957. Scubapro introduced the stabilization jacket (BC or BCD) in 1971, followed by the dive computer in 1972. Cousteau's famous Conshelf 2 experiment in underwater living took place in 1963 at Shaab Rumi reef in the Sudanese Red Sea. By the early 1960s SCUBA diving was an integral part of the tourism offering from the Red Sea and Indian Ocean, right across the Pacific and into the Caribbean. Humankind was enthusiastically exploring and discovering a new world full of colour, adventure and beauty—a world that had existed for millennia but which had been tantalizingly out of reach until SCUBA changed everything.

Reports of aggregations of COTS not surprisingly mirrored this rapid increase of underwater observers. The mere 'discovery' of 'new' starfish outbreaks (i.e., previously unreported aggregations) was offered as evidence that reefs were facing unprecedented threats of imminent destruction. There were few voices questioning this apparently simplistic analysis and vested interests, particularly in terms of research grant applications (Sapp 1999), appeared to obstruct a more balanced examination of the cause of the ominous starfish aggregations that so alarmingly transformed once flourishing reefs to blanched desolate seascapes. The massive scale of COTS outbreaks on the Great Barrier Reef and other Indo-Pacific reefs caught the attention of world media, the general public and a somewhat perplexed scientific community.

The 'noise' around COTS during the early 1970s included claims that this was the beginning of the end for the world's coral reefs! Theo Brown (Brown and Willey 1972)

Fig. 13.1 The Crown of Thorns Starfish *Acanthaster planci* adult in the Sudanese Red Sea (© Sjoeholm)



wrote as follows: “As the infestation is allowed to spread unchecked, I believe the ultimate survival of the reef is in doubt. I believe the starfish plague is the first of a series of major ecological disturbances that will have far reaching and devastating effects on mankind. Perhaps through the Crown of Thorns infestation, we are witnessing the beginning of the end.” Peter James authored a book on this subject (*Requiem for the reef: The story of official distortion about the Crown-of-Thorns starfish*. James et al. 1976).

A well-balanced analysis of the debate surrounding COTS is provided by Ian Sapp (1999) in *What Is Natural? Coral Reef Crisis*.

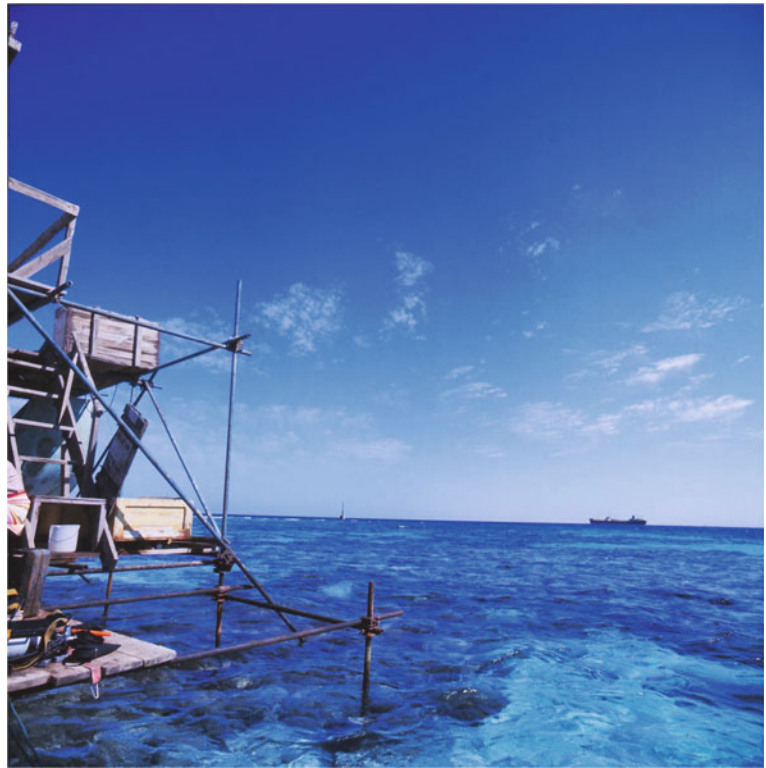
Joining the Cambridge Coral Starfish Research Group (CCSRG) (Fig. 13.2) in 1971, the author had been following with interest a public debate between Richard Chesher (Chesher 1969), Thomas Dana (Dana et al. 1972) and William Newman. Chesher favoured the view that, more often than not, Man had a direct hand in the population explosions being witnessed throughout the Indo-Pacific and therefore the starfish should be controlled. He suggested that starfish larvae are heavily preyed upon by live coral polyps and that predatory pressures may have been reduced by mechanical damage to reefs, such as reef blasting. On the other hand, Newman and Dana held the view that they were primarily natural events in the long-term life of coral reefs (Dana et al. 1972). Thomas Dana published evidence of previous aggregations and proposed that a likely trigger for reef disturbance, leading to *A. planci* outbreaks, was storm damage caused by cyclones and wave surge that could also wreak havoc on shallow reefs, uprooting and killing many coral

colonies. In a letter to the present author, Dana emphasized that this could be one of several natural events that trigger the outbreaks. “...if we have a potentially unstable situation, a number of parameters need to be considered, and perhaps all will form part of the model. We think storms are involved —typhoon, rain and wave types, but this does not exclude the other involvements” (pers. comm.).

The Scientific Director of the CCSRG, Dr. Rupert Ormond (Ormond and Campbell 1974), discussed the possible outbreak mechanisms for COTS and proposed a ‘Special Instability’ hypothesis that draws attention to a feedback mechanism whereby coral-eating starfish also create habitats (bare feeding scars) that are potential sites for even greater numbers of settled larvae. It has since been shown that the COTS larvae most frequently settle on pink coralline algae (e.g., *Porolithon* or *Hydrolithon*) that tend to colonise newly exposed surfaces of dead coral, playing a crucial role in cementing the reef structure. The pivotal significance of CCA on coral reefs is an integral part of the COTS story and is discussed in relation to several topics covered in this chapter.

By the early 1970s COTS was a global media phenomenon heavily laden with unsubstantiated claims regarding causes and extent of outbreaks. Despite reports of widely scattered aggregations of COTS on Indo-Pacific coral reefs, there was mounting evidence that many of these could be natural events and as such may well, in the medium to long term, be a contributor to reef development rather than reef destruction. The author’s views, as presented in a number of publications (Vine 1970, 1973), aligned in most respects

Fig. 13.2 Cambridge Coral Starfish Research Group (CCSRG) Platform (Head and Ormond 1978) on Harvey Reef provided a living laboratory to study life on the reef (© Vine)



with those of Ormond and Campbell, together with Newman and Dana, in acknowledging the likelihood that *A. planci* aggregations are fundamentally naturally occurring events that may also be triggered by reef disturbances attributable to Man.

Our knowledge and understanding of COTS has been greatly advanced by the many studies that have taken place since the early spate of studies in the late 1960s and early 1970s. First of all, we now know that there are effectively four species of COTS in the Indo Pacific, as demonstrated by mitochondrial clades, from the Red Sea, the Pacific (Pac), the Northern (NIO) and the Southern Indian Ocean (SIO) that, taken together, form a species complex (Vogler et al. 2008).

In a Letter to Nature published in 1978, Richard Moore set forth his view that *A. planci* outbreaks are naturally occurring events. “I believe that a more detailed consideration of the ecology of *A. planci* ... suggests violent population fluctuations without the assistance of Man’s activities.” It was a theory that he developed over the next ten years, finding much evidence to corroborate his early observations (Moore 1978).

In terms of effort, endurance, tenacity and scientific achievement, attention must be drawn to the impressive report by Moore of the Queen Mary College 1984 Red Sea Expedition to Dungonab Bay entitled ‘A Study of an Outbreak Area of the Crown of Thorns Starfish’ (Moore 1985). After conquering a long list of logistical challenges that

included rescuing a heat-exhausted team member from the sea, being left to carry on alone, sailing off one of Sudan’s most remote and poorly charted coastlines, suffering a terminal breakdown of the expedition’s compressor, self-medicating for potentially crippling ‘coral ear’ and finding that his underwater camera had not produced a single usable picture, he modestly reports: “In spite of this catalogue of mishaps, far more research was implemented than on previous visits to Dungonab Bay, and the original objectives of the expedition were largely fulfilled. In all, perhaps 15 man-days of field work were realized, including the surveys of reefs between Port Sudan and Dungonab” (Moore 1985).

Rick Moore’s study of Dungonab confirmed previous observations of the common occurrence of COTS in the bay and of the impact of food supply on their behaviour. Where live corals were scarce, the starfish tended to remain exposed in daytime, feeding on a range of items, including soft corals. In areas with a healthier coverage of scleractinian corals, the starfish remained hidden in daytime, emerging to feed at night. He showed that the nutrient-rich shallow waters of Dungonab Bay area, well known as a spat collection and nursery area for pearl oysters, were also a long-term source of *A. planci* larvae that could seed COTS outbreaks on an annual basis. He noted evidence for larval settlement close to the entrance of the bay and suggested that localized changes in temperature or salinity (that are quite marked in this area) could stimulate settlement of the

brachiolaria larvae. As for those larvae that drift out of Dungonab Bay and enter the main body of the central Red Sea, Moore drew attention to a gyre that sweeps from outside Dungonab, across toward Jeddah, then down past the Farasan Bank and back to Sudan where it flows northward from Suakin and Port Sudan, completing the circle off the Mohammad Quol area. He pointed to the common occurrence of COTS on the Farasan Bank, suggesting that this population might have seeded an outbreak off Port Sudan in 1970.

Given the special instability of their recruitment figures and the widespread occurrence of ‘plagues’, an increasing number of scientists felt it unlikely that dense aggregations of COTS had not occurred naturally, long before Man’s impact on coastal environments reached the levels we see today. Natural events such as previous climate change, sea level alteration, hurricane damage or volcanic activity might all be expected to disturb the ecological balance, impacting survival of reef fishes and invertebrates, and from time to time triggering COTS outbreaks. Coral reefs have lived with this threat for a very long time!

Anthropogenic impacts, perceived as potentially creating similar impacts to natural events, include pollution, run-off (caused by agriculture or coastal developments), ocean warming, acidification, dive tourism, anchoring, dredging, reef blasting and over-fishing—all of which exact their toll on healthy ‘natural’ coral reefs and may lead to COTS (Dulvy et al. 2004) outbreaks.

The overriding question remains: by what mechanism does the normal ‘control’ on COTS populations break down, triggering the massive aggregations that can wipe out nearly all the live corals along wide sections of coral reef?

Zann et al. (1987) studied juvenile *Acanthaster* on reefs in Fiji. They found juveniles ‘hiding’ among loose algal encrusted coral rocks on the reef front, on the bases of dead *Acropora* in more sheltered locations and among the interstices of the crevices on the reef crest. Recruitment was studied over a nine-year period and was shown to be normally very low, with 8 month-old juveniles recorded at 0.004 per m² in the boulder zone. However, a massive recruitment occurred in 1984, resulting in densities of 7 month-old juveniles at 8.3 per m² in the same zone. By measuring, over a two-year period, sizes of individuals in the ‘outbreak cohort’, they demonstrated a sigmoidal growth curve with maximum diameter increases of “2.6, 16.7 and 5.3 mm/month in the algal-feeding, early coral-feeding and adult phases, respectively”. At 13–15 months, the young starfish switched from feeding on coralline algae to feeding on scleractinian corals but they continued in their cryptic behaviour, withdrawing into crevices in daytime and generally being more active at night. This finally changed at around 20 months when they formed aggregations and could be seen out on the reefs during daytime. By this stage they

were almost ready to breed, becoming sexually mature at 23 months. Zann and colleagues concluded that recruitment is erratic and that an outbreak results from a “single massive settlement”.

