Crown-of-thorns starfish, *Acanthaster solaris* by virtue of their Pacific origin and red / brown colouration as well as consistency with the observations of Keesing and collaborators from 2019. The Australian Institute of Marine Science © courtesy of Hall et al. 2017, Nature, and The Creative Commons Attribution Licence.

Reef Focus: Crown-of-Thorns Starfish

Chris Aslett

Crown-of-thorns starfish (COTS) of the genus *Acanthaster* (Echinodermata: Asteroidea) are distributed throughout most tropical regions including the Red Sea (Goreau 1964) and the Indian and Pacific Oceans (Pratchett et al. 2014) as far east as Panama (Glynn 1973) but they have never been described in the wider Caribbean or indeed anywhere in the Atlantic (Vine 1973; Kayal et al. 2012; Pratchett et al. 2014). They regularly scourge the ecosystems of Brunei (Lane 2012), Fiji (Zann et al. 1987; Zann et al. 1990), French Polynesia (Kayal et al. 2012), Guam (Chesher 1969), southern Japan (Deaker & Byrne 2022), the Chagos Archipelago (Roche et al. 2015), the Coral Triangle (CT; Baird et al. 2013), New Caledonia (Conand 1985), Samoa (Birkeland 1981), The Great Barrier Reef (GBR; Deaker & Byrne 2022), India (Roche et al. 2015), Tonga (Birkeland 1981), and the South China Sea (Lane 2012) where they amass in incalculable numbers to denude vast areas already threaten by well-known stressors. Historic literature catalogued their dispersal off Portuguese India (Goa) in 1743; the Philippines in 1781; Java in 1793; Mauritius in 1885; GBR in 1913 (Clark 1921), Low Isles from where Livingston's 1928 to 1929 expedition radiated (Livingstone 1932; Vine 1973), American Samoa in 1938 (Flanigan & Lamberts 1981, cited in Birkeland 1981), and New Caledonia in 1950 (Catala, cited in Conand 1985).

Sightings have been comparatively well-documented since the 1930s (Vine 1973), yet it was challenging to appraise their impact until the advent of scuba (Westcott et al. 2016). Nonetheless, when the threat was finally revealed, strong emotional responses inspired common names like mother-in-law's cushion: arguably the least offensive of which, is used today, COTS (Branham 1973). The press gleefully engaged in stirring up public opinion which was still raging 25 years later, where the scientific community was implicated in a "conspiracy of silence" as laypersons feared the worst (Zann 1987a). Numerous biocontrol measures were therefore kneejerk and disproportionate to ecological impairment (Westcott et al. 2016).

Despite decades of research and copious investment, it is still unclear what aspects of their natural history enable them to go from manageable populations to an advancing multitude of half a metre-wide corallivorous sea stars virtually overnight (Deaker & Byrne 2022). The author was thus motivated to examine the affluence of evidence to an end of shedding some measured and objective light on this tantalising mystery.

Taxonomy

The ancestral lineages of starfish of the genus *Acanthaster* are being extensively revised (Webb et al. 2024) where the morphology and locality of the original description's topotypes, matches the candidate specimen and its distribution, which appraises con- and inter-specific phenotypic plasticity within a species-substantiating framework (Aslett 2024a; Bridge et al. 2024). See: Appendix I for geographic range and type localities. Despite COTS being the most widely studied kind of starfish, there are merely three unequivocally named congeners: *Acanthaster planci* Linnaeus 1758, *Acanthaster mauritiensis* de Loriol 1885, and *Acanthaster brevispinus* Fisher 1917, with the former two nested within the *Acanthaster planci* species group which occur exclusively and respectively in the northern and southern regions of the Indian Ocean (Haszprunar & Spies 2014; Haszprunar et al. 2017). Consequently, uncertain nomenclature may be designated *incertae sedis*.

Keywords: COTS; crown-of-thorns starfish; natural history; outbreak causation; reef ecological impact; starfish control; venomous spines.

Evidence of these sea stars was chronicled from the beginning of the 18th century insofar as a remark made by Rumphius in 1705 preceded a formal description by Plancus and Gualtieri in 1743 (Vine 1973). The father of modern taxonomy, Carl Linnaeus (Manktelow 2010) paid homage to their contribution when he subsequently erected *Asterias planci*. The accepted genus, *Acanthaster* Gervais 1841 replaced *Echinaster* Gray 1840 which was erected by Müller and Troschel in 1844 to absorb *Asterias solaris* Schreber 1793 (Haszprunar & Spies 2014). *Acanthaster*'s affiliates including *A. planci* Linnaeus 1758 are ranked in the kingdom Animalia, the phylum Echinodermata, the subphylum Asterozoa, the class Asteroidea, the subclass Ambuloasteroidea, the infraclass Neoasteroidea, the superorder Valvatacea, the order Valvatida, and the family Acanthasteridae (WoRMS 2026). *Acanthaster* cf. *solaris* initially appeared genetically-indistinguishable from *A. planci* and were thus nested together (Hall et al. 2017), whereas deepwater-dwelling *A. brevispinus* Fisher 1917 scarcely venture into well-illuminated (euphotic) milieus (Birkeland & Lucas 1990, cited in Pratchett et al. 2014; Haszprunar et al. 2017). Stable first generation (F_1) hybrids of *A. planci* and *A. brevispinus* have been reared for several years in the laboratory, whilst F_2 and backcrosses proved mostly inviable (Lucas 1984; Haszprunar et al. 2017). F_1's life histories were not too dissimilar to *A. planci*'s (Lucas 1984). *A. ellisii* once thought peculiar to the eastern Pacific were hitherto considered valid, where Caso erected two subspecies: *A. ellisii ellisii* and *A. e. pseudoplanci* (Caso 1962, cited in Moran 1988); however, later comparative sequence analyses discovered they were significantly homologous to *A. planci* and *A.* cf. *solaris* and thus formed a convincing unsynonymised complex (Appendix I; Glynn 1974; Vogler et al. 2013).

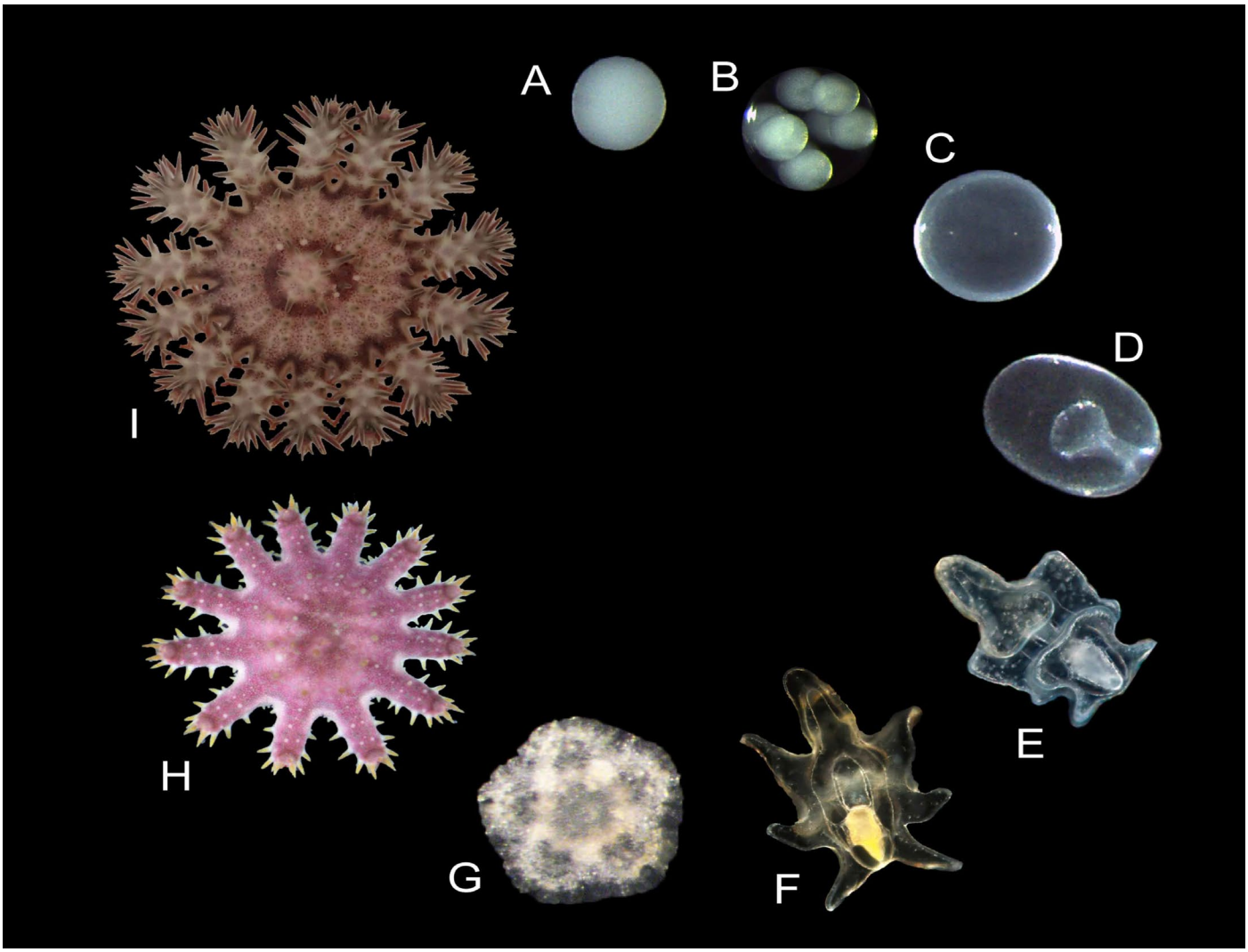


Fig. 1. The life cycle of crown-of-thorns starfish: [A to F] waterborne; [G to I] substratum established; [A] unfertilised egg; [B] eight blastomere outcome of third cleavage; [C] blastula; [D] gastrula with rudimentary mouth and gut (archenteron); [E] feeding bipinnaria with a fully developed digestive tract capable of transverse binary fission; [F] phytoplanktivorous brachiolaria with settlement-expediting limbs and a posterior budding competence; [G] newly settled juvenile; [H] late stage herbivorous juvenile, and [I] corallivorous adult (Fig. 16.). Lacks kidney-shaped dipleurula and early bipinnaria between D and E (Uthicke et al. 2019). Micrograph "E" Dr. Jonathan Allen © and micrograph "F" Dr. Paulina Selvakumaraswamy ©. Courtesy of Deaker and Byrne 2022 and the Creative Commons Attribution License 4.0 (CC BY-NC-ND).