Scientists have proposed a number of possible causes of massive settlement and survival (Moran 1986). Run-off of nutrient rich waters associated with coastal flooding may boost growth rates and hence survival at planktonic and early settled phases. There is experimental evidence to suggest that COTS outbreaks are predominantly controlled by phytoplankton availability. Heavy rain causing run off to the sea of nutrient rich water may lead to COTS outbreaks since it is known that larval development and growth is directly affected by the concentration of the phytoplankton on which COTS larvae feed. It has been shown, for example, that doubling concentrations of large phytoplankton can create an almost 10-fold increase in larval development, growth and survival of COTS.

Rising sea temperatures (Raitsos et al. 2011) shortening the time larvae spend in the plankton, or juveniles spend as vulnerable algal feeding bottom-dwellers, have also been proposed as potential population growth triggers (Uthicke et al. 2015). The latter showed that in a nutrition medium containing 5,000 cells per ml, “a 2 °C increase may shorten developmental time by 30% and may increase the probability of survival by 240%. The main contribution of temperature is to ‘push’ well-fed larvae faster to settlement.” They concluded that warmer sea temperatures connected to climate change are important co-factors promoting COTS outbreaks.

However, there seems to be two schools of thought with regard to the possible impact on COTS of a 2 °C temperature rise. Whilst Uthicke et al. (2015) indicate that such a rise may speed larval development and survival, Kamya et al. (2014, 2016) draw attention to a negative impact of such heightened temperatures on late stage brachiolaria larvae.

They (Kamya et al. 2014, 2016) have focused on predicting possible side-effects of ocean warming on COTS. Reporting on experiments to examine the effects of temperature and acidity on larvae of *Acanthaster*, they showed that whilst there was no impact on fertilization or early larval development of 30 °C and pH 7.6, there was a marked negative impact on later larval stages—a contrary finding to that of Uthicke et al. (2015).

Conjecturing that such a 2 °C rise might lead to a *reduction* in COTS success on low latitude coral reefs (where sea temperatures are expected to reach these levels), they also suggest that the warmer seas may result in migration of the starfish to higher latitude coral reefs where temperatures are closer to 28 °C. They also point out that *Acanthaster* has a higher tolerance to temperature rise than do most reef building corals. This work may be of particular relevance to the central and southern Red Sea where temperatures are

already higher than at comparable latitudes of the open Indo-Pacific Ocean and where a sudden 1 °C rise has recently been reported.

Raitsos et al. (2011) reported an increase of 1 °C over the previous 15 years in the Red Sea, resulting in both bleaching and a 30% reduction in coral growth—a trend that threatens to halt coral growth in the central Red Sea by 2070, especially in proximity to cities such as Yanbu, Jeddah, Gizan, Aqaba, Eilat, and Port Sudan (Sawall and Al-Sofyani 2015). Where such changes result in algal dominance over reef-building corals, COTS may be expected to experience significant recruitment fluctuations, accompanied by a probable decrease in coverage of live corals.

In a further development of this work Kanya et al. (2017) pointed to another potential set-back for COTS in the form of increased acidity of ocean waters (OA). More acid waters are expected to negatively impact on the CCA on which many juvenile *Acanthaster* depend for food (and, incidentally, coral larvae depend for settlement). Meanwhile, the increased acidity may enhance feeding rates by COTS's herbivorous juveniles (Uthicke et al. 2013). This team found that settlement of COTS larvae “was significantly reduced on crustose coralline algae (known settlement inducers of COTS) that had been exposed to OA conditions for 85 days prior to settlement assays”. Reduced settlement may be the largest bottleneck for overall juvenile production and their results indicate that “reductions in fertilization and settlement success alone would reduce COTS population replenishment by over 50%”. They conclude however that it is “unlikely that this effect is sufficient to provide respite for corals from other negative anthropogenic impacts and direct stress from OA and warming on corals”.

A complicating factor in predicting the impact of such changes is that COTS' ability to withstand or adapt to the environmental changes associated with projected climate change effects (raised sea temperature and lowered pH levels) has been shown to differ, depending on parental identity (Sparks et al. 2017).

Given the dramatic impact of increasing phytoplankton cell concentration in seawater containing COTS larvae (see above), it is not surprising that the presence of heightened concentrations of nutrient-rich waters is a major suspect behind outbreaks of the starfish. The impact of nutrient levels was also suggested by Birkeland (1982) as a key factor in boosting larval development and survival. A boost in nutrient levels caused by run off during the breeding season, especially around mainland associated islands rather than on offshore reefs, might lead to high larval survival, settlement and early growth. Resulting outbreaks of COTS might become obvious, in terms of recorded numbers of adults, one to two years after such heightened nutrient levels boosted larval survival. Wolfe et al. (2017) have however

questioned this, showing that eutrophic levels are not required for outbreak conditions.

COTS larvae have been successfully raised on a monoculture diet of phytoplankton such as *Dunaliella primolecta* (M. Barker, pers. comm. 1973; Yamaguchi 1973; Lucas 1982, 1984). They may remain in the plankton for as short as ten days or as long as 50 days, depending on a variety of environmental factors, including sea temperature and density of phytoplankton food.

As many authors have asserted, it is hardly surprising that *A. planci* populations are known to undergo dramatic changes and they are not alone among echinoderms in this regard (Calderwood et al. 2016). The intrinsic nature of their reproductive biology plays a significant role in their tendency to undergo sudden population explosions (Ormond and Campbell 1974). Ormond et al. (1973), noting the chemical attraction of other COTS to a feeding starfish, considered the local mini-aggregations could result in greatly increased fertilization success in breeding individuals, otherwise widely spaced on the reef. A single individual may release over a million eggs during one spawning episode and up to 50 million in a single season. “Outbreking populations (ca. 100000 starfish per reef) will kill thousands of square metres of coral, equivalent to hundreds of kilograms' dry weight of soft tissues per day” (Keesing 1990).

Mass synchronized spawning guarantees very high rates of egg fertilization, over 80% in samples taken at the peak of a major spawning event and 50 to 20% in animals 30–60 m apart—much higher than recorded in other invertebrates (Babcock and Mundy 1992). These numbers speak for themselves. In order to replace two adults, 20 million eggs would undergo a survival rate of about 0.00000001% where the larvae recruit. A jump in survival rate to 0.1% (one in a thousand) of 20 million eggs would result in 20,000 adult starfish where the larvae have recruited. Given the logic dictated by these figures it seems likely that survival rates of larvae and young juveniles are a crucial element in the tendency of *A. planci* to undergo population explosions.

Cowan et al. (2016) reported on various planktivorous damselfishes' appetite for *Acanthaster* larvae. They showed that some species have the capacity to buffer against population fluctuations and may contribute toward the stability of COTS populations. This suggests that removal of planktivores from reef shallows would raise the prospect of higher survival rates of *Acanthaster* larvae, potentially leading to peaks in settlement of their late brachiolaria larvae.

When the late brachiolaria larvae are ready to settle, they commence probing the reef for suitable locations in terms of refuge from predators, such as puffer fish (Fig. 13.3), and availability of food. Based on studies to date, it is clear that, like a number of other echinoderms, they actively seek out their preferred habitat of CCA (Fig. 13.4) that is abundant on Red Sea reefs. This tends to flourish in moderately

exposed sections of the reef crest and shallow reef-face where it is often found encrusting dead *Acropora* corals.

The young starfish's bright pink colouration, merging with that of the encrusting alga, combined with their cryptic behavior, provide camouflage and refuge from potential predators. By two weeks old, their mouths are developed and they start feeding on the CCA, leaving small white feeding scars, much as the adults do on corals, but on a much smaller scale (Henderson and Lucas 1971; Lucas 1973; Hughes et al. 2014; Yokochi and Ogura 1987). Coralline algae are thus a key component in settlement and survival of young COTS on the reef and, as we shall see in the next section, their distribution on the shallow reef is affected by fish that 'farm' the reef, such as *Stegastes nigricans*, with little or no coralline algae growing in damselfish protected 'farms' where algal turf predominates.

COTS begin feeding on live coral at 6–15 months old (depending on growth rates), when they are fully developed young adults with an effective protection of toxic spines and well-developed stomachs that spread over the coral polyps in an impressive display of extra-oral digestion (Barnes et al. 1970). Coral feeding COTS attract other COTS to the same location, tending to form aggregations. Individuals that become associated with such aggregations may forsake their cryptic behaviour and expose themselves on coral reefs as they feed in daylight, unlike their younger stages that are usually hidden beneath coral heads or in crevices during daytime, only emerging to feed at night.

As mentioned above, despite their adults' capacity to lay bare huge tracts of live coral, larval and juvenile phases of

the starfish are themselves vulnerable to predation by both fish and corals. It has also been noted that COTS aggregations feeding on live coral (creating surfaces for coralline algae to flourish) may also positively impact on the available surfaces for their own larvae to settle—creating favourable conditions for secondary outbreaks, potentially larger than initial ones in a given area (Ormond and Campbell 1974).

Notwithstanding the degree of impact of the feedback mechanism proposed by Ormond and Campbell (1974), the role played by coralline algae cannot be over emphasized. Space, food and protection from predation are critical factors influencing survival of settled starfish (Hughes et al. 2014). As stated above, crustose coralline algae play a vital role in stabilizing reef structure and are a common feature of healthy coral reefs. Not only do they help to build the reef form, cementing dead coral rubble together, but they also provide larval settlement surfaces for many invertebrates (including corals and starfish) and create crevices for starfish to hide, as well as food for a range of invertebrates, including COTS. Development of these encrusting algae is, as we shall see below, dependent on the scraping and browsing activities of reef fish and other invertebrate herbivores such as young *Acanthaster* themselves or sea urchins (e.g., *Diadema*). Experiments have shown that once new, clean, surfaces appear on reefs in the Red Sea, the first colonisers of such surfaces are crustose coralline algae.

A series of experiments related to algal growth in pomacentrid territories (Vine 1974) (see below) undertaken on a Sudanese reef, poses a number of questions regarding the role of herbivorous and grazing fish on the shallow water

Fig. 13.3 The pufferfish, *Arothron hispidus* was shown to be an opportunistic predator on *Acanthaster* adults (Ormond et al. 1973). We kept several in cages on the reef to study their behaviour (© Vine)

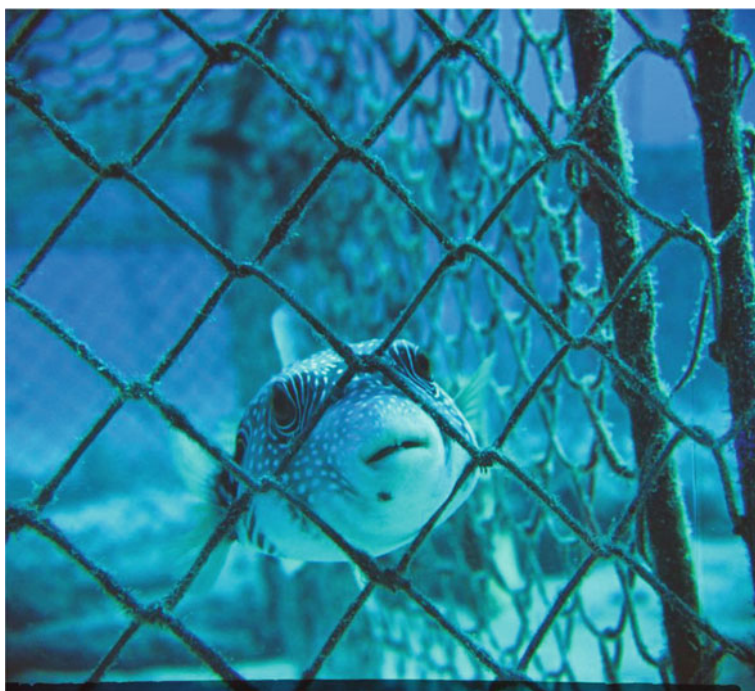
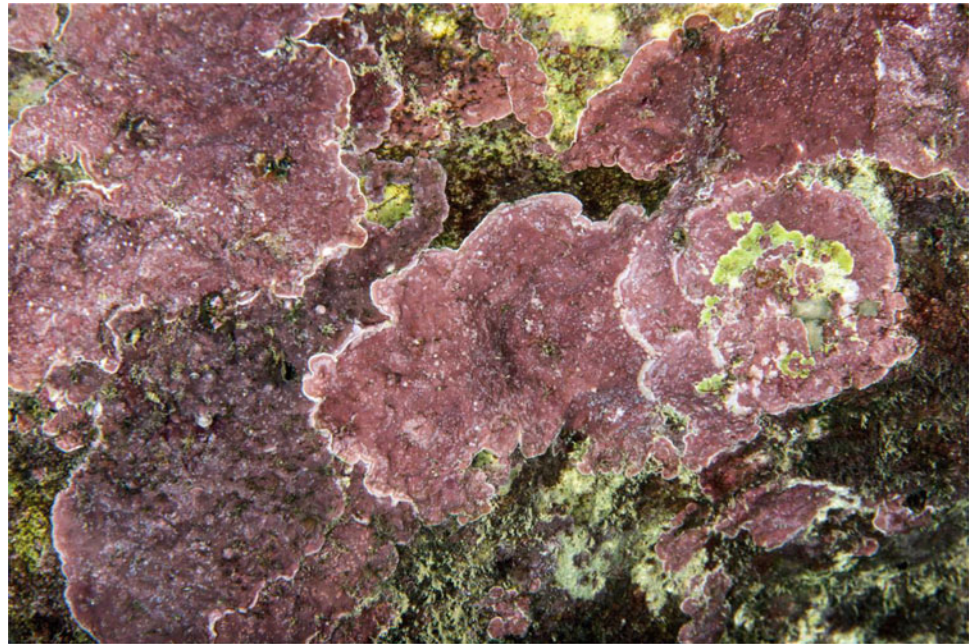


Fig. 13.4 Crustose coralline alga (CCA)—prime settlement substrate for many invertebrates including corals' and *A. planci* larvae (© Sjoeholm)



reef structure, including their influence over settlement and growth of coralline algae. The author demonstrated that these important calcareous algae are absent from damselfish 'farms', limiting their growth to areas where reef herbivores are more active.

Randall (1972) also proposed that fish play an important role in survival of recently settled COTS. "Plant and detritus feeding animals may be among the more important consumers of newly transformed starfish. Many of these animals such as fishes, echinoids and gastropods are not very discriminating as they graze. Small benthic animals, though ingested incidentally, may be eaten in great numbers".

In April 1996, Charles Birkeland re-visited areas in Palau that he had recorded as being severely impacted by COTS in 1977–78. Writing to Jan Sapp, author of the book *What is Natural? Coral Reef Crisis* (Sapp 1999), he stated: "These areas have not only failed to recover after nearly 20 years, but they have deteriorated further. I think it is over fishing of herbivorous fishes so the coral recruits cannot get a start. The areas are all covered with algae. This is in great contrast to the beautiful healthy reefs which COTS did not infest in the 1970s."

Pratchett et al. (2014) brought the state of our knowledge of *Acanthaster* research from 1990 to 2014 up to date. Evidence is mounting of a crucial relationship between the presence of herbivorous fish and the recruitment of COTS (Jessen et al. 2014), both in terms of the initial outbreaks and indefinite recovery periods due to algae preventing the re-establishment of reef building corals. There is a globally recognized trend toward loss of coral cover and increase in algal cover on many tropical reefs. A study on the Great

Barrier Reef showed that a phase shift from coral dominance to algal dominance was associated with low diversity of herbivorous fishes and low abundance of algal browsers such as rabbit fish (Siganidae), and of grazers/detritivores such as surgeonfish (Acanthuridae) (Cheal et al. 2010, 2012).

Other episodic intrusions such as run-off after torrential rainfall (as noted above, larval development, growth and survival increases almost ten-fold with doubled concentrations of large phytoplankton; Brodie et al. 2005), hurricanes (Brown 1997), smothering of shallow habitats by dredge tailings or eutrophication from sewage outflows could all trigger conditions for high recruitment figures and these could be natural or anthropogenic in nature.

Regardless of the causes, outbreaks of COTS on coral reefs can have serious implications. In areas such as the Great Barrier Reef where a 17 year cyclical pattern of outbreaks has been postulated, efforts have been made to introduce effective management control strategies based on methods employed for control of invasive species (which *A. planci* is not). The options and challenges involved have been discussed by Jessica Hoey et al. (2016), and include use of a robotic submersible known as *COTSbot* that is designed to search out and inject a toxin into individual starfish.

The full story may be somewhat more complex than the linear nature of the various hypothetical cause and effect scenarios discussed above. Nevertheless, we are getting closer to understanding COTS biology than we were in the 1960s and 1970s. As we move forward it is important to recognize that coral reef ecosystems are dynamic regimes

that respond in complex ways to different conditions and that multiple factors are likely to be involved. Mayer (2004) discusses the importance of a holistic approach in attributing ‘blame’ for COTS outbreaks.

Notwithstanding the multiple cause and effect scenarios alluded to above, it remains clear that protection of reef fishes, especially herbivores, is a vital step in reef conservation and in supporting healthy coral growth. This is a field of research worthy of closer attention since it impacts directly on development of management strategies for coral reefs (Dulvy et al. 2004; Hughes et al. 2014).

Corals–V-Algae and the Influence of Herbivorous Fish on the Outcome

Whilst working with the CCSRG off Port Sudan, the author was a regular visitor to the reef shallows of ‘Harvey Reef’ (part of the Towartit reef complex) where a research platform was situated. Dart (1972) studied echinoids on this reef and hypothesized that their grazing of filamentous algae could contribute to coral larval settlement. One of the author’s regular swims from the platform to a point along the reef edge took him close to a patch of reef characterized by loose algal-coated dead coral rubble, defended from intruders (both fish and Man) by pugnacious damselfish (Fig. 13.5). The rubble mound was adjacent to an area of shallow sand where the author regularly photographed fish.

In a paper published by Vine (1974), the author wrote:

... one way of encouraging parrotfish and surgeonfish to feed in front of the camera was to remove loose pieces of algal covered rubble from the reef and to place them on sand. Each time this was done many fish (mainly Acanthuridae, Siganidae, Chaetodontidae and Balistidae) commenced browsing on the displaced rock and, within about 30 min, the green matting of

filamentous algae previously covering the rock had been consumed by fish, leaving the rubble fragments to merge inconspicuously with the colour of the lagoon sand. The question arose: why do these herbivorous fish not eat the green alga growing on the rocks in situ? The intensity of their browsing on displaced rocks was so great as to suggest that the in situ rocks would not have such a thick matting of green filamentous algae if they were grazed by surgeon and parrotfishes.

Suspecting that the reef’s architecture was being influenced by aggressive pomacentrids that were protecting their occupied rubble patches from reef grazers, the author set up a series of experiments to probe deeper.

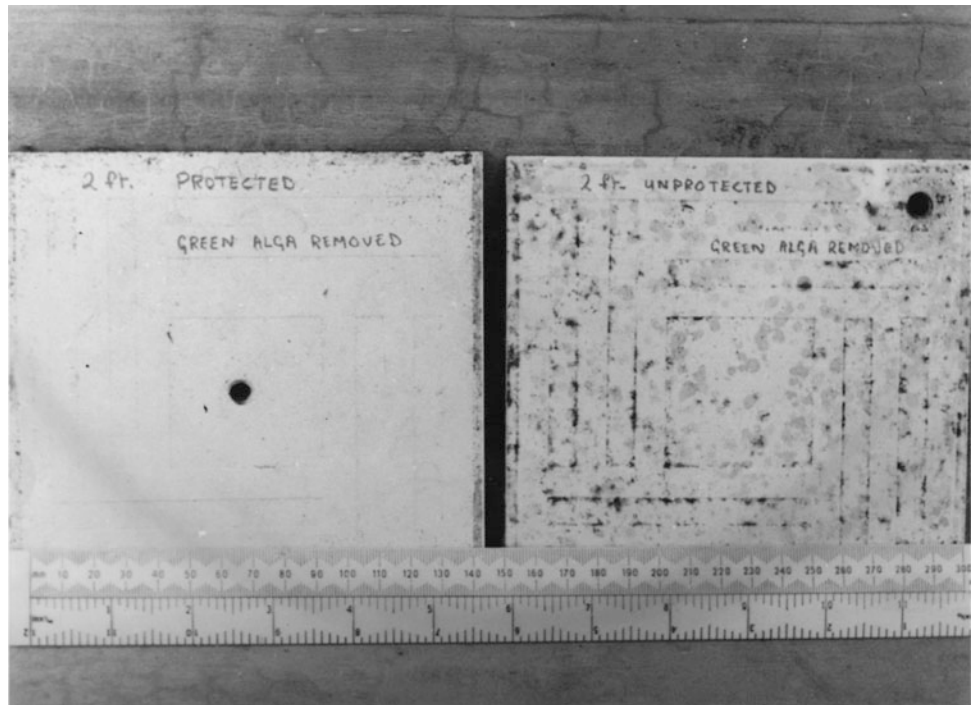
Several other characteristics of the damselfish territories were noted during the course of this work. Fragments of dead coral were often poorly cemented and therefore easy to remove as ‘bait’ for other reef fish. In addition, there was little live coral growing among algal covered rocks, whereas around the edges of their territories encrusting corals were associated with relatively high densities of the serpulid tubeworms, *Spirobranchus* sp.

The study (Vine 1974) led to some unexpected findings that provided a deeper understanding of the processes at work in a balanced coral reef environment. The essence of the field experiment was that bathroom tiles were screwed onto the reef in shallow water to act as settlement plates. Some were protected by wire netting cages, preventing access to herbivorous fishes (thus mirroring the effect of aggressive damselfish chasing away competitors or of over-fishing), whilst other tiles were left unprotected, permitting all fish to graze on their surfaces. After periods of 2–4 weeks the plates were lifted, weeds were removed, dried and weighed, and the surfaces examined for attached organisms. A photograph of two such settlement plates after one of the experiments is shown here (Fig. 13.6). It clearly illustrates the impact of reef grazing fish on reef structure.

Fig. 13.5 *Stegastes nigricans* (previously *Pomacentrus lividus*) ‘farming’ filamentous algae. The fish chases intruding individuals away, preventing herbivores from grazing on the algal turf. This sets in train a chain reaction that involves, among other effects: increased sedimentation, prevention of settlement and growth of crustose coralline algae, loss of favoured coral settlement sites and weakening of reef structure (© Sjöholm)



Fig. 13.6 Settlement plates after filamentous algae have been removed. The protected (left-hand) plate had significantly more 'algal turf' but no settlement of crustose coralline algae (CCA). The right-hand plate that was exposed to reef grazers had significantly less algal turf formed by filamentous algae (since this had been grazed) but dense settlement by CCA. The latter are preferred settlement surfaces for coral planula larvae, *A. planci* larvae and the main source of food for young COTS, before they begin feeding on corals. This work was first described in Vine (1974)



The left-hand plate (that was protected by a wire netting cage) had a clean surface after removal of a thick mono-specific algal turf formed by a matting of green filamentous algae. In contrast, the right-hand plate, that had been left exposed on the reef, adjacent to the protected plate, had a high percentage covering of CCA that was clearly visible after removal of the much thinner covering of filamentous algae. The latter was due to the fact that browsing and grazing reef fish, constantly scraping at the unprotected plate, efficiently cropped the algal turf and created fresh surfaces for settlement and growth of coralline algae.

The twin tiles in the photograph taken during the above experiments in 1973 tell a compelling tale, pointing to several impacts of fish on coral reef development.

One of the first conclusions was that green filamentous algae coating the protected tiles would cover much of the reef top if it were not for the grazing/browsing activities of a healthy population of herbivorous reef fishes that are largely responsible for controlling the extent of its growth. It was also clear that the aggressive behaviour of damselfish (Fig. 13.5) led to growth of green filamentous algae within their territories. Subsequent researchers have categorized such fish as 'farmers'. The experiments also showed how the filamentous algae were so successful in blanketing hard surfaces that they inhibited the settlement and growth of encrusting CCA that are one of the main instruments of reef cementation (and main food of young *A. planci*—see above discussion). The author concluded that the reason that the damsel fish territories comprised loose rubble rather than firmly attached fragments was connected to the aggressive

behavior of the damselfish that prevented other fish from cropping the filamentous algae. The settlement experiments also showed how small sessile invertebrates such as spirorhids were much less frequent among the cage protected weed-covered settlement plates than on those that had been exposed to reef grazers (Fig. 13.7).