Early genotypic disparities suggested there were at least two species (Roche et al. 2015) where colour morphs of grey-green to red-brown were said to crop up in the Pacific, whilst those that were blue to pale red predominated in the Indian Ocean (Benzie 1999). Homologues encoding mitochondrial cytochrome oxidase I's (COI's) barcoding region were redolent of speciation in the Red Sea, the Pacific, and southern and northern Indian Oceans (Vogler et al. 2008; Vogler et al. 2013; Pratchett et al. 2014; Hall et al. 2017).

Contemporary analyses of the microsatellite biomarkers of COTS DNA have revealed *Acanthaster planci* Linnaeus 1758 inhabit India's northern ocean from the Sea of Oman to North Sumatra, whereas *A. mauritiensis* de Loriol 1885 occur mainly in India's west, but also around Chagos and Christmas Island (Vogler et al. 2013). A third nominally toxic unassigned species is found exclusively in

the Red Sea that is reported to have a maximum of 13 to 14 arms as opposed to the 23 of other COTS (Haszprunar et al. 2017) whilst still to be formerly classified, *Acanthaster solaris* Schreber 1793 are prevalent throughout the Pacific (Vogler et al. 2008; Haszprunar & Spies 2014; Haszprunar et al. 2017; Wilmes et al. 2018). *A. planci* and *A. solaris* are now described as iridescent purple and red to brownish orange respectively (Appendix I; Keesing et al. 2019) while *A. mauritiensis* are rust coloured to light blue (Haszprunar et al. 2017). Moreover, the phylogeny of *A. solaris* infers further diversification and subspeciation (Yasuda et al. 2006, cited in Haszprunar et al. 2017; Timmers et al. 2012; Tuso et al. 2016, cited in Haszprunar et al. 2017).

Acute pathologies have not been reported by divers that have handled the Red Sea variants, yet those pricked by the spines of Pacific species presented with abscesses, preprogrammed cell death, anaemia, and bone destruction, and recounted hours of severe pain to weeks of nausea and fever (Birkeland & Lucas 1990, cited in Haszprunar et al. 2017). Spine venom has likely evolved to deter predation, which may clarify why Red Sea COTS are nocturnal (Wörheide personal observation, cited in Haszprunar et al. 2017). Fijian, Palauan, and Samoan fishermen place the sea star's mouth over the wound so it can suck out the poison, which appears to have been devised by ancient islanders three times in isolation (Birkeland & Randall 1979).

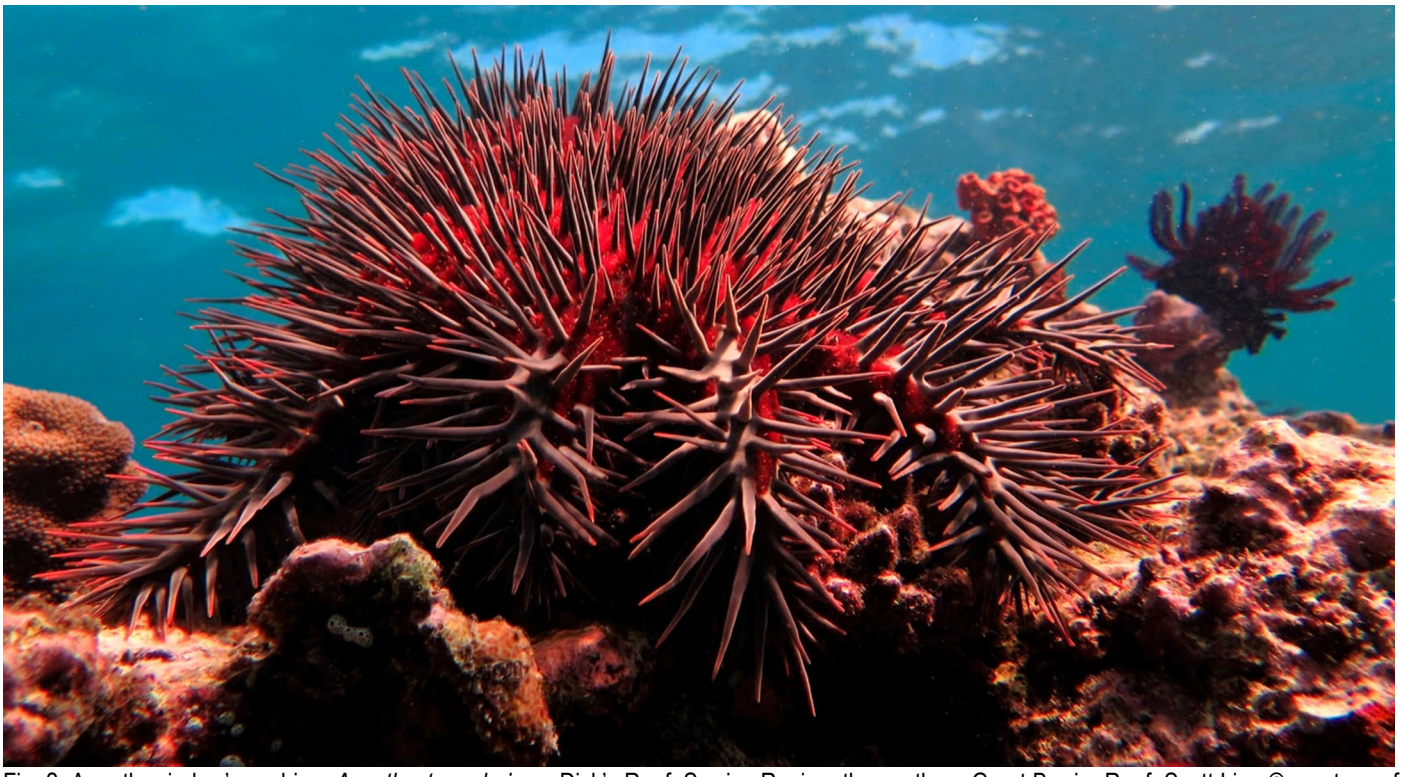


Fig. 2. A mother-in-law's cushion, *Acanthaster solaris* on Dick's Reef, Swains Region, the southern Great Barrier Reef. Scott Ling © courtesy of Cowan et al. 2017, Diversity, and The Creative Commons Attribution licence.

Impacts on Reef Habitats

COTS outbreaks increase the time it takes reefs to recover from abiotic disturbances like anomalous weather (Wakeford et al. 2008; De'ath et al. 2012) as they digest first polyps, juveniles, and adult colonies alike (Keesing 1993), whose replenishment may take several decades (Pearson 1981). Their dietary preference extends to rapid-growing but bleach prone species of *Acropora* (Keesing et al. 2019) that conceivably deposited most of the calcium carbonate in the Indo-Pacific since the late Oligocene some 28 to 23 million years ago (MYA; Wallace & Rosen 2006). These corals are thus foundation species upon which much of the regional ecology relies (Zhao et al. 2021). Nevertheless, the accelerated growth of acroporans means coral cover should be replenished within 15 years (Zann 1987a). All the same, the prevailing rigours of climate change were yet to be felt when this observation was made by Leon Zann towards the end of the 1980s. The Complexa Acroporid genera, *Montipora* (Pratchett et al. 2014) and *Isopora* (Dana 1970; Dana et al. 1972) are also targeted, whereas the genera *Heliopora*, *Hydonophora*, *Leptastrea*, *Oxypora*, and *Turbinaria* seem indigestible (Pratchett et al. 2014), whereas Ormond and colleagues saw *Goniastrea* and *Turbinaria* being voraciously consumed by a different species in the Sudanese Red Sea (Ormond et al. 1973). *Pocillopora damicornis* (Robusta: Pocilloporidae) are either a favourite or merely sustenance which are forcefully defended by their symbiotic pistol shrimp (Glynn 1987; Moran 1988; Cowan et al. 2016), whilst their polyps are half as nourishing as *Acropora nasuta*'s, yet they retain a competency for capturing and consuming zooplanktonic COTS (Yamaguchi 1974). Even so, these kinds of appraisals rarely yield worthwhile data insofar as populations endemic to certain subregions assume dissimilar dietary preferences (Baird et al. 2013), which are diversified further when hordes of starfish descend during epizootics (Keesing et al. 2019). Intriguingly, all captive corallivorous juveniles died after eating an exclusive diet of *Echinopora lamellosa* which may reflect mesenteric defence, whilst dietary preferences appear uninfluenced by nutritional value which are likely determined by environmental preconditioning (Fig. 17.; Johansson et al. 2016). Favoured nourishment may be symptomatic of accessibility (Potts 1981) and thus prevalence and colonial morphology (Keesing 1990; Pratchett 2007) which is probably resolved as sea stars mature (Johansson et al. 2016). After outbreak densities of *Acanthaster solaris* off northwestern Australia's Montebello and Barrow Islands have devoured their preferred prey, they go on to absorb extensive populations of the families Faviidae, Merulinidae, and Poritidae (Keesing et al. 2019). COTS find it challenging to cling to massive

smooth colonies like some species of *Porites* and are thus prone to dislodgment during their unavoidably lengthy feeds in turbulent environments (Chesher 1969; Pratchett et al. 2014), where colonial mucogenesis counters adherence.