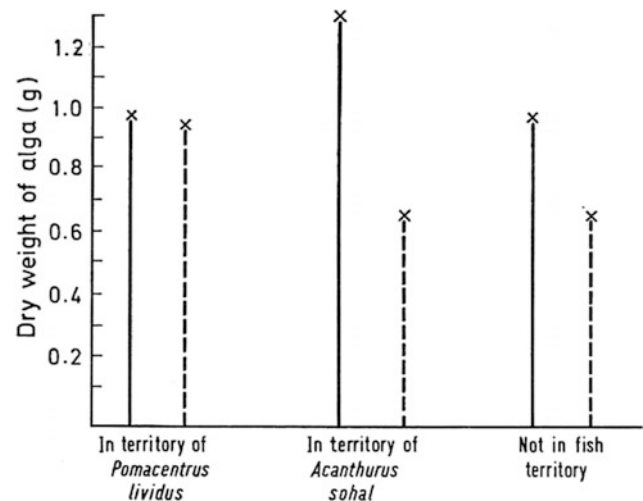


Fig. 13.7 Impact of *Stegastes nigricans* (previously *Pomacentrus lividus*) on development of algal turf formed by filamentous algae. Continuous lines are plates protected by wire netting cages; broken lines are unprotected settlement plates. It is clear that within the *Stegastes* territory the cages have little or no impact because the pomacentrids are performing the same task of excluding herbivores as are the cages. Outside the damsel fish territories there is a marked difference between algal growth in protected (caged) plates and those accessible to reef herbivores

Later studies on the impact of herbivory in damselfishes confirmed the author's observations (e.g. Jessen et al. 2014) and have thrown new light on the significance of these fish in shaping reef form and invertebrate diversity (Lobel 1980, 1981; Schopmeyer and Lirman 2015; Gordon et al. 2015; Hiroki and Kato 2002). At the time of writing, over 240 research papers have cited the above research (Vine 1974) and, thanks to such studies, we now have a clearer understanding on the influential role that damselfish can play in reef morphology and ecology. A paper by Lobel (1980) affirms that scraping of the substrate by herbivores promotes the growth of corals and coralline algae by reducing the abundance of filamentous algae (Stephenson and Searles 1960; Dart 1972; Vine 1974; Wonders 1977). Competition between corals and algae on coral reefs has been investigated by McCook et al. (2001).

Meanwhile, Rasher et al. (2012) are in no doubt that herbivorous fish are pivotal in reducing algal cover with its associated sedimentation whilst creating surfaces for settlement and growth of corals. They showed that removal of herbivores resulted in proliferation of macroalgal cover by 9–46 times, macroalgal biomass by 23–84 times and cyanobacteria cover by 0–27 times whilst decreasing cover of encrusting coralline algae by 46–100% and short turf algae by 14–39%. These results are in line with those recorded by the present author in his investigations on Harvey reef, Sudanese Red Sea (Vine 1974) and are reflected in the settlement plate image shown here.

Meanwhile, Hata and Kato (2002) studied *Stegastes nigricans* on reefs in Japan where they found that its fastidious 'gardening' of its 'algae farms' resulted in a nearly monocultural mat of the erect filamentous rhodophyte, *Womersleyella setacea*. They found *S. nigricans* unusual in this regard with other herbivorous damselfish maintaining more species rich 'farms'. *S. nigricans* was observed to weed out the less digestible algae, leaving more space for the digestible *W. setacea*.

Interestingly, Lobel points out that the pomacentrids he studied feed primarily on epiphytes rather than the alga itself since they lack cellulases or other enzymes capable of digesting plant cell walls. He also states that whilst the red algal mat may not constitute an actual food resource, it is important as a vital refuge for small invertebrates and its variation in size affects the area available for epiphytic growth. He also points to the fact that benthic invertebrates and demersal plankters live within the algal mat including juvenile crabs, snails, polychaetes, brittle-stars and others.

Commenting on the author's observations in the Red Sea (Vine 1974), Lobel stated "pomacentrids can be regarded as a detriment to the physical development of the reef framework" and "it is becoming increasingly clear that grazing fishes (and other benthic rasping feeders) are important agents controlling spatial utilization and competitive

outcomes among corals, algae and other benthic organisms". Furthermore, Potts (1977) suggested that pomacentrids may be such decisive factors in reef ecology that they may be responsible for "exclusion of certain coral species from an otherwise favorable habitat".

Ceccarelli et al. (2005) studied three species of territorial damselfish in a seasonally *Sargassum* dominated algal coastal zone at Magnetic Island in Queensland, Australia. They noted that these fish can play a significant role in defining reef dynamics on coral reefs because they frequently occupy a large proportion of the substratum—*Pomacentrus tripunctatus*, *P. wardi* and *Stegastes apicalis* occupied 60% of available surface in the area of their study. As with related species on Red Sea reefs, their presence promoted the abundance of algal food in their territories. They concluded that damselfish "appear to readily co-exist with large unpalatable macroalgae as they can use them as a substratum for promoting the growth of palatable epiphytes."

It is clear that damselfish and corals are uneasy bed partners and promotion of algal coverage (inhibiting coral settlement and growth) may not be the fish's only impact on corals. Kaufman (1977) showed that *Eupomacentrus planifrons* from the Caribbean actively kills corals, thus expanding available areas for algal growth. In a zone where competition between corals and algae is intense, such damselfish exert an "important influence on the outcome of competition between corals and algae". Others reached similar conclusions on the impact on species diversity that pomacentrids can exert. Potts (1977) showed that corals became smothered by algae and sediment when placed in pomacentrid territories. Soft corals suffered a similar plight.

On the other hand, Birkeland (1977) showed how grazing fishes have an opposite effect, reducing filamentous algae, creating free spaces into which coralline algae and juvenile invertebrates such *Acanthaster* or corals can settle.

Head (1987) re-emphasised the importance of balanced reef grazing on the recruitment and survival of reef corals: "The larvae [of corals] always require a hard algal-free substrate to settle, so it is important that new bare substrate be continually formed on reefs. In consequence there is a non-linear relationship between the rate of grazing by such animals as echinoids and the recruitment success of corals. Too little grazing and no bare substrate is available, too much and the newly settled spat are killed before they are properly established (Sammarco 1980)" (Fig. 13.8).

It is becoming increasingly clear that grazing fishes (and other benthic rasping feeders) are important agents controlling spatial utilization and competitive outcomes among corals, algae and other benthic organisms (Lobel 1980).

A pomacentrid may be such a decisive factor as to be responsible for exclusion of certain coral species from an otherwise favorable habitat (Potts 1977).

Fig. 13.8 A healthy coral reef where scleractinian corals and crustose coralline algae create a vibrant habitat for fish and invertebrates (© Sjöholm)



It is now clear that turf algae ('farmed' by pomacentrids) promote sedimentation, negatively impacting larval settlement and early growth of coral recruits. The consequential impact on cover by corals and coralline algae has been well described by a number of researchers (e.g., Ceccarelli et al. 2006). Meanwhile, CCA—also obstructed by turf algae—are essential elements of healthy reefs, contributing to calcification and inducing larval settlement of many reef organisms such as corals, soft corals, echinoderms and gastropods.

This is an area of coral reef research that can provide valuable insights into the processes at work on the reef, particularly with regard to the tendency for coral dominated reefs to shift toward algal domination (Figs. 13.9 and 13.10). Rasher et al. (2012) undertook field experiments in adjacent areas where herbivorous fish were, on the one hand protected from fishing, and on the other hand unprotected and scarce. They showed how corals developed much more successfully on the blocks that were exposed to grazing by the herbivores. The effects were not confined to the algal turf created by filamentous forms. Their support for reef herbivores is unambiguous: "herbivores strongly suppress macroalgal colonization and growth, lessen damage to corals, and promote coral recruitment and growth". Of particular interest from a management control viewpoint is that the presence of reef herbivores is of much greater significance than moderately elevated levels of nutrients. Whilst lowering nutrient levels is unlikely to reverse a shift toward algal domination, increasing the density of herbivores on the reef is a possible tool to shift the balance in favour of corals, given time for their impact to be felt (Jessen et al. 2014).

These effects are being recognized at more and more tropical sites around the globe and humans are frequently,

but not always, the culprits responsible, as a result of ignorance and/or lack of controls, for removing herbivores and bringing about the decline of reefs whose 'health' and diversity they depend on for food (Burke et al. 2011; Lewis 1986; Hughes 2010; Rasher et al. 2012; Burke et al. 2011). Lirman (2001) studied the impact that algae have on coral growth rates in the Caribbean, basically concluding that increased algae resulted in significant slowing of coral growth. The mechanism by which algae suppress coral growth and survival seems to be that the algae release compounds that enhance microbial activity on live coral surfaces, causing mortality of corals and stimulation of further algal growth (Smith et al. 2006).

An interesting study by Katie Barott and colleagues (Barott et al. 2009), utilizing hyperspectrometry, demonstrated that whilst the impact of fleshy algae on corals in the Line Islands creates a zone of hypoxia and altered pigmentation, the combination of corals and CCA is not accompanied by such a disturbance. This reflects the fact that such coralline algae are often present among reef building corals without any obvious negative impact on the corals, whereas the same cannot be said for the damage that turf or fleshy algae cause to reef building corals (Fig. 13.9). The above findings were confirmed by Barott et al. (2011) who compared reactions of *Montastraea annularis* corals to the macroalgae *Dictyota bartayresiana* and *Halimeda opuntia*, together with a mixed consortium of turf algae. They once again showed that contact between all of the above algae and the coral resulted in hypoxia on the adjacent coral tissue. However, CCA and *M. annularis* "did not appear to be antagonistic at any scale. These zones were not hypoxic, the microbes were not pathogen-like and the abundance of

Fig. 13.9 *Sargassum* weed dominating on what was previously a coral dominated reef (© Sjoeholm)

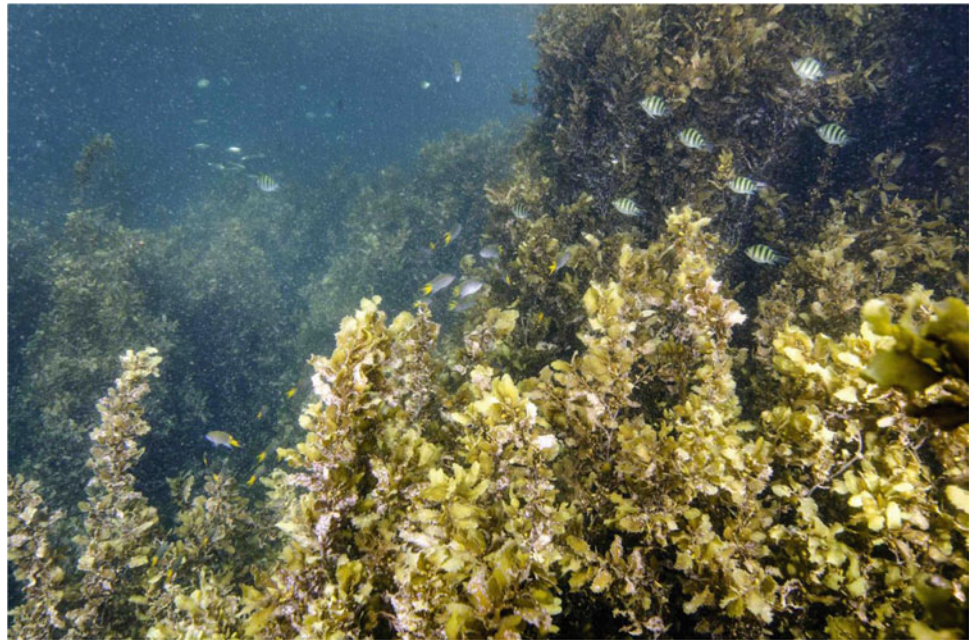


Fig. 13.10 *Sargassum* weed often smothers reef building corals that are stressed by environmental factors (© Sjoeholm)



coral–CCA interactions was positively correlated with per cent coral cover”. In other words, a healthy reef can be expected to host extensive stands of CCA, subject to restrictions on farming fish such as *Stegastes lividus* which, as we have seen above, promotes development of algal turf and consequently discourages settlement of CCA. Barott and colleagues proposed “a model in which fleshy algae and some species of turf macroalgae alter benthic competition dynamics by stimulating bacterial respiration and promoting invasion of virulent bacteria on corals. This gives fleshy

algae a competitive advantage over corals when human activities, such as overfishing and eutrophication, remove controls on algal abundance.”

prioritization of management approaches that protect critical processes, such as herbivory, that bolster coral reefs against phase-shifts to macroalgae should slow reef decline and facilitate coral recovery from the numerous stresses impacting present day reefs (Rasher et al. 2012).

What began for the author as an academic study of whether fish behaviour plays a significant role in defining

reef structure has turned out to be a much more critical line of enquiry in terms of management and conservation of coral reefs and our ability to reverse what are increasingly frequent 'phase shifts' from coral dominated to algal dominated reefs.

Corals-V-Sponges and Ecological Impact of the Battle for Dominance

A SCUBA diver's view of Red Sea coral reefs inevitably reveals an intricate and varied, apparently haphazard, arrangement of surfaces created by a wide range of species. Among the predominant forms are corals, algae (including calcareous forms), Bryozoa and sponges. Pressed close to each other, they are in constant competition to occupy the available space, keeping their adversaries at bay, whether these be separate colonies of the same species or opposing taxa. Close study of the interface between these invertebrate rivals has always been a source of fascination to the author since there seemed to be little understood forces at play in both the manner of attack and defence.

In his book, *Red Sea Invertebrates* (Vine 1986), the author describes observations of the coral-killing sponge, *Terpios viridis* (Figs. 13.11 and 13.12), in the Sudanese Red Sea. The species was originally described by Keller (1891) from specimens collected on corals in the *Stylophora* zone on reefs close to Suakin. During the author's own survey of reefs in this region in 1975, he noted large tracts of a thin blue-grey slimy sponge literally blanketing sections of reefs. Closer inspection revealed that the sponge, identified as *T. viridis*, was extensively overgrowing corals and thus killing them. A series of photographs of the sponge coral interface, taken at regular intervals, demonstrated the alarming rate at which this was taking place. At one site the sponge extended its coverage to an area of 400 m² during the summer months. This occurred at 15–20 m deep along a 40 m stretch of reef face on which virtually all the smothered corals were killed. Studies in Guam at that time, reported by Bryan (1973), described similar events with sponge growth rates on colonies of *Porites* coral at 2.3 cm per month. In the central Red Sea, maximum growth of *Terpios* occurred during summer months, from May to October (when coral growth was suppressed), with a distinct slowdown in winter when the affected corals seemed to have greater success in repelling the invasions. *Galaxea* coral appeared to have a greater ability to defend against *Terpios*, but no species was immune. *Terpios* was by no means the only sponge to threaten live corals—at least 15 encrusting species were recorded—including some other members of the family Suberitidae (to which *Terpios* belongs)—but it was the most prolific.

It was clear that damage to reef building corals caused by these aggressive sponges could be just as devastating to a

well-balanced reef as could an invasion of *Acanthaster*. Furthermore, both species may sometimes combine to the detriment of reef corals. Corals attacked by COTS could be more susceptible to sponge invasion than healthy corals that have an ability to 'fight back'. It is also worth noting that damage inflicted on live corals by *Terpios viridis* and related species is not confined to the immediate impact of sponge-carpeted dead reefs. Once established, the sponge may persist for years and during this period resettlement of corals and possible reef recovery is delayed until more coral-conducive conditions return, accompanied by a breakdown of the sponge layer (Plucer-Rosario 1987).

Whilst the macro view of corals and sponges fighting it out on Red Sea reefs was engaging enough for this inquisitive biologist, it raised more questions than it answered. There was clearly a need to take a closer view of what was happening at the cellular level. Microscopic and biochemical studies on both corals and sponges, particularly at the leading edge of sponge encroachment, were undertaken by several researchers. Tang et al. (2011) examined this interface between the encrusting sponge *Terpios* and the corals that it killed. They suggested that the dominance of sponge over coral is established at the leading edge of the encrustation by extension of arm- or tube-like structures that create a 'scaffold' for subsequent sponge invasion. Whilst the invasion activity is concentrated at the interface, reaction in corals seems to be more general with the coral associated bacterial community undergoing changes depending on distance from the sponge-coral junction. The coral's defence mechanisms are induced by those areas of coral in direct contact with the sponge where a high concentration of nematocysts was observed. The most lethal damage inflicted by *Terpios* sponges in their assault on corals may be the fact that they block out the light, preventing photosynthesis of the coral's symbiotic algae.

Rützler (2002) has reviewed the ecological impact of crustose clonid sponges on Caribbean reef corals, emphasizing that they can have a dramatic effect on coral coverage, particularly on stressed corals whilst virile colonies are mostly able to resist being overgrown by these sponges. Triggers for rapid sponge extension may come from temperature changes (warmer or colder), sedimentation, organic pollution and physical damage caused by fish, boat anchors or other means. These boring sponges excavate cavities below the coral surface, depriving colonies of their structural base, or simply overgrow dying colonies, blanketing out the light on which they depend. Non-boring sponges such as *Terpios* and *Chondrilla* may rapidly extend their growth over corals whose resistance has been weakened by pollution or by a range of other impacts, both natural and anthropogenic.

Studies on reef associated sponges and soft corals have drawn the attention of the pharmaceutical industry. Vacelet

Fig. 13.11 The invasive sponge, *Terpios viridis* attacks a coral colony. It is a battle that can be won by either side but corals under stress from other factors often fail to resist the sponge's attack (© Sjoeholm)

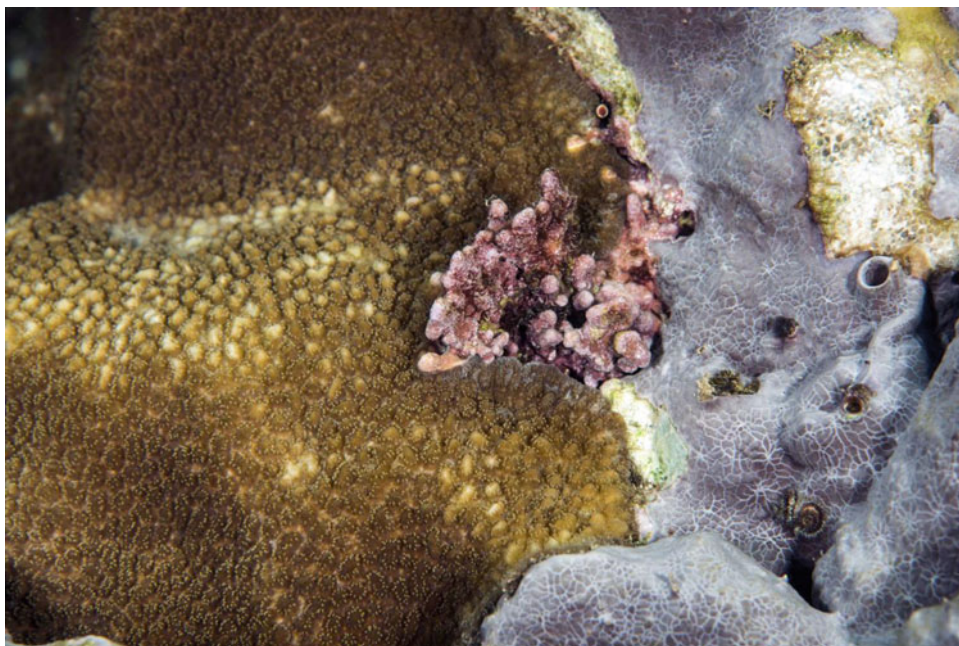


Fig. 13.12 *Chalinula saudiensis* is a distinctive vivid blue sponge that has strong antiviral properties (© Sjoeholm)



et al. (2001) described *Chalinula saudiensis* (Fig. 13.12), a distinctive vivid blue sponge that has strong antiviral properties. Hassan et al. (2010) isolated compounds from the soft coral *Cladiella pachyclados* and evaluated them for their ability to inhibit growth, proliferation, invasion and migration of prostate cancer cells. They state that “some of the new metabolites exhibited significant anti-invasive activity”.

The impact of sponges on coral reefs remains an important topic for both field and laboratory research, since sponges not only play a key role in the health of coral reefs, but they may also provide inspiration for life-saving

pharmaceutical medicines. The above observations are just a brief introduction, based on the author's observations and interests.

General Reef Ecology and Conservation

A field study of 30 reef locations in the Sudanese Red Sea, conducted by the author over a four-year period (Vine and Vine 1980), emphasized the difficulty faced by biologists attempting to impose order over such a complex array of

interconnected habitats. Notwithstanding the intricacies and pitfalls involved in comparing different habitats, a few features were regarded as suitable for data recording. These included biodiversity as displayed by distribution of reef fishes, physical aspects of different reefs in vertical profile, and growth rates of reef corals (Vine and Head 1977). In addition to these studies, the author also collected spirorbid tube worms as part of a taxonomic and zoogeographic survey of the group (Vine 1972).

The main study was presented at the Symposium on Coastal and Marine Environment of the Red Sea, Gulf of Aden and Tropical Western Indian Ocean, whose results were published in the proceedings of that event (Vine and Vine 1980).

Approximately 250 species of reef-associated fish were recorded during the work and their presence was noted at each transect. One hundred and ninety-two species were recorded in Suakin harbour alone. Forty settled fauna and flora types were recognised and logged on transect illustrations. Transects were made on reefs at Sanganeb (Fig. 13.13), Wingate, the Umbria wreck, Towartit and Suakin. Coral growth rates were measured for corals growing on the Conshelf 2 garage at Shaab Rumi reef (Fig. 13.14). Four reef types were present: fringing reefs, shallow patch reefs, barrier reefs and offshore reefs or atolls. Standard features of many offshore reefs were a shallow reef-top that drops steeply from close to the surface to about 8–10 m where it is followed by a gently inclined terrace sloping down to around 15 m, followed by a second steep reef face from about 15 m to 30 m. This is then followed by a second incline that culminates in a steeper slope extending into deep water beyond the reach of divers on normal mix compressed air. On south and north reef faces this pattern is often compressed into an almost vertical reef face reaching from close to the surface to 30 m with no intervening terrace. It is beside such steep, deep reef faces that the larger ocean pelagic species of fish were found, such as schools of scalloped hammerhead sharks and barracuda.

A notable feature of the Sudanese Red Sea is Sanganeb atoll with its prominent lighthouse. The author's description of its underwater habitats in the 1970s is one that still evokes a sense of wonder at how unspoiled the reefs were at that time.

The sea around Sanganeb is always clear and the biotopes are varied and flourishing. Species range from typically oceanic ones such as large tuna, sailfish, greater hammerhead sharks, and *Carcharhinus longimanus* to a wide range of reef dwelling species and lagoonal forms such as the delicately coloured *Pseudochromis flavivertex* and many invertebrates more typical of lagoons or harbours than of open-water coral reefs. There is a semi-resident school of dolphins, frequently sighted turtles and manta rays, schools of barracuda and a variety of migratory sharks and other large pelagic fish. In winter months, especially November to April, hammerhead sharks tend to form schools at

the south-west and north-east points of the atoll. These may be observed at shallow depths, around 20 m, in the early morning (before 0900) or in the evening, immediately prior to sunset. During May and June, sailfish are relatively common around the atoll and they enter the shallow water on top of the reef and in the lagoon. There is a peak of zooplankton during January and February when many of the planktivorous species appear to be most active...We have heard it described as one of the most magnificent diving locations in the world (Figs. 13.15 and 13.16).