One team of researchers remarked in 2015, that although numbers had been raised, they were unlikely to have reached plague densities on the northern warmer territories of GBR (Miller et al. 2015) where widespread thermal-stress-induced bleaching occurred in 2015 and 2016 (Hughes et al. 2018). Notwithstanding, Westcott and colleagues alluded to outbreaks in the north between 2008 to 2010, whereas the coral cover of northeastern Australia decreased by as much as 50 percent from 1985 to 2012 (Westcott et al. 2020).

Akin to the transformations of reef communities that accompany the localised enrichment of dissolved inorganic nitrogen and phosphorus (DIN and DIP) whereby several become fleshy macroalgae-dominated (Barile & Lapointe 2005; Lapointe et al. 2010; Honig & Mahoney 2016) which retain an inertia and are unlikely to revert (Bulleri et al. 2018; Schmitt et al. 2019; Aslett 2023; Smith et al. 2023), COTS have elicited phase shifts since the 1960s, where reefs become rubble wastelands predisposed to subsidence adorned by macroalgae, soft corals, and sponges (Sano et al. 1987; Hughes 1994). Widespread digestion of coral flesh followed by mass starfish die off is likely to kickstart these ecological transitions, as it cannot fail to lead to upsurges of dissolved inorganic nutrients. Besides the impact on other corallivores, a loss of three-dimensional habitat can lead to mass extinctions and / or over predation as numerous animals do not have the ability to migrate (Deaker & Byrne 2022), whilst dredging may free up COTS-nurturing niches (Walsh et al. 1971; Moran 1988). Waves of *Acanthaster* have coincided with elevated rates of calcite bioerosion (Musso 1993), the dwindling of coral head-sheltering zooplanktivorous damselfish (Pratchett et al. 2012) and corallivorous butterflyfish (Kayal et al. 2012), accompanied by an influx of sizeable shoals of herbivorous teleosts (Hart et al. 1996; Han et al. 2016). Local ecology is thus significantly perturbed (Pratchett 2007; Pratchett et al. 2020) and ripe for starfish inhabitation (Pratchett et al. 2014).

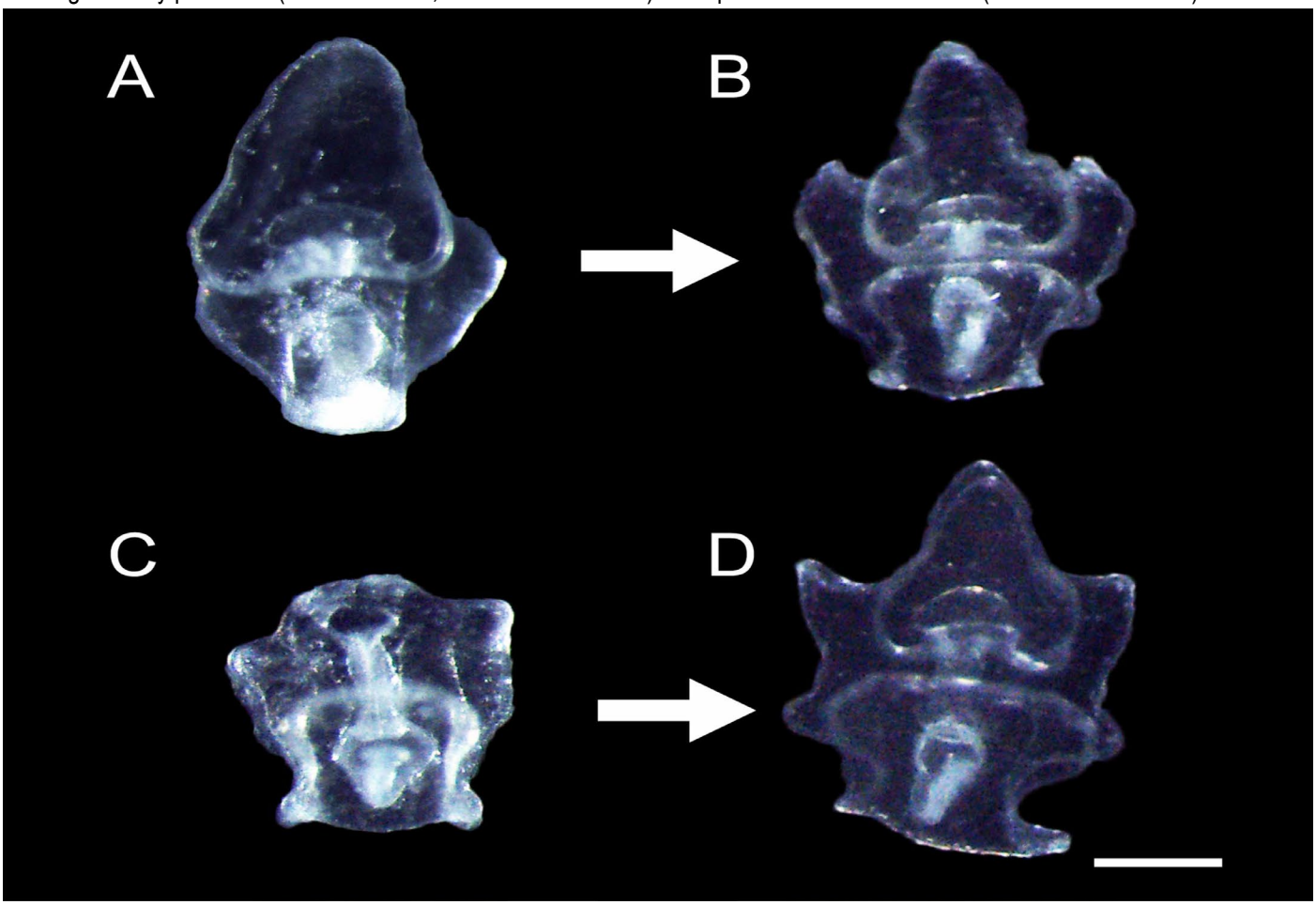


Fig. 3. The outcome of transverse binary fission in zooplanktonic bipinnaria with a 200-micron (µm) scale bar: [A & C] respective partially regenerated anterior and posterior; [B & D] almost fully regenerated four days after separation (Fig. 1. E). Courtesy of Deaker and Byrne 2022 and the Creative Commons Attribution License 4.0 (CC BY-NC-ND).

The foremost proficient primary-producing tropical saltwater ecosystems require ultrapure water, where nearshore fringing reefs or flats are invariably polluted by dense human settlements and nearby pastoral or arable farming and their land runoff and sewage discharge (Frias-Lopez et al. 2002; Aslett 2024), whereas nutrient enrichment (eutrophy) exacerbates coral bleaching and disease (Voss & Richardson 2006; Cunning & Baker 2013; Ho 2013; Vega Thurber et al. 2014). The most anthropogenically-degraded once thriving reef ecosystems occur off the densely-populated landmasses of the Caribbean, East Africa, and Southeast Asia (Wilkinson 2004, cited in Pratchett et al. 2014) which is worsened by overfishing (Pratchett et al. 2014). While it is challenging to state with any certainty insofar as reports date back to merely the 1930s, outbreaks that were ostensibly occurring every 50 to 80 years, now happen every 15 (Fabricius et al. 2010; Babcock et al. 2020; Deaker & Byrne 2022), which may erupt every seven in certain subregions (Potts 1981). Given that eutrophic environments support the growth of benthic microscopic “algae” (Aslett 2024), and that newly-settled larvae will monopolise on this smorgasbord, attacks could indeed be influenced by human population density.

Natural History

Adults have a poisonous spike-embellished discoid, albeit uncalcified dorsum, which is unlike most warmwater sea stars (Kettle & Lucas 1987, cited in Deaker & Byrne 2022), surrounded by 10 to 23 calcite-armoured and thorny limbs, with a sizeable ventral eversible stomach approaching 50 percent of their diameter (Birkeland & Lucas 1990, cited in Pratchett et al. 2014; Lawrence & Moran 1992), that envelops and digests all underlying coral which leaves a wake of slimy denuded skeleton (Zann 1987a; Birkeland 1989). However, this process can take from three to six hours (Goreau 1964; Brauer et al. 1970). Consuming from 5 to 10 square metres (m^2) of coral flesh per year (Chesher 1969; Glynn 1973; Birkeland 1989; Johansson et al. 2016), and unlike other corallivores whose predation does not exhaust local populations, they currently remain strong candidates for the foremost biotic threat to reef ecology (Chesher 1969). Their digestive repertoire includes extraordinary enzymes capable of degrading wax esters, which are major components of coral tissue (Glynn 1973, cited in Caballes 2017; Deaker et al. 2020a).

Crabs and pistol shrimp of the genera *Trapezia* and *Alpheus* forcefully defend their respective hosts: *Stylophora* and *Pocillopora* (Glynn 1987; Stella et al. 2011), whereas "acropora" crabs like *Tetralia cavimana* proactively protect colonies (Moran 1988; Glynn 1987; Stella et al. 2011; Cowan et al. 2016). Such companions are mostly discarded by aquarists following their detachment using coral prophylactics. Retrieve from the bottom of dipping vessels and reunite them with colonies as they significantly lessen parasitisations (Fig. 6.; Aslett 2024) yet painstakingly identify as many harmful crabs arrive as hitchhikers; however, these look meaningfully less wholesome (Fig. 10.).