Monitoring the status of Red Sea reefs is a vital management task in terms of highlighting threats and mitigating their impact (Kotb et al. 2004; Götz et al. 2003). Klaus (2015) provides an interesting account of the less well-known reefs to the south, where conditions for coral growth are generally more challenging than in the central Red Sea areas of Sudan, Saudi Arabia, and some of the southern sections of Egypt and Jordan. Head (1980), Sheppard (1982), Sheppard and Sheppard (1991), and Sheppard et al. (1992) also provided valuable reviews of the diversity and zonation of reef building corals along the Red Sea's coastlines, whilst a recent paper by Nasr (2015) concentrates on reefs in Sudanese waters and Bruckner and Dempsey (2015) summarise conditions for the Saudi Arabian reefs. Several authors have stated that the Red Sea offers ideal conditions for investigation of potential acclimatization or adaptation mechanisms in corals to some of the predicted scenarios implicit in climate change and ocean acidification (Sawal and Al-Sofyani 2015). Cantin et al. (2010) studied the impact of surface sea temperature (SST) rise on coral growth, using *Diploastrea heliopora*. They demonstrated that growth rates were inversely proportional to SST and postulated that predicted sea temperature rise in the central Red Sea would impact severely on calcification rates of this and other Red Sea corals.

Efforts to provide greater protection for Sudan's coral reefs are taking place within the context of intensifying pressures and notable decline in certain areas. Reinicke et al. (2003) presented results of an eleven-year photographic study of selected transects at Sanganeb. They summarised the status of reef habitats in the Red Sea and the threats they faced:

major local threats include land fills, dredging, sedimentation, sewage discharge and effluents from desalination plants, mostly around towns, cities and tourist development sites. There is local reef damage around major tourism areas, caused by people and boat anchors, along with other threats. Fish populations are declining in some areas, because of increased demand for and fishing pressure on food and ornamental species. Destructive fishing practices such as trawling in fragile habitats is increasing. There has been an influx of illegal fishing vessels seeking to meet demands of the export market and more affluent and growing populations locally. The other major threats are from pollution and shipping accidents, and future bleaching. Monitoring these reefs is becoming increasingly important, as climate change and warmer waters near the limits for coral growth.

Fig. 13.13 Sanganeb atoll reef with lighthouse (© Vine)



Fig. 13.14 Cousteau's underwater garage is the remains of the Conshelf 2 project. It is an ideal structure for studying coral ecology (© Sjoeholm)



Meanwhile, Riegl et al. (2012) studied coral colony sizes over two decades and provided evidence that Red Sea reefs are already being affected by climate change. "Coral size, measured as corrected average intercept of corals in transects, had decreased from 1997 to 2009, after having remained constant from 1988 to 1997. Recruitment had remained stable (~ 12 juvenile corals per m^2). Size distributions had not changed significantly but large corals had declined over 20 years. Thus, data from a wide range of sites taken over two decades support claims by others that climate

change is indeed beginning to show clear effects on Red Sea reefs" (Riegl et al. 2012).

Salam (2006) reviewed the state of affairs regarding Marine Protected Areas (MPAs) in the Red Sea in 2006. He stated that 12 MPAs were selected for a Regional Network of MPAs for the Red Sea and Gulf of Aden. These included two sites in Djibouti to the south, two sites in Egypt (Ras Mohammed National Park and Red Sea Islands), Aqaba Marine Park in Jordan, the Straits of Tiran bordered by both Saudi Arabia and Egypt, Al Wejh Bank and Farasan Marine

Fig. 13.15 Manta ray filter feeding in the Red Sea (© Sjoeholm)

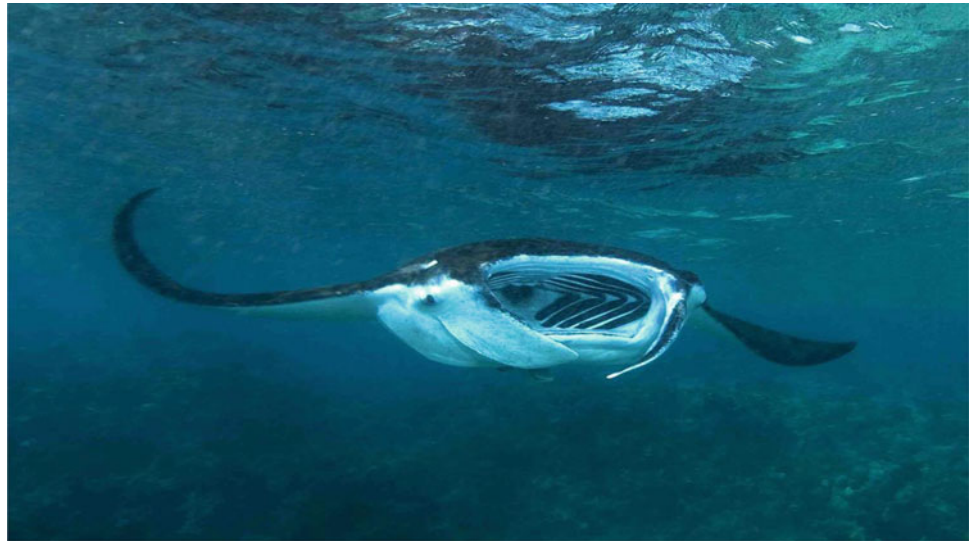


Fig. 13.16 Whale sharks are the world's largest fish and are filter feeders (© Sjoeholm)



Protected Area in Saudi Arabia, Aibat and Saad ad-Din Islands in Somalia, Sanganeb National Park, Dungonab Bay and Mukkawar Island in Sudan together with sites in Yemen including Socotra Islands Group National Protected Area and the Bir Ali–Belhaf area. Some of these had already been established for some years whilst others were to be newly formed as protected areas.

Approximately ten years later, on 17 July 2016, the World Heritage Committee declared eight new sites, including Sanganeb atoll and Dungonab Bay—Mukkawar Island Marine National Park. The committee noted that the designation applied to two separate areas: Sanganeb: “an isolated, coral reef structure in the central Red Sea and the only atoll, 25 km off the shoreline of Sudan. The second element of the property is made up of Dungonab Bay and Mukkawar Island, situated 125 km north of Port Sudan. It includes a highly diverse system of coral reefs, mangroves,

sea-grass beds, beaches and islets. The site provides a habitat for populations of seabirds, marine mammals, fish, sharks, turtles and manta rays. Dungonab Bay also has a globally significant population of dugongs.”

The move was widely welcomed by marine scientists who have long been aware of the unique fauna and flora of these areas. Up to date information on the park is available online at www.sudanmarineparks.info.

It is clear however, that the mere designation of MPA status does not provide any guarantees that coral reefs will be protected from anthropogenic impact. All the author’s work to date, and the overriding conclusion of the present review, confirms the interconnected nature of life on coral reefs. Remove reef grazers in the form of shallow reef fish such as parrotfish or surgeonfish (Fig. 13.17) and the consequences will soon be felt in terms of a phase shift from coral to algal dominated reefs. Along with that will come

greater coverage by sponges, migration of coral eating fish and decline of predatory species—in other words, a whole chain of events that leads to a dramatic collapse in biodiversity on the reefs (Gladstone et al. 2003).

Policy makers need to understand this and also to have faith in the positive impact that properly managed MPAs can initiate and sustain. Marine Parks in coral areas are only as good as the conservation that they achieve. They will only be successful in attracting visitors if they have extraordinary ‘coral gardens’ vibrating with colourful species. In order to achieve this, the priority is to establish programmes that arrest ecological decline and start to put the clock back in terms of biodiversity. It sounds like an impossible dream but it has already been achieved in some cases and there are signs that much more can be achieved in the coming years.

The methodology and efficacy of MPAs in promoting reef building corals rather than blanketing seaweeds is discussed in some detail by a number of authors (Burke et al. 2011; Carilli et al. 2009; Knowlton and Jackson 2008; Mumby and Harborne 2010; Selig and Bruno 2010 and Burke et al. 2011). Their findings all reiterate the important role played by herbivorous reef fishes and unanimously recommend that protection of these species should be a first line of defence in terms of MPA management. Given the inextricable connection between reef herbivores and reef health there is an inescapable requirement to protect the fish communities that keep reefs healthy and can start the ball rolling in terms of reef recovery (Burke et al. 2011). This means that ‘no take’ rules are at the top of the list of conservation priorities in MPAs set up within coral reef areas.

Mora et al. (2006) reviewed the global situation with regard to Marine Protected Areas around the world and concluded that whilst some ‘worked’, overall there was an urgent need for reassessment and room for considerable improvement. They created a verified database containing 980 MPAs and 98,650 km² (18.7%) of the world’s coral reef habitats. Based on levels of poaching “as an indirect measurement of management performance”, they found that only “88 coral reef MPAs covering 1.6% of the world’s coral reefs are managed in such a way as to prevent such activities.”

This does not mean that MPAs are not effective management tools. It does, however, indicate that the vast majority of MPAs are not being effectively managed. Creation of no-take areas is never a popular measure until the benefits of such measures trickle through to fishermen who realize that the stocks on which they depend are slowly recovering, thanks to restrictions imposed by the marine park authorities. Establishment of effective marine parks requires vision, scientific support, regional coordination and community leadership together with government facilitation/legislation, financial resources and multi-party commitment. Public awareness is an essential tool to achieve these goals.

Selig and Bruno (2010) found that MPAs can be very effective in maintaining stable coral cover. “MPA benefits may appear modest in the short term, but over several decades could lead to large and highly ecologically significant increases in coral cover as the cumulative importance of small annual effects becomes more important and the

Fig. 13.17 Surgeon fish *Acanthurus sohal* are herbivores and detritivores constantly picking at the shallow reef surface, usually near the reef crest (© Sjoeholm)



number of years of MPA protection increases. However, it remains to be seen whether the observed benefits of MPAs are sufficient to offset coral losses from major disease outbreaks and bleaching events, both of which are predicted to increase in frequency with climate change. Given the time lag for maximizing MPA effectiveness, implementing new MPAs and increasing enforcement should help maximize the ability of MPAs to prevent future coral loss”.

Taxonomy of Red Sea Marine Life

Much of the marine biological research in the Red Sea has had a taxonomic bias—collecting, recording, preserving, describing and naming new species of fish and invertebrates. Given the high degree of endemism in the Red Sea, it has provided rich pickings for enthusiastic amateurs and dedicated professionals alike. Indeed, the dividing line between hobbyists and experts has frequently been blurred by the cooperation that takes place between amateur collectors and professional taxonomists. Among fish experts one particular ichthyologist deserves special mention: Dr. J. E. Randall. The author was fortunate enough to welcome Dr. Randall on his first visit to Sudan and to dive with him on numerous occasions when he was building up his first-hand knowledge of Red Sea reef fishes. An illustrated summary for the general public was first published by Randall (1983). Jack Randall, as he is best known, has described over 799 new fishes and more coral-reef species than anyone else in history. He has authored over 906 publications in marine biology, nine of which are regional guides on the fishes of the Caribbean Sea, Hawaiian Islands, Red Sea, Oman, and Great Barrier Reef of Australia. Since 1970 he has been senior ichthyologist at the Bishop Museum, Honolulu.

The present author described four new species of serpulids (Polychaeta) from the Red Sea including a new genus and new subgenus. Within a small group of probably twenty or so active serpulid taxonomists spread across the globe, these were significant discoveries, but beyond that highly specialized interest there was no impact whatsoever.

Those of us that have contributed to the task of identifying, classifying, describing and naming the seemingly inexhaustible array of species with which we share the planet are increasingly aware that taxonomy is entering a period of rapid change, becoming less subjective or intuitive and more formulaic in nature. DNA does not lie. Genetic analysis provides definitive evidence for the process of separation and speciation. This involves new skill sets that differ from those of traditional taxonomy. Meanwhile, fewer and fewer specialized taxonomists are engaged in this science and as these people retire, unique skills and knowledge are being lost.