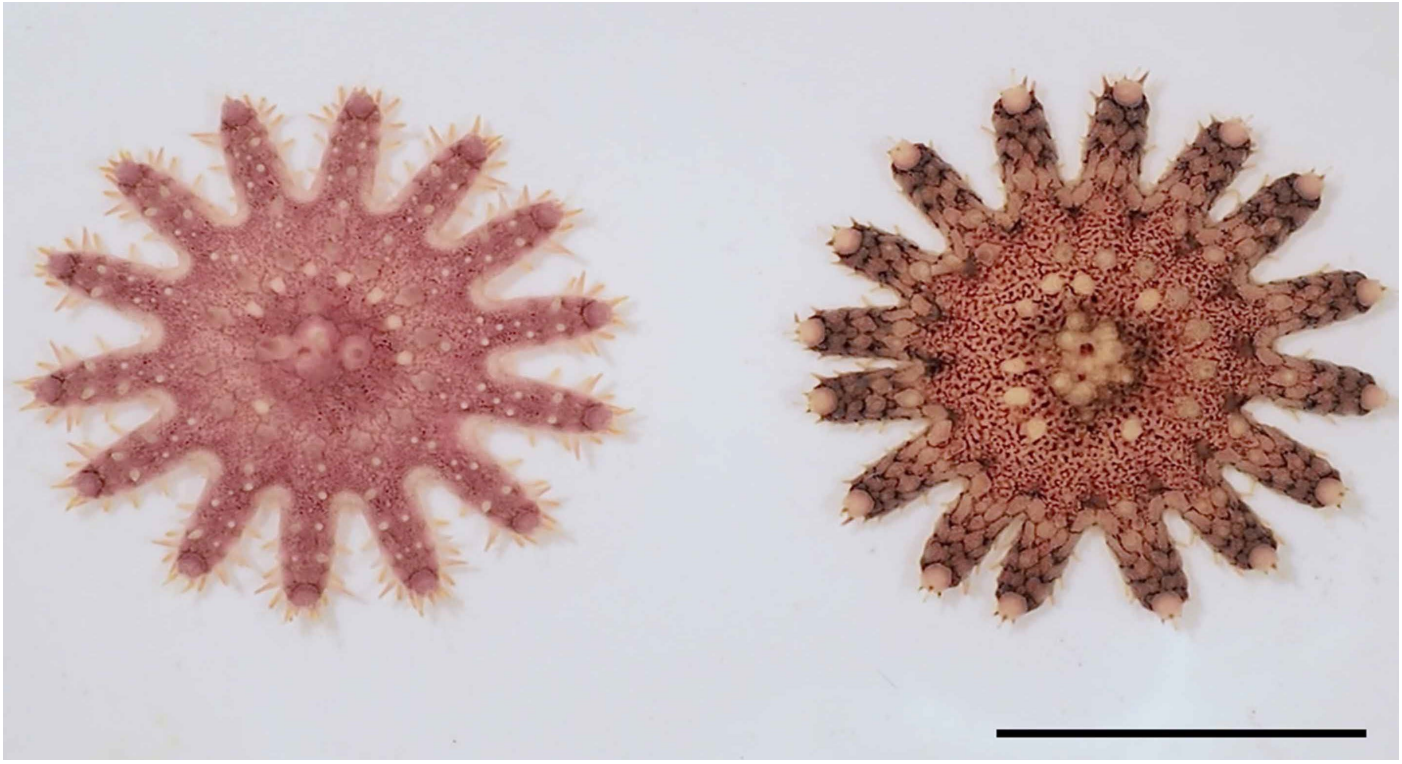


Fig. 4. Magnified photographs of respective one-year-old and six-and-a-half-year-old developmentally-arrested herbivorous COTS with a 1-centimetre scale bar. Yamaguchi referred to pallid central papulae (pimples) and a ring that manifests in up to 150-millimetre juveniles that becomes inconspicuous in adults by virtue of the withdrawal of pimples inside the central disc (Yamaguchi 1974). This description is most likely applicable to what is evident here, whereas the central disc of a youthful adult is unmistakable on the title photograph. Of note are the nascent thorn buds along the upper surfaces of the arms of the younger, which appear to have been transformed into scales on the chronically herbivorous elder. See: Appendix I for clarification. Courtesy of Deaker and Byrne 2022 and the Creative Commons Attribution License 4.0 (CC BY-NC-ND).

Found in numerous tropical environments, they enjoy a zooplanktonic phase, whereupon they settle and transform into herbivorous miniature starfish until around 8 millimetres when they commence to eat coral flesh. Their nomadic lifestyle and dietary plasticity are considered major contributors to their population explosions. Although this kind of "boom and bust" (Uthicke et al. 2009) manifests in other species, most notably insects of the genera *Locusta* and *Nomadacris*, Nature tends to be parsimonious where locusts return to a solitary life after swarming. However, cyclic fluctuations in procreative competency (fecundity) occur in lemmings of the genera *Lemmus*, *Synaptomys*, and *Dicrostonyx* which lead to four litters of up to eight, as opposed to the two litters of five in non-migration years. Like COTS, lemming consortia eventually run out of food, whilst their southward frenzied foraging has on occasion forced those at the advancing front into the ocean where they drown (Bertin et al. 1971).

Whilst a lack of living Scleractinia has been held responsible for mass starfish die off, which ultimately leads to the "bust" phase of an outbreak, the findings of Burkholder's study published in 1973 inferred that COTS can only mount a weak defence against gram positive bacteria, whilst they remain entirely vulnerable to gram negative (Burkholder 1973). Captive examples often become infected and die from bacteriological disease (Lucas 1984; Sutton et al. 1988). *Vibrio harveyi*, *V. tubiashi*, *V. campbellii*, and the genera *Pseudomonas* and *Moraxella* were isolated from those exhibiting lesions / ulcerations, tissue necrosis, and a collapse of turgidity and the orientation of their spines (Sutton et al. 1988). The same symptoms were described by Pratchett around northern GBR's Lizard Island which arose in ostensibly healthy starfish exposed to water contaminated with necrotic tissue (Pratchett 1999). Most meaningfully, the disease coincided with the widespread demise of starfish approaching the zenith of an outbreak, but before the

exhaustion of local corals (Pratchett 2005, cited in Pratchett et al. 2014; Pratchett 2010) where their multitudes expedite transmission (Pratchett et al. 2014). The density-dependent prophylaxis hypothesis proposes immunity is naturally upregulated to prevent the spread of disease when individuals congregate, where the elevated defence of COTS is commensurate with outbreaks and nutritional abundance (Mills 2012). Under normal circumstances, they allocate significant resources to constituent immunity, whilst reserves are finite whose depletion can lead to immunosuppression (Rivera Posada 2012, cited in Pratchett et al. 2014). Injecting the bacterial isolates of Sutton and allies into ostensibly healthy well-nourished starfish did not cause the same illness, yet those that are malnourished (Zann et al. 1990; Sutton et al. 1988) remain particularly vulnerable to Vibrionaceae (Rivera Posada 2012).

Despite them taking several years to grow into monsters (Yamaguchi 1974; Lucas 1984) which may attain a diameter of one metre or more (Moran 1988; Deaker & Byrne 2022) lemming-like fluctuations in reproductive output (Caballes 2017) may partly explain their amassment. Nevertheless, their predatory hoards have likely impacted reef communities for millennia (Vine 1973, cited in Deaker & Byrne 2022; Zann 1987a; Walbran et al. 1989) but without the consequences of anthropogenic activities. Research findings are indicative of attacks becoming more frequent (Fabricius et al. 2010; Babcock et al. 2020; Deaker & Byrne 2022).

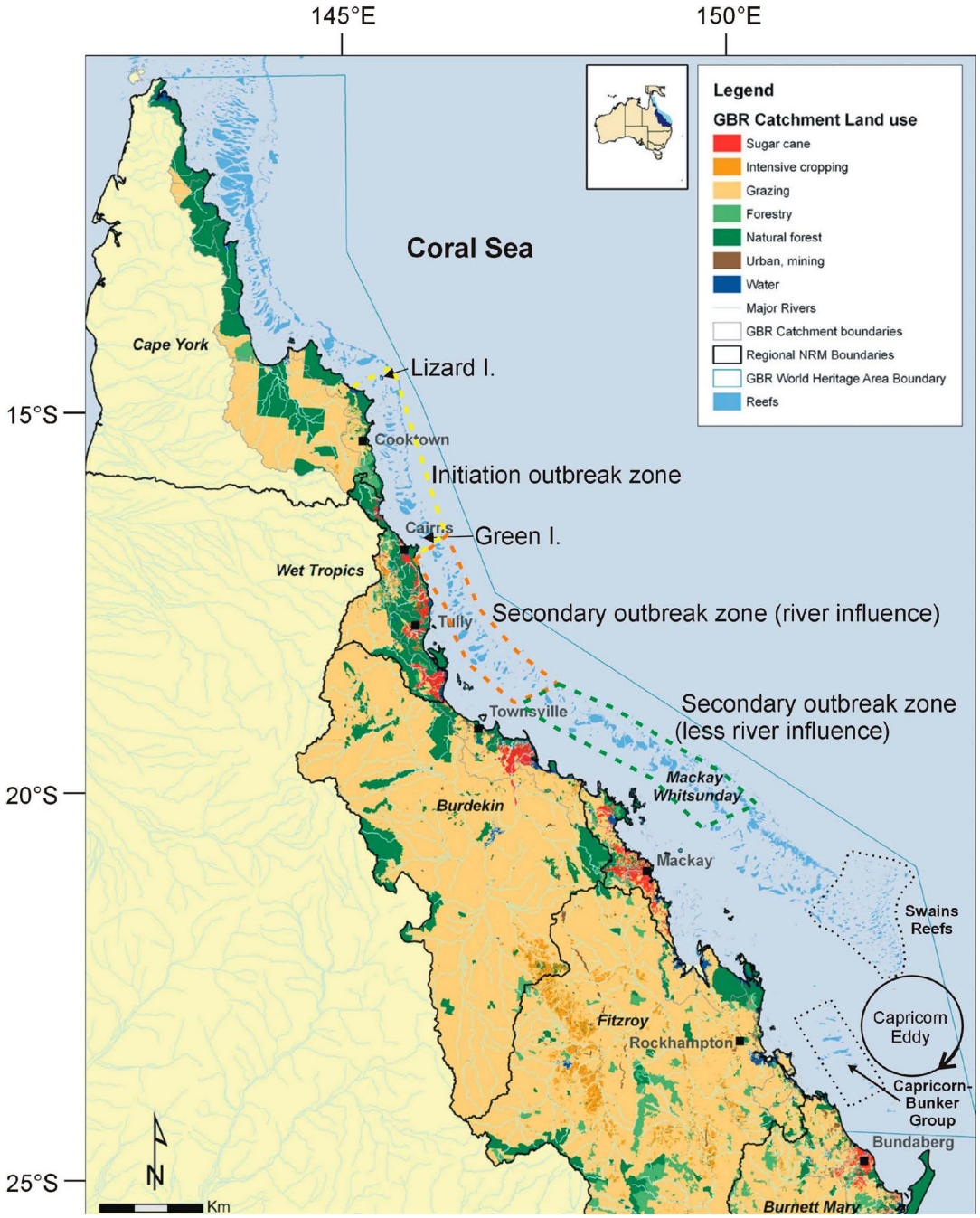


Fig. 5. A map of the northeastern coastline of Australia illustrating the COTS initiation box enclosed by the yellow dotted line, and two further outbreak zones fuelled by eutrophic riverine discharge. Features nutrient-enriching land usage and natural forestry. Courtesy of Brodie et al. 2017, Diversity, and The Creative Commons Attribution Licence.