The situation is further complicated by the relatively recent discovery of the phenomenon of cryptic-speciation (Bickford et al. 2006), whereby individuals previously assigned to a single species have sufficiently distinct genetic make-up for them to be regarded as different species. An example of this is provided by the grouper *Cephalopholis hemisktos* which occurs in the Red Sea/Gulf of Aden as well as the Gulf of Oman/Arabian Gulf. The two populations have been isolated from each other for more than 800,000 years and have developed differences in pectoral fin size, pectoral fin ray count, oblique scale rows and asymptotic size (Randall and Ben-Tuvia 1983; Priest et al. 2016).

Given the high levels of endemism in the Red Sea (14% in fishes according to Randall 1994), a function of its Pleistocene exposure to dramatic shifts in sea levels and sea temperatures, together with restricted access via the Straits of Bab al Mandeb, we can expect to find many cases of cryptic-speciation across a wide range of the marine fauna of the region.

In an article published in Bioscience, Lisa Drew (Drew 2011) discussed the threatened ‘extinction of taxonomists’. The figures are astounding and daunting! Almost two million species have been identified. In 2008 the figure was actually 1,922,710. In that year alone researchers newly described and named 18,225 living species (2010 State of Observed Species Report, University of Arizona). The decade-long Census of Marine Life, which ended in 2010, estimates that the ocean holds more than one million marine species, excluding microbes. The task of recognizing, describing and preserving the holotypes and paratypes, depositing them in museums and publishing this work is overwhelming. It is also, on a broad scale, inadequately valued or funded. As a result of climate change and our impact on nature, threatened communities in the Red Sea may be destroyed before their unique species are even recognized (Hobbs et al. 2011). The question is, does this really matter? It is a debate that needs to take place among scientific organisations before it is too late to turn back the clock.

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References

- Babcock RC, Mundy CN (1992) Reproductive biology, spawning and field fertilization rates of *Acanthaster planci*. *Australian J Marine Freshwater Res* 43(3):525–533
- Barnes DJ, Brauer RW, Jordan MR (1970) Locomotory responses of *Acanthaster planci* to various species of coral. *Nature Lond* 228:342–344
- Barott K, Smith J, Dinsdale E, Hatay M, Sandin S, Rohwer F (2009) Hyperspectral and physiological analyses of coral-algal interactions. *PLoS ONE* 4(11):e8043
- Barott K, Rodriguez-Mueller B, Youle M, Marhaver KL, Vermeij MJA, Smith JE, Rohwer FL (2011) Microbial to reef scale interactions between the reef-building coral *Montastraea annularis* and benthic algae. *Proc R Soc B* 279:1655–1664
- Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I (2006) Trends in ecology and evolution. *Sci Dir* 22(3):148–155
- Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. In: Taylor DL (ed) *Proceedings Third International Coral Reef Symposium. Vol. 1: Biology*. Rosenstiel School of Marine and Atmospheric Science, Miami, Florida, pp 15–21
- Birkeland C (1982) Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). *Mar Biol* 69(2):175–185
- Brodie J, Fabricius K, De'ath G, Okaji K (2005) Are increased nutrient inputs responsible for more outbreaks of crown of thorns starfish? An appraisal of the evidence. *Mar Pollut Bull* 51(1–4):266–278
- Brown T, Willey K (1972) *Crown of thorns*. Angus and Robertson, Sydney, p 128
- Brown BE (1997) Disturbances to reefs in recent times. In: Birkeland C (ed) *Life and Death of Coral Reefs*. Kluwer Academic Publishers, Boston, MA, pp 354–379
- Bruckner AW, Dempsey AC (2015) The status, threats and resilience of reef-building corals of the Saudi Arabian Red Sea. In: Rasul NMA, Stewart ICF (eds) *The Red Sea: the formation, morphology, oceanography and environment of a young ocean basin*. Springer Earth System Sciences, Berlin Heidelberg, pp 471–486
- Bryan PG (1973) Growth rate, toxicity and distribution of the encrusting sponge *Terpios* sp (Hadromerida, Suberitidae) in Guam, Mariana Islands. *Micronesia* 9:237–242
- Burke L, Reynter K, Spalding M, Perry A (2011) *Reefs at risk revisited*. World Resour Inst
- Calderwood J, O'Connor NE, Roberts D (2016) Efficiency of starfish mopping in reducing predation on cultivated benthic mussels (*Mytilus edulis* Linnaeus). *Aquaculture* 452:88–96
- Cantin NE, Cohen AL, Karnauskas KB, Tarrant AM, McCorkle DC (2010) Ocean warming slows coral growth in central Red Sea. *Science New Series* 329(5989):322–325
- Carilli JE, Norris RD, Black BA, Walsh SM, McField M (2009) Local stressors reduce coral resilience to bleaching. *PLoS ONE* 4(7):e6324. <https://doi.org/10.1371/journal.pone.0006324>
- Ceccarelli DM, Jones GP, McCook LJ (2005) Effects of territorial damselfish on an algal-dominated coastal coral reef. *Coral Reefs* 24(4):606–620
- Ceccarelli DM, Hughes TP, McCook LJ (2006) Impacts of simulated overfishing on the territoriality of coral reef damselfish. *Marine Ecology Prog Ser* 309:255–262
- Cheal AJ, MacNeil MA, Cripps E, Emslie MJ, Jonker M, Schaffelke B, Sweatman HM (2010) Coral-macroalgal phase shifts or reef resilience: Links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs* 29(4):1005–1015
- Cheal AJ, Emslie M, Miller I, Sweatman H (2012) The distribution of herbivorous fishes on the Great Barrier Reef. *Mar Biol* 159:1143–1154
- Chesher R (1969) Destruction of Pacific corals by the Sea Star *Acanthaster planci*. *Science* 165:280–283
- Cousteau JY, Dumas F, Dugan J (1953) *The silent world*. Harper & Brothers, New York
- Cowan ZL, Symon AD, Ciemon FC, Prachett MS (2016) Predation on crown-of-thorns starfish larvae by damselfishes. *Coral Reefs* 35(4):1253–1262
- Dana TF, Newman WA, Fager EW (1972) *Acanthaster* Aggregations: interpreted as primarily responses to natural phenomena. *Pacific Sci* 26:355–372
- Dart JKG (1972) Echinoids, algal lawn and coral recolonization. *Nature* 239:50–51
- Drew LW (2011) Are we losing the science of taxonomy? *Bioscience* 61(12):945
- Dulvy NK, Freckleton RP, Polunin NVC (2004) Coral cascades, starfish outbreaks and exploitation. *Ecol Lett* 7: 410–416
- Gladstone W, Krupp F, Younis M (2003) Development and management of a network of marine protected areas in the Red Sea and Gulf of Aden region. *Ocean Coastal management* 46(8):741–761
- Gordon T, Cowburn B, Sluka R (2015) Defended territories of an aggressive damselfish contain lower juvenile coral density than adjacent non-defended areas on Kenyan lagoon patch reefs. *J Intl Soc Reef Studies* 34(1):13–16
- Götz B, Stralsund F, Kroll DK, Schuhmacher H (2003) Patterns and changes of reef-coral communities at the Sanganeb-Atoll (Sudan, Central Red Sea):1980 to 1991. *Facies* 49(1):271–297
- Hass H (1952a) *Diving to Adventure*. Jarrolds, 236 pp
- Hass H (1952b) *Under the Red Sea with Spear and Camera*. English translation by James Cleugh, Rand McNally & Co, p 208
- Hassan MH, Khanfar MA, Elnagar AY, Mohammed R, Shaala LA, Youssef DTA, Hifnawy MS, El Sayed KA (2010) Pachycladins A-E, prostate cancer invasion and migration inhibitory eunicellin-based diterpenoids from the Red Sea soft coral *Cladiella pachyclados*. *J Nat Prod* 73(5):848–853
- Hata H, Kato M (2002) Weeding by the herbivorous damselfish *Stegastes nigricans* in nearly monocultural algae farms. *Marine Ecology Prog Ser* 237:227–231
- Head SM, Ormond RFG (1978) A platform as a base for coral reef studies. In: Stoddart DR, Johannes RE (eds) *Coral reefs, research methods*. UNESCO, Paris, pp 109–118
- Head SM (1980) *The ecology of corals in the Sudanese Red Sea*. Ph.D. Thesis, University of Cambridge, 471 pp