Predominantly gonochoric (Deaker & Byrne 2022), individuals are typically male or female, yet a contrasting study unearthed hermaphroditism (Guerra et al. 2020) which may or may not be spontaneous, and as such, could induce self-fertilisation (selfing; Hart et al. 2021; Uthicke et al. 2021; Horoiwa et al. 2022). These findings also infer sequential protandry where other sea stars begin life as males then transform into females or hermaphrodites (Achituv & Sher 1991). Male dominated populations are not uncommon (Stump 1994) where genders are easily discerned when sea stars permit the inspection of their ventrums, insofar as ovaries are spherical and yellow to orange whereas testes are cream to pale yellow with far more abundant and tinier lobes (Pratchett et al. 2014). Iteroparity and semelparity describe the reproductive strategies of yearly seasonal, or a single lifetime event followed shortly by death, both of which have been exploited by COTS (Stump 1994). Intriguingly, gonads are reabsorbed in those that are malnourished which probably reflects a life-saving reallocation of resources (Cheney 1974, cited in Caballes 2017).

Profoundly fecund broadcast spawners with a summer trajectory (Uthicke et al. 2019; Caballes et al. 2021), sizeable females can liberate up to and over a hundred million eggs, or over two hundred million per season (Babcock et al. 2016). Procreative competency rises disproportionately with starfish diameter insofar as recently matured adults of less than 30 centimetres and around two years of age liberate between one half and two and a half million ova per annum, whereas 40-centimetre sea stars broadcast

roughly forty-five to forty-six (Birkeland & Lucas 1990, cited in Pratchett et al. 2014). Up to 34 percent of the body mass of a 44.5-centimetre female, might be monopolised by egg production, yet the gonads of respective maternal and paternal sea stars typically amount to 16 and 12 percent (Babcock et al. 2016). The distances over which these starfish can achieve elevated rates of successful fertilisation are two orders of magnitude higher than other marine organisms. It is unclear if sexual reproduction is limited to annual events in certain subspecies (Babcock & Mundy 1992) or whether communities undergo multiple spawns (Conand 1983, cited in Pratchett et al. 2014), where the warmer seas surface temperatures (SSTs) of lower latitudes in the tropics, may influence the maturation of gonads and broadcasting. Despite the discovery of four clades, all COTS likely adopt analogous mating (Pratchett et al. 2014). The gametogenic cycles occurring between September and February of 1990 / 91 equating to the Austral spring and summer, were indicative of multiple events which were dominated by a sizeable early December spawn followed by two smaller bouts of broadcasting mid- to late -January. Intriguingly, on the night of the former, numerous sessile invertebrates were also observed reproducing including numerous corals and bivalves. Participation of this kind is not uncommon (Babcock & Mundy 1992) despite procreation being strictly regulated and cue-dependent in Scleractinia (Lin et al. 2021; Davies et al. 2023). Reproductive gatherings (Guerra et al. 2020) increase the likelihood of cross-fertilisation (Babcock & Mundy 1992; Evans & Marshall 2005), where the results of aquarium-based experiments suggested that the pheromones of both sexes drive aggregations of broadcast-ready sea stars which assist the synchrony of spawns (Beach et al. 1975). Molecular analyses indicate reproduction transpires throughout epizootics (Uthicke et al. 2015). *A. planci* do not release gametes if the distance of a male to the nearest female is too great (Babcock et al. 1994), hence outcomes are significantly impacted by proximity (Vine 1973) and gender ratios (Stump 1994). Reproduction does not appear to be influenced by lunar cycles, but most events are initiated on a tidal ebb or within one hour of low tide, before which starfish appear unusually active. The spawning of wild and captive sea stars often initiates reciprocation in others. Ascending to higher elevations, many rear up to adopt a typically dorsally-concaved posture, when eggs or sperm are liberated from rows of gonopores that run along the undersides of each arm (Pratchett et al. 2014). Remarkably, nighttime populations may subside by as much as 37 percent over the next two days, whilst daytime densities remain consistent. Notwithstanding, most spawns have been observed in the afternoon with the occasional early morning sighting (Babcock & Mundy 1992).

Abrupt rises in phytoplankton and / or 4^{o}C induce spawning in males but not in females, whilst waterborne sperm stimulate meiocyte shedding in either. Hormone- and pheromone-liberating procreating males and spermatozoa, trigger endocrinal cascades in others that culminate in mass-broadcasting. Water-soluble compounds associated with eggs excite male gametes, whereas early larval stages can withstand extensive variances in temperature, salinity, and pH and are thus climate change-adapted. Females that were starved or fed *Porites rus* developed slender ovaries with reduced-diameter eggs compared to females that were satiated on *Acropora abrotanoides*. Larvae from coral-fed adults were larger with well-evolved stomachs most of which unlike larvae from malnourished parents, progressed through late bipinnaria to early brachiolaria. Larval development was expedited in those originating from *Acropora*-fed females compared to the progeny of *Porites*-eating or starved mothers, whose offspring failed to reach mid- to late brachiolaria (Caballes 2017).

These sea stars have comparatively large 220-micron (µm) eggs that are significantly yolky (isolecithal), which sustains and lessens the prey-dependency of their planktonic larvae (George 1999; Byrne et al. 2008; Moran et al. 2013; Caballes 2017). Larger ova raise fertilisation likelihood (Levitan 2006), whereas plumes of zooplankton are evident after the spawning of profuse assemblages (Uthicke et al. 2015) whose densities increase around two hours beforehand (Babcock & Mundy 1992). Nevertheless, egg size diminished in starfish conditioned to the increased temperatures and acidity of foreseen climate change, but this exerted a negligeable impact on fertilisation success. However, rates of zygotic fusion are more than three-fold less towards the end of spawning seasons when mean SSTs increase by 2^{o}C (Hue et al. 2020). Bipinnaria are smaller when pH is supressed and temperature increases (Kamya et al. 2014). The outcomes of wild surveys and genetic analyses are indicative of the geographic retention of larvae (Timmers et al. 2012; Vogler et al. 2013; Miller et al. 2015) where the so-called COTS “initiation box” is said to occur on reefs betwixt GBR’s Lizard Island and Cairns (Fig. 5.; Pratchett et al. 2014; Brodie et al. 2017). However, northeastern Australia’s waterborne DNA would suggest larval dissemination can also occur over 320-kilometre (km) spatial extents (Uthicke et al. 2015), while there appears a lack of interconnectivity between profoundly isolated reefs such as those off Hawai’i and Moorea as well as numerous archipelagos in the central Pacific (Birkeland 1982; Timmers et al. 2012). Regardless, spawning appears to be a localised phenomenon (Babcock & Mundy 1992) and although larval dissemination is likely to be small-scale, sea star migrations could conceivably occur in a stepwise manner throughout multiple spawning years (Horoiwa et al. 2018).

Echinoderms embody the phenotypic trait of dietary plasticity (Strathmann et al. 1992; George 1994; Caballes 2017; McAlister & Miner 2018), together with an expansion of the prey-capturing ciliated bands of their planktonic larvae during periods of nutritional dearth (Strathmann et al. 1992; Wolfe et al. 2015; Caballes 2017; McAlister & Miner 2018). However, progeny from starved females had insufficient reserves to expand these structures when phytoplankton were scarce, which highlights the provision of sizeable isolecithal ova from *Acropora*-fed mommas (Caballes 2017). COTS bipinnaria appear well-suited to nutrient-poor oligotrophic reef ecosystems (Olson 1985; Olson 1987; Wolfe et al. 2017; Deaker & Byrne 2022). Nevertheless, it is likely that the maternal donation of significant yolk (Caballes 2017) means that starvation and / or depletion of reserves is more pertinent for late pre-settling brachiolaria (Lucas 1982). Suzuki and collaborators concluded that feeding was more critical for early zooplankton (Suzuki et al. 2016) because the intake of “algae” declines before settlement. However, during gluts of phytoplankton, most cells pass through the gut undigested as larvae appear unable to moderate intake (Lucas 1982). Contrary to the terrestrial high-island runoff hypothesis which posits nutrient enrichment boosts phytoplanktonic populations which underpins the zooplanktonic phases and benthic recruitment of sea stars (Birkeland 1981), bipinnaria are not perturbed by low to moderate waterborne phototrophs (Lucas 1982; Fabricius et al. 2010; Suzuki et al. 2016; Caballes 2017; Pratchett et al. 2017; Wolfe et al. 2017) which apparently prevail in the wet

season when embryos metamorphose into brachiolaria (Wolfe et al. 2015, cited in Deaker & Byrne 2022; Brodie et al. 2017). Nevertheless, deluges encourage land runoff and upsurges of "algae"-fuelling nutrients. Larval survival and settlement were optimised when the concentrations of phytoplankton (*Proteomonas sulcata*) were 10^4 cells per millilitre (cells ml^{-1}) yet unexpectedly, survival was attenuated at 10^5 cells ml^{-1} (Wolfe et al. 2015; Pratchett et al. 2017). All the same, settlement was delayed in brachiolaria exposed to 10^3 (Pratchett et al. 2017) and these algae liberate allelopathic compounds that may kill larvae at higher densities (Google.com 2026). Olson's 1985 and 1987 experiments were replicated by different teams under rigorous nutrient management protocols whose findings lend credence to Birkeland's hypothesis (Keesing & Halford 1992; Ayukai et al. 1996; Fabricius et al. 2010; Brodie et al. 2017).

Larval gut microbiota may comprise nutritionally-advantageous fluorescent phototrophs (Olson 1987; Wolfe et al. 2015, cited in Deaker & Byrne 2022; Carrier et al. 2018; Allen et al. 2019), whilst they appear competent at gaining nourishment from dissolved amino acids and organic matter (DOM) such as coral mucus (Hoegh-Guldberg 1994; Nakajima et al. 2016). Their digestive microbiomes comprise exceedingly diverse communities of commensals and mutualists that are attuned by diet and distinct from those found environmentally (Carrier et al. 2018). Exploitation of a variety of sustenance including nanoplanktonic bacteria (Olson & Olson 1989) and the biofilms of all wet surfaces, likely contributes to persistence throughout shortages and boosts their development when conditions are bountiful (Deaker & Byrne 2022). Be that as it may, Ayukai found that larvae gain significant nourishment from phytoplankton such as cyanobacteria which are cleared from the gut 10 times slower than other kinds of unicellular life, but they do not ingest vast numbers of bacteria (Ayukai 1994).

Fig. 6. Symbiotic "acropora" crabs of the genus *Trapezia* or *Tetralia* have been known to defend colonies from juvenile COTS (Moran 1988; Cowan et al. 2016), where they nip their tube feet and spines (Glynn 1987).

COTS larvae exploit binary fission (Allen et al. 2019) whereas the findings of genetic analyses are redolent of clonal populations and those likely to arise from selfing (Hart et al. 2021; Uthicke et al. 2021; Horoiwa et al. 2022). Transverse division of the anterior and posterior of bipinnaria fully regenerates within days, whose rates appear enhanced by buoyant phytoplanktonic populations (Fig. 3.; Birkeland 1981; Birkeland 1982; Allen et al. 2019), whilst brachiolaria bud posteriorly (Fig. 1. F; Suzuki et al. 2016, cited in Deaker & Byrne 2022).

Temperatures of more than 32°C appear nonpermissive for bipinnaria while less than 25°C arrests their development (Henderson & Lucas 1971; Lucas 1973). Late brachiolaria appear particularly temperature-sensitive (Habe et al. 1989, cited in Caballes 2017) which is likely to forestall settlement during marine heatwaves (MHW), whereas gastrulating embryos can withstand from 13°C to 34°C. Moreover, embryonation takes 31 and 11 hours at 20 and 32°C respectively (Habe et al. 1989, cited in Caballes 2017).

Bipinnaria are also significantly euryhaline tolerating salinities far outside the natural range (35 parts per thousand; ppt; ‰; ~1.026 SG), yet brachiolaria are strictly stenohaline which can perish when salinity varies by only 2‰ (Henderson & Lucas 1971). However, 30‰ enhances bipinnarial survival (Lucas 1973) which infers that the early zooplanktonic phases of COTS are suited to heavy downpours (Birkeland 1982) whilst these stages predominate in the rainy season (Wolfe et al. 2015, Deaker & Byrne 2022; Brodie et al. 2017) when Birkeland's highland runoff is likely to prevail (Birkeland 1981; Birkeland 1982).

Fig. 7. Recently denuded predation scars and culling of *A. solaris* by lethal injection on northeastern Australia's Great Barrier Reef. Injecting an upper arm with 10 millilitres of 8 grams per litre (g l^{-1}) of oxbile induces mortality within 24 hours (Rivera Posada 2012; Rivera Posada et al. 2013; Rivera Posada et al. 2014a). Matthew Curnock © courtesy of Deaker and Byrne 2022 and the Creative Commons Attribution License 4.0 (CC BY-NC-ND).

After around two to three weeks of waterborne transformations, cues from their preferred source of benthic nutrition, crustose coralline algae (CCA; Zann et al. 1987; Johnson et al. 1991), or the holobionts thereof (Johnson et al. 1991), induce settlement metamorphoses, yet equally, they may be attracted by other signals from adult populations (Chesher 1969; Lucas et al. 1979; Black et al. 1995), which may represent a replenishing stratagem to succeed senility (Pratchett et al. 2014) or declining populations (Deaker

& Byrne 2022). Exceedingly nutritious species of CCA include *Lithothamniurn pseudosorum* and *Porolithon onkodes* (Johansson et al. 2016). Feeding starfish liberate a waterborne substance or substances that are detected by chemoreceptors whose downstream cascades likely drive aggregations (Vine 1973; Ormond & Campbell 1974). All the same, the findings of ex situ experiments indicate that late herbivorous juveniles are not so keen to gather with corallivorous adults (Webb et al. 2024). Well-nourished zooplankton retain spontaneous settling competencies where they typically alight ubiquitous life-sustaining biofilms (Fig. 1.; Wolfe et al. 2015; Deaker et al. 2020a). However, biofilm was not favoured by captive juveniles which merely supported decelerated growth resulting in over 40 percent mortality and moderate shrinkage, where survivors were smaller with fewer arms. Growth rate accelerated when these sea stars were finally offered CCA, but speed and arm tally did not recover. Half of one of these chronically biofilm-fed juveniles degraded whilst the remaining tissue regenerated into a fully developed sea star which was reminiscent of the fissiparity of other asteroids (Achituv & Sher 1991; Deaker et al. 2020a). Juveniles grow well on frond-forming calcified algae of the genus *Amphiroa* around which they wrap themselves when they are more challenging to discern (Deaker et al. 2020a). The findings of one study suggested the algal microbiome liberates a settlement-inducing morphogenic substance that is not produced by these bacteria when not inhabiting CCA (Johnson & Sutton 1994). Nevertheless, COTS can extend their zooplanktonic phase (Yamaguchi 1973) in some instances to 42 days (Pratchett et al. 2014). Settlement took 22 at optimal phytoplanktonic concentrations of 10^4 cells ml^{-1} whilst few brachiolaria survived at 10^5 (Pratchett et al. 2017).

The arms of late stage imminent-settling brachiolaria elongate to expedite locomotion (Olson et al. 1988) and their primordium swells (Birkeland 1989; Suzuki et al. 2016) as they descend rear first, when they tentatively land to test the substratum (Fig. 16.; Yamaguchi 1973) because COTS are extraordinarily particular about where they settle. They can detect predators like polychaete (bristle) worms amongst benthic fauna, which is not always off-putting, but their presence influences settlement success (Cowan et al. 2016). Typically favouring micro-topologically-complex rubble, their likely aim is predation avoidance (Lucas 1975). Cowan and allies were unable to recover two-day-old juveniles from predator-abundant substrate following the settlement of brachiolaria which emphasises the competency of benthic fauna for eradicating this vulnerable life stage (Keesing & Halford 1992; Cowan et al. 2016), yet equally, they demonstrate a keen reluctance to settle on animal-inhabited rubble (Cowan et al. 2017).

Fig. 8. [b] a giant triton snail (*Charonia tritonis*) about to ingest a reddish-brown COTS, which are usually only half eaten and thus take merely a few months to regenerate (Chesher 1969). Oceanwide Images © courtesy of Hall et al. 2017, Nature, and The Creative Commons Attribution Licence.

The anterior of brachiolaria has been absorbed after two days of settlement (Yamaguchi 1973) as they have transformed into 0.3- to 0.7-millimetre algivorous juveniles with five appendage buds (Fig. 1. G), each equipped with two tube feet, a terminal tentacle, and a compound eye frequently referred to as a red optic cushion (Henderson & Lucas 1971; Yamaguchi 1973; Lucas 1975; Korsvig-Nielsen et al. 2019). Optic centres continue to develop at the arm tips of adults (Appendix I; Korsvig-Nielsen et al. 2019). Pairs of fully-developed limbs are added each fortnight from the third week, when their dorsums turn pink so they can covertly browse upon CCA (Yamaguchi 1974; Lucas 1975; Birkeland & Lucas 1990, cited in Pratchett et al. 2014). Their arms develop thorns as they grow,

whilst many ascend their ex situ containers to float upside-down on the meniscus with extended tube feet. They fall to the bottom when the surface is disturbed (Deaker et al. 2020a), while other infant asteroids exhibit analogous behaviours (Soliman & Nojima 1984, cited in Deaker et al. 2020a; Byrne 1995, cited in Deaker et al. 2020a). Uncommon circumstances are required for them to benefit, whereas floating juveniles will remain susceptible to predation from above and below.

They ingest other forms of coralline algae (Wilmes et al. 2020), but their growth is accelerated when dining on CCA (Deaker et al. 2020a), likely thanks to its superior dietary worth (Martinez et al. 2017, cited in Deaker & Byrne 2022). These tiny and vulnerable herbivores prefer rubble strewn environments presumably for protection, until four to six months when they are 8 to 18 millimetres when they emerge and commence a corallivorous lifestyle (Fig. 1.; Yamaguchi 1974; Deaker et al. 2020). Notwithstanding, they remain partial to filamentous and leafy macroalgae which they digest when corals are lacking (Deaker & Byrne 2022). As they mature, their chemoreceptors and compound eyes confer an aptitude for identifying and migrating to prime reef locations (Appendix I; Brauer et al. 1970; Korsvig-Nielsen et al. 2019). Zooplanktonic COTS can detect and avoid being captured and consumed by corals, where brachiolaria will not settle, and actively-feeding adults attract others (Ormond & Campbell 1974).