- Head SM (1987) Corals and coral reefs of the red sea. In: Edwards AJ, Head SM (eds) Key Environments: Red Sea. Pergamon Press, pp 128–151
- Henderson JA, Lucas JS (1971) Larval development and metamorphosis of *Acanthaster planci* (Asteroidea). *Nature* 232:655–657
- Hiroki H, Kato M (2002) Weeding by the herbivorous damselfish *Stegastes nigricans* in nearly monocultural algae farms. *Marine Ecology Prog Ser* 237:227–231
- Hobbs JPA, Jones GP, Munday PL (2011) Extinction risk in endemic marine fishes. *Conserv Biol* 25(5):1053–1055
- Hoey J, Campbell ML, Hewitt CL, Gould B, Bird R (2016) *Acanthaster planci* invasions: Applying biosecurity practices to manage a native boom and bust coral pest in Australia. *Management Biological Invasions* 7(3):213–220
- Hughes TP (2010) Rising to the challenge of sustaining coral reef resilience. *Trends Ecology Evolution* 25(11):633–642
- Hughes RN, Hughes DJ, Smith IP (2014) Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster* spp). *Oceanography Marine Biol: Annual Rev* 52:133–200
- James P, Endean R, Robert R (1976) Requiem for the reef: the story of official distortion about the Crown-of-Thorns starfish. Foundation Press, Brisbane
- Jessen C, Voolstra CR, Wild C (2014) In situ effects of simulated overfishing and eutrophication on settlement of benthic coral reef invertebrates in the Central Red Sea. *PeerJ Preprints* 2:e227v1, <https://doi.org/10.7287/peerj.preprints.227v1>
- Kamya PZ, Dworjanyn SA, Hardy N, Mos B, Uthicke S, Byrne M (2014) Larvae of the coral eating crown-of-thorns starfish, *Acanthaster planci* in a warmer-high CO2 ocean. *Glob Change Biol* 20:3365–3376
- Kamya PZ, Byrne M, Graba-Landry A, Dworjanyn SA (2016) Near-future ocean acidification enhances the feeding rate and development of the herbivorous juveniles of the crown-of-thorns starfish. *Acanthaster planci*. *Coral Reefs* 35(4):1241
- Kamya PZ, Byrne M, Mos B, Hall L, Dworjanyn SA (2017) Indirect effects of ocean acidification drive feeding and growth of juvenile crown-of-thorns starfish, *Acanthaster planci*. *Proc Roy Soc B* 284 (1856). <https://doi.org/10.1098/rspb.2017.0778>
- Kaufman L (1977) The three spot damselfish: effects on benthic biota of Caribbean coral reefs. *Proc 3rd Int Coral Reef Symp* 1:559–564
- Keesing JK (1990) Feeding biology of the crown-of-thorns starfish, *Acanthaster planci* (Linnaeus). Ph.D. dissertation, James Cook University
- Keller C (1891) Die Spongienfauna des rothen Meeres (2) *Zeitschrift für Wissenschaftliche Zoologie* 52:294–368
- Klaus R (2015) Coral reefs and communities of the central and southern Red Sea (Sudan, Eritrea, Djibouti, and Yemen). In: Rasul NMA, Stewart ICF (eds) The Red Sea: the formation, morphology, oceanography and environment of a young ocean basin. Springer Earth System Sciences, Berlin, Heidelberg, pp 409–452
- Knowlton N, Jackson JBC (2008) Shifting baselines, local impacts, and global change on coral reefs. *PLoS Biol* 6(2):54
- Kotb M, Abdulaziz M, Al-Agwan Z, Alshaikh K, Al-Yami H, Banajah A, Devantier L, Eisinger M, Eltayeb M, Hassan M, Heiss G, Howe S, Kemp J, Klaus R, Krupp F, Mohamed N, Roupheal T, Turner J, Zajonz U (2004) Status of coral reefs in the Red Sea and Gulf of Aden in 2004. In: Wilkinson C (ed) Status of coral reefs of the world. Australian Inst Marine Sci, Townsville, Queensland, Australia, pp 137–154
- Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol Monogr* 56(3):183–200
- Lirman D (2001) Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19(4):392–399
- Lobel PS (1980) Herbivory by Damselfishes and their role in coral reef community ecology. In: Biology of Damselfishes. Rosenstiel school of marine and atmospheric science, University of Miami, *Bull Marine Sci* 30:273–289
- Lobel PS (1981) Trophic biology of herbivorous reef fishes: Alimentary pH and digestive capabilities. *J Fish Biol* 19:365–397
- Lucas JS (1973) Reproductive and larval biology of *Acanthaster planci* (L.) in Great Barrier Reef waters. *Micronesica* 9:197–203
- Lucas J (1982) Quantitative studies of feeding and nutrition during larval development of the coral reef asteroid *Acanthaster planci* (L.). *J Experimental Marine Biol Ecol* 65(2):173–194
- Lucas JS (1984) Growth and maturation of *Acanthaster planci* (L.) (Asteroidea) and hybrids in the laboratory, including observations on the effects of diet. *J Exp Mar Biol Ecol* 79:129–147
- Mayer AL (2004) The dynamic regime concept for ecosystem management and restoration. *Bioscience* 54(11):1013–1020
- McCook L, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *J Intl Soc Reef Studies* 19(4):400–417
- Moore RJ (1978) Is *Acanthaster planci* an r-strategist? *Nature* 271:56–57
- Moore RJ (1985) A study of an outbreak of the Crown-of-Thorns Starfish *Acanthaster planci*. Report of the Queen Mary College (1984) Red Sea Expedition to Dungonab Bay. School of Biological Sciences, Queen Mary College, University of London, Sudan, p 91
- Moore RJ (1988) Persistent and transient populations of the Crown-of-Thorns Starfish, *Acanthaster planci*. In: *Acanthaster and the Coral Reef: a theoretical perspective*. Proceedings workshop held at the Australian institute of marine science, Townsville, Aug. 6–7, 1988
- Mora C, Andréfouët S, Costello MJ, Kranenburg C, Rollo A, Veron J, Gaston KJ, Myers RA (2006) Coral reefs and the global network of marine protected areas. *Science* 312(5781):1750–1751. <https://doi.org/10.1126/science.1125295>
- Moran PJ (1986) The *Acanthaster* phenomenon. *Oceanogr Mar Biol Ann Rev* 24:379–480
- Mumby PJ, Harborne AR (2010) Marine reserves enhance the recovery of corals on Caribbean reefs. *PLoS ONE* 5(1):e8657
- Nasr DH (2015) Coral reefs of the Red Sea with special reference to the Sudanese coastal area. In: Rasul NMA, Stewart ICF (eds) The Red Sea: the formation, morphology, oceanography and environment of a young ocean basin. Springer Earth System Sciences, Berlin Heidelberg, pp 453–469
- Ormond RFG, Campbell AC, Head SM, Moore RJ, Rainbow PR, Sanders AP (1973) Formation and breakdown of aggregations of the Crown-of Thorns Starfish *Acanthaster planci*. *Nature* 246:167–168
- Ormond RFG, Campbell AC (1974) Formation and breakdown of *Acanthaster planci* aggregations in the Red Sea. *Proc 2nd Int Coral Reef Symp* 1:595–619
- Plucer-Rosario G (1987) The effect of substratum on the growth of *Terpios*, an encrusting sponge which kills corals. *Coral Reefs* 5 (4):197–200
- Potts DC (1977) Suppression of coral populations by filamentous algae within damselfish territories. *J Experimental Marine Biol Ecol* 28 (3):207–216
- Pratchett MS, Caballes CF, Rivera-Posada JA, Sweatman HPA (2014) Limits to understanding and managing outbreaks of Crown-of-Thorns Starfish (*Acanthaster* spp). *Oceanography Mari Biol Ann Rev* 52:133–200
- Priest MA, DiBattista JD, McIlwain JL, Taylor BM, Hussey NE, Berumen ML (2016) A bridge too far: dispersal barriers and cryptic speciation in an Arabian Peninsula grouper (*Cephalopholis hemistiktos*). *J Biogeogr* 43:820–832

- Raitsos DE, Hoteit I, Prihartato PK, Chronis T, Triantafyllou G, Abualnaja Y (2011) Abrupt warming of the Red Sea. *Geophys Res Lett* 38:L14601. <https://doi.org/10.1029/2011GL047984>
- Randall JE (1972) Chemical pollution in the sea and the crown of thorns starfish (*Acanthaster planci*). *Biotropica* 4:132–144
- Randall JE (1983) Red Sea Reef Fishes. Immel Publishing, 192 pp
- Randall JE, Ben-Tuvia A (1983) Review of the groupers (Pisces: Serranidae: Epinephelinae) of the Red Sea, with descriptions of a new species of *Cephalopholis*. *Bull Marine Sci* 33:373–426
- Randall JE (1994) Twenty-two new records of fishes from the Red Sea. *Fauna of Saudi Arabia* 14:259–275
- Rasher DB, Engel S, Bonito V, Fraser GJ, Montoya JP, Hay ME (2012) Effects of herbivory, nutrients, and reef protection on algal proliferation and coral growth on a tropical reef. *Oecologia* 169 (1):187
- Reinicke GB, Kroll DK, Schuhmacher H (2003) Patterns and changes of reef-coral communities at the Sanganeb-Atoll (Sudan, Central Red Sea): 1980 to 1991. *Facies* 49(1):271–297
- Riegl BM, Bruckner AW, Rowlands GP, Purkis SP, Renaud P (2012) Red Sea coral reef trajectories over 2 decades suggest increasing community homogenization and decline in coral size. *PLoS ONE* 7: e38396. <https://doi.org/10.1371/journal.pone.0038396>
- Rützler K (2002) Impact of crustose clonid sponges on Caribbean reef corals. *Acta Geologica Hispanica* 37(1):61–72
- Salam MYA (2006) Marine and Coastal Environment Conservation in Sudan: The Role of Marine Protected Areas. UNEP
- Sapp J (1999) What is Natural?. Oxford University Press, Coral Reef Crisis, p 275
- Sammarco PW (1980) *Diadema* and its relationship to coral spat mortality: Grazing, competition and biological disturbance. *J Exp Mar Biol Ecol* 45:242–272
- Sawall Y, Al-Sofyani A (2015) Biology of Red Sea corals: Metabolism, reproduction, acclimatisation, and adaptation. In: Rasul NMA, Stewart ICF (eds) *The Red Sea: the formation, morphology, oceanography and environment of a young ocean basin*. Springer Earth System Sciences, Berlin Heidelberg, pp 487–509
- Schopmeyer SA, Lirman D (2015) Occupation dynamics and impacts of Damselfish territoriality on recovering populations of the threatened staghorn coral. *Acropora cervicornis*. *PLoS ONE* 10 (11):e0141302. <https://doi.org/10.1371/journal.pone.0141302>
- Selig ER, Bruno JF (2010) A global analysis of the effectiveness of marine protected areas in preventing coral loss. *PLoS ONE* 5(2): e9278. <https://doi.org/10.1371/journal.pone.0009278>
- Sheppard CRC (1982) Coral populations on reef slopes and their major controls. *Mar Ecol Progr* 7:83–115
- Sheppard CRC, Sheppard ALS (1991) Corals and coral communities of Arabia. *Fauna Saudi Arabia* 12:3–170
- Sheppard CRC, Price A, Roberts C (1992) Marine ecology of the Arabian region: patterns and processes in extreme tropical environments. Academic Press, London, p 359
- Smith JE, Shaw M, Edwards RA, Obura D, Pantos O, Sala E, Sandin SA, Smriga S, Hatay M, Rohwer FL (2006) Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecology Lett* 9(7):835–845
- Sparks KM, Foo SA, Uthicke S, Byrne M, Lamare M (2017) Paternal identity influences response of *Acanthaster planci* embryos to ocean acidification and warming. *Coral Reefs* 36(1):325–338
- Stephenson W, Searles RB (1960) Experimental studies on the ecology of intertidal environments at Heron Island. I. Exclusion of reef fish from beach rock. *Australian J Marine Freshwater Res* 2:241–267
- Tang SL, Hong MJ, Liao MH, Wann-Neng J, Chiang PW, Chen CB, Chen CA (2011) Bacteria associated with an encrusting sponge (*Terpios hoshinota*) and the corals partially covered by the sponge. *Environmental Microbiol* 13(5):1179–1191
- Uthicke S, Pecorino D, Albright R, Negri AP, Cantin N, Liddy M, Dworjanyn S, Kamy P, Byrne M, Lamare M (2013) Impacts of ocean acidification on early life-history stages and settlement of the coral-eating Sea Star *Acanthaster planci*. *PLoS ONE* 8(12):e82938. <https://doi.org/10.1371/annotation/b03dc5d7-0cfd-4182-b39d-fb9299275d5c>
- Uthicke S, Logan M, Liddy M, Francis D, Hardy N, Lamare M (2015) Climate change as an unexpected co-factor promoting coral eating seastar (*Acanthaster planci*) outbreaks. *Sci Reports* 5:8402. <https://doi.org/10.1038/srep08402>
- Vacelet J, Al Sofyani A, Al Lihaibi S, Kornprobst J-M (2001) A new haplosclerid sponge species from the Red Sea. *J Marine Biol Assoc UK* 81(6):943–948
- Vine PJ (1970) Field and laboratory observations of the Crown of Thorns starfish, *Acanthaster planci*. *Nature* 228:341–342
- Vine PJ (1972) Spirorbinae (Polychaeta: Serpulidae) from the Red Sea, including descriptions of a new genus and four new species. *Zool J Linnean Soc* 51(2):177–201
- Vine PJ (1973) Crown of Thorns (*Acanthaster planci*) plagues: The natural causes theory. *Atoll Res Bull* 166:1–10
- Vine PJ (1974) Effects of algal grazing and aggressive behaviour of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral-reef ecology. *Marine Biol* 24(2):131–136
- Vine PJ, Head SM (1977) Growth of corals on Commander Cousteau's underwater garage at Shaab Rumi (Sudanese Red Sea). *Jeddah Nature J*, pp 6–17
- Vine PJ, Vine MP (1980) Ecology of Sudanese coral reefs with particular reference to reef morphology and distribution of fishes. *Proc Symp on The Coastal and Marine Environment of the Red Sea, Gulf of Aden and Tropical Western Indian Ocean*. Khartoum, 9–14 Jan, University of Khartoum
- Vine P (1986) Red Sea Invertebrates. Immel Publishing, 224 pp
- Vine P, Schmid H (1987) Red Sea Explorers. Immel Publishing, 206 pp
- Vogler C, Benzie J, Lessios H, Barber P, Wörheide G (2008) A threat to coral reefs multiplied? Four species of crown-of-thorns starfish. *Biology Lett* 4(6):696–699
- Wolfe K, Graba-Landry A, Dworjanyn SA, Byrne M (2017) Superstars: Assessing nutrient thresholds for enhanced larval success of *Acanthaster planci*, a review of the evidence. *Marine Pollution Bull.* <https://doi.org/10.1016/j.marpolbul.2016.12.079>
- Wonders JBW (1977) The role of benthic algae in the shallow reef of Curaco (Netherlands Antilles). III. The significance of grazing. *Aquatic Botany* 3:357–390
- Yamaguchi M (1973) Recruitment of coral reef asteroids, with emphasis on *Acanthaster planci* (L.). *Micronesica* 9(2):207–212
- Yokochi H, Ogura M (1987) Spawning period and discovery of juvenile *Acanthaster planci* (L.) (Echinodermata: Asteroidea) at northwestern Iriomote-Jima, Ryukyu Islands. *Bull Marine Sci* 41(2):611–616
- Zann L, Brodie J, Berryman C, Naqasima M (1987) Recruitment, ecology, growth behaviour of juvenile *Acanthaster planci* (L.) (Echinodermata: Asteroidea). *Bull Marine Sci* 41(2):561–575