Conversely, maze-confined juveniles around the age amenable to herbivory-corallivory ontogenic switching, were directly and swiftly attracted to waterborne chemicals from rubble-enveloped CCA and to a lesser extend corals, but meandered away from adult signals. When both former cues were present, they demonstrated a preference for coral, yet adult / coral combinations appeared to incite motionless confusion. As COTS feeding is likely indiscriminate insofar as anything underlying their stomachs may be digested, juveniles may be vulnerable to incidental cannibalism. Water from coral rubble collected from reef habitats powerfully attracted most sea stars which may reflect a profound desire to be return to their nursery, whereas the decision to move towards coral took the longest towards which taxis remained modest, which suggests vigilant hesitancy. Embarking on a corallivorous lifestyle is significantly perilous for COTS, whereas waterborne cues from feeding adults may be integral to a negative feedback loop that hinders a shift from algivory to a corallivory when adults are plentiful. Numerous young sea stars remained stationary with elevated arm tips redolent of sensing their environment, while restrained movement may be a defensive trait (Webb et al. 2024). Zann and allies discovered that 15- to 40-millimetre juveniles took two years to migrate 800 metres from their reef flat nursery to the neighbouring crest (Zann et al. 1987, cited in Webb et al. 2024).

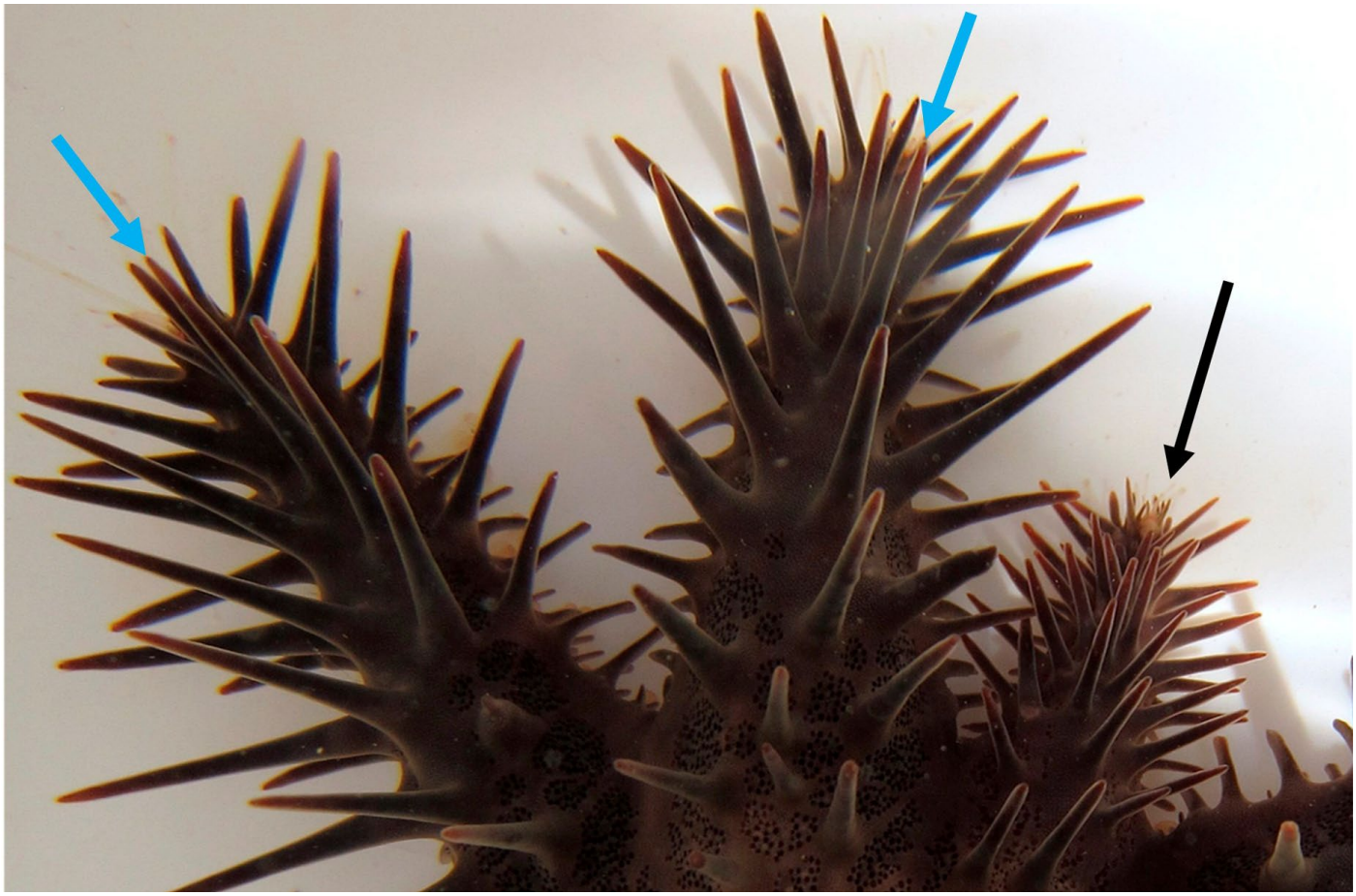


Fig. 9. [black arrow] a regenerating arm of *Acanthaster* cf. *solaris* whose original was likely lost or discarded during a strike from a predator consistent with the observations of Rivera Posada et al. 2014. Blue arrows specify spines ostensibly amenable to age determination as described by Stump and Lucas in 1990. Adapted from and courtesy of Messmer et al. 2017, Diversity, and The Creative Commons Attribution License.

During the first 40 days of corallivory, they are stung by numerous kinds of polyp tentacles where most sustain injuries, some of which prove fatal (Yamaguchi 1974; Deaker et al. 2021a). The estimated recouperation of wounded juveniles is said to be around three and a half months (Deaker et al. 2021a) during which many revert to CCA (Deaker & Byrne 2022). Nevertheless, despite a significant detriment to their health (Lawrence & Vasquez 1996), these tenacious starfish persevere with their new way of life, where 90 percent of surveyed juveniles appeared to be in a state of regeneration (Wilmes et al. 2019). COTS seem to lack a flight response to harmful and lethal stimuli (Yamaguchi 1994), so their capacity to feel pain appears comparatively dulled, which is fortuitous insofar

as initial control measures included living in situ dissections or bringing them ashore to be buried alive (Westcott et al. 2016).

In an ex situ study, settled algivorous COTS grew to 4.5-millimetre corallivores in just 90 days (Deaker & Byrne 2022), from whence accelerated development yields sexually mature sea stars with 20-centimetre diameters after two years (Yamaguchi 1974; Lucas 1984; Pratchett et al. 2014). Their body walls are not calcified like other tropical sea stars (Kettle & Lucas 1987, cited in Deaker & Byrne 2022) which means their growth requires fewer resources, whilst their expansive stomachs expedite nutritional uptake (Birkeland & Lucas 1990, cited in Pratchett et al. 2014; Lawrence & Moran 1992). At two years, their growth rate subsides, likely thanks to devoting significant resources to gonad development (Kettle & Lucas 1987; Birkeland & Lucas 1990, cited in Pratchett et al. 2014). 70- to 75-centimetre sea stars have been recorded (Lucas 1984; Moran 1988; Endean & Cameron 1990, cited in Pratchett et al. 2014), whilst researchers have strived to develop precise ways of evaluating age.

The skeletons of echinoderms are composed of numerous small, calcified bones secreted by mesodermal stroma. Each continuously-developing ossicle is composed of a latticework of linear centres of accretion known as trabeculae (Nothdurft & Webb 2007) whose pores are interspersed with calcite-depositing stroma (Smith 1980; Stump & Lucas 1990).

Fig. 10. A small hitchhiking example of potentially destructive *Pilumnus* cf. *vespertilio* (Eumalacostraca: Pilumnidae) which looks remarkably more harmful than beneficial *Tetralia cavimana* (Eumalacostraca: Tetraliidae; Fig. 6.).

The bands on the longest spine ossicles of *A. planci* that run along the aboral surfaces of each arm that are furthest from the mouth of sexually mature adults, are deposited seasonally (Fig. 9.; Stump & Lucas 1990; Stump 1994). However, this was later contested by researchers who analysed numerous spines including those from the tips and on regenerating arms (Souter et al. 1997). Yet the longest spines precisely selected from the proximal area of the entire arm that were specified by Stump and Lucas and corroborated by Stump in 1994, reveal defined patterns of banding (Stump & Lucas 1999). Six-months of development is marked by a light and dark stripe deposited at their base which may be emphasised by tetracycline and viewed under ultraviolet (Stump & Lucas 1990). Ages from one to 17 have thus been estimated. 35-centimetre five-year-olds are regarded by some as senile because despite their expansive stomachs, heavyweights cannot be fuelled proficiently (Keesing 1990) when they frequently begin to degenerate (Pratchett et al. 2014). Regardless, sea stars whose age exceeds 14, are testament to surviving the "bust" of an outbreak (Stump 1996), whereas growth rapidity may be an independently plastic trait and / or determined by numerous environmental factors (Stump 1994; Stump & Lucas 1999). Consequently, sea star diameter is a poor sign of age.

Outbreak-expediting behaviours could be better understood with permanent and unique ways of tagging starfish for several years of recurrent capture and release. Avoiding permanently tagging thus far, their ability to discard limbs could not thwart in vitro trials of complex, laborious, and somewhat hazardous methodologies involving monofilament and the inhumane procedure of drilling holes in the aboral region of their disk, which had not been deployed in the wild in 2014 (Rivera Posada 2012 unpublished data, cited in Pratchett et al. 2014).

Aside from those inhabiting the Red Sea, the risk of predation lessens as they grow (Keesing et al. 2018; Balu et al. 2021) as divulged by their behaviour insofar as covert photophobic foraging (Korsvig-Nielsen et al. 2019) is succeeded by daylight gluttony (Keesing 1995; De'ath & Moran 1998).

Candidate Outbreak Inducers

A COTS outbreak can be qualitatively defined as a profound and inexplicable proliferation of sea stars that cannot be sustained by local resources (Potts 1981; Pratchett et al. 2014). Either solitary and nomadic, or gregarious, the motive and driver of the formation of a consortium remains largely enigmatic. Nevertheless, Vine and Ormond and Campbell remarked that feeding sea stars attract others (Vine 1973; Ormond & Campbell 1974). Unsustainability is an inescapable aspect of an outbreak; however, coral cover varies from subregion to subregion and may in some instances fluctuate over tens of square metres. Furthermore, global reefs are deteriorating at accelerated rates, whereas mean starfish diameters and their distribution introduce other unaccommodatable variables. By necessity, any definition must account for two covariates: (a) mean percent coral cover, and (b) starfish density or, average numbers spread over a geographic area. There are established protocols for appraising the former as sessile invertebrates

do not move; however, starfish behaviour and motility confound determinations of the latter. Their ability to switch from covert nocturnal foraging to overt daytime gorging may not only give the appearance of a sudden increase in numbers but also prevents accurate appraisals of localised populations. Moreover, outbreak densities are such that an almost uniform carpet of sea stars can be spread over a comparatively small area whilst there are very few scattered on the surrounding substratum (Pratchett 2005). Hence any defined threshold can be exceeded over a couple of transects (Ormond et al. 1973; Moran & De'ath 1992) whereas averaging these quantities over the remaining reef can yield underwhelming densities. Therefore, surveys typically appraise outbreaks that are "spot" or "reef-wide" (Engelhardt 1999) or either "incipient" or "active" (Sweatman et al. 2008, cited in Pratchett et al. 2014). The causes and consequences of epizootics are clearer when a high frequency of recurrent surveys measure the densities as well as the diameters of starfish (Moran 1988) which had only been conducted in the 21st century by Pratchett and Kayal and collaborators whose findings were published in 2005 and 2012 respectively.

The polymerase chain reaction (PCR) amplified the mitochondrial DNA of COTS from samples of plankton originating from Christmas- and full moon-proximate spawns on northeastern Australia's reefs of Agincourt and Moore. Natural declines in adult populations coincide with analogous decrements in the abundance of zooplanktonic sea stars (Uthicke et al. 2019) which infers that epizootics are seeded by procreations occurring during summer plagues.

Endean's postulation of a secondary outbreak is instigated by multitudes of COTS with a unimodal size structure with diameters that differ by as little as 150 millimetres or less, which are thus members of the same cohort that originate from weeks to months of rapid development from the same spawning year (Chesher 1969; Branham et al. 1971; Dana et al. 1972; Glynn 1973, cited in Caballes 2017; Endean 1974; Potts 1981; Zann et al. 1987; Birkeland & Lucas 1990, cited in Pratchett et al. 2014; Johnson 1992). Primary initiating outbreaks, however, with a multimodal size structure composed of starfish with diameters that vary by as much as 650 millimetres, are an assortment of cohorts originating from up to five or six spawning years (Stump 1996; Engelhardt 1999; Pratchett 2010) and are thus created gradually (Zann et al. 1987; Zann et al. 1990; Stump 1996; Pratchett 2005). These vast communities are said to amass in the Lizard Island to Cairns "initiation box" (Engelhardt et al. 2002; Brodie et al. 2017). Hence secondary outbreaks appear to be the outcome of primary accumulations of starfish which then spawn in synchrony (Endean 1974; Johnson 1992; Stump 1996). However, Birkeland and Lucas maintained that gradual amassment is at odds with the definition insofar as outbreaks must reflect sudden manifestations (Birkeland & Lucas 1990, cited in Pratchett et al. 2014), thus primary accruals may epitomise the generation of a fecund community capable of spawning an outbreak (Pratchett et al. 2014). Covert primary seeding might be succeeded by an overt secondary mass parasitisation on the remote and isolated reefs off Hawai'i and Moorea and the archipelagos of the central Pacific (Birkeland 1982; Timmers et al. 2012), or they may arise from a typically unexplained single momentous influx of larvae (Birkeland 1982). Migrations to distant reefs could occur step by step over multiple spawning years (Horoiwa et al. 2018).

Numbers can increase by up to six orders of magnitude in the one or two years that precede a plague (Birkeland & Lucas 1990, cited in Pratchett et al. 2014). For instance, 1 or 2 starfish became 200000 from 1976 to 1977 off American Samoa's Tutuila Island (Birkeland & Randall 1979, cited in Pratchett et al. 2014), and likewise, 0.1 per hectare (ha^{-1}) became 1000 ha^{-1} on Guam's Tanguisson Reef throughout 1967 (Chesher 1969). Further 10-fold increases amounting to 151650 starfish per square kilometre (km^2) were reported on the northern barrier reef of French Polynesia's Moorea in just one year (Kayal et al. 2012).

Despite extensive deliberations (Lane 2012; Pratchett et al. 2014; Miller et al. 2015) the biotic mechanisms that underpin outbreaks remain largely enigmatic. The hitherto extensively supported (Pratchett et al. 2014) terrestrial runoff theorem proposed by Charles Birkeland postulates that intermittent deluge-driven highland overspill causes nutrient enrichment which in turn boosts phytoplanktonic populations which reinforce the zooplanktonic phases and settlement of COTS (Birkeland 1981; Birkeland 1982; Fabricius et al. 2010; Brodie et al. 2017). Birkeland deduced from his conversations with indigenous people that outbreaks of COTS predominated around the reefs of the lofty islands of Micronesia, Melanesia, and Polynesia where *Acanthaster* were known by numerous monikers, but were less conspicuous around low-lying atolls where they were absent from the vernacular (Birkeland 1981). Most remarkably, there is no Marshallese word for *Acanthaster* despite over 12,000 for other wildlife including marine animals (Abo et al. 1976, cited in Birkeland 1981). Phytoplankton in non-anthropogenically-impacted areas such as coral islands surrounded by deep oligotrophic ocean or remote areas, are said to receive nutrients, as they always have, via upwellings or bird guano (Roche et al. 2015; Brodie et al. 2017). Contributions of the latter may be tangible around atolls like the Pacific's Midway which is a nursery for albatross chicks (Aslett 2024) or the Indian Ocean's Great Chagos Bank which supports extensive nesting populations of red-footed booby (*Sula sula*); however, there are no such communities on Eagle Island which is also uninhabited by humans, where COTS amass in great numbers (Roche et al. 2015). Accrual of bioinformatics and complex statistical analyses would be necessary to elucidate the significance of bird droppings. The findings of Brodie and allies strongly supported this hypothesis, insomuch as Townsville- and MacKay-proximal secondary outbreak initiation zones were identified on GBR that were fuelled by nutrient-rich riverine discharges that occur each year during the wet season (Fig. 5.; Brodie et al. 2017), whereas the findings of historic studies are redolent of limited larval survivorship when food is scarce (Lucas 1982; Ayukai 1994; Okaji et al. 1996; Okaji et al. 1997). Furthermore, elevated nutrients encourage the proliferation of sizeable phytoplankton which COTS larvae find more nourishing (Mellin et al. 2017, cited in Brodie et al. 2017).

Birkeland's runoff hypothesis relies on the premise that phytoplankton are nutrient-limited and scarce in oligotrophic environments. One comparative enrichment study affirmed that a ceiling is imposed on the numbers of the dinoflagellate zooxanthellae of corals insofar as nitrogen is much easier to derive from ammonium as opposed to nitrate (Ezzat et al. 2015) which is unlikely to be peculiar to dinoflagellates. It does, however, clarify why ammoniotelic fish appear prerequisite for hermatypic culture, albeit clearly, corals do not benefit from the continuous presence of this potentially lethal toxin. Phytoplankton's nourishment like

irradiance downwelling and ammonium are supplied in pulses. The former by surface water lensing, and the latter by shoals of fish (Stramski & Legendre 1992; Delbeek & Sprung 1994), yet supplementary dissolved inorganic nutrients are delivered by infrequent upwellings of deep ocean water (DOW; Delbeek & Sprung 1994). Nevertheless, denser phytoplanktonic communities seem to stimulate the transverse binary fission of their waterborne larvae (Allen et al. 2019) which if not innately moderated, could lead to substantial increases (Fig. 3.; Deaker & Byrne 2022).

When coral is lacking, 16- to 18-millimetre juveniles can cease development and revert to herbivory for a number of years (Deaker & Byrne 2022) which has been observed in vitro (Lucas 1984; Keesing et al. 1997; Deaker et al. 2020) and simulated in situ (Wilmes et al. 2020a). Prolonged herbivory and deferred-development that was monitored for six years in the laboratory, did not impact their growth after they resumed coral digestion (Fig. 4.; Deaker et al. 2020). Despite the risk of being eaten as juveniles (Keesing et al. 2018), over one-year-old 10- to 20-millimetre examples have been observed on GBR (Wilmes et al. 2017). This ability to halt their development through dietary preference, lends credence to the "juveniles-in-waiting" hypothesis of Deaker and allies that proposes multitudes of young amass in reef rubble over several years until they emerge to germinate a host of corallivorous adults (Deaker et al. 2020). The timing of this herbivory-corallivory ontogenic switch, is likely influenced by coral proximity and health (Zann et al. 1987), probably detected by their chemoreceptors (Vine 1973; Ormond & Campbell 1974). The outcomes of Webb and colleagues' seminal maze experiments suggest this kind of dietary shift could be prohibited by a glut of adults (Webb et al. 2024) whose decline could trigger the emergence of the "hidden army" of Deaker and allies to seed the next outbreak. Equally, corallivory may be elicited by manual methods of sea star attenuation which mitigate adult competition (Deaker et al. 2020; Webb et al. 2024), yet killing sizeable adults followed by routine frequent culls, has a long-term positive impact on coral cover (Westcott et al. 2020).

Given that the wildfires of forestry catalyse evolution and diversification and assist the reestablishment of ancestral lineages of foundation species (McLauchlan et al. 2020), COTS may be Nature's way of cleansing and repopulating (Goreau 1964, cited in Vine 1973; Colgan 1987, cited in Webb et al. 2024; Zann 1987a). A purge of this kind would likely prove beneficial every 50 to 80 years as long as conditions were exemplary for coral regrowth. Conversely, it may be that this dynamic epitomises the increase of populations that are decimated and scattered over sizeable geographic extents, yet this does not entirely clarify the occurrence of mass assemblages. Assumed to be a natural phenomenon in the early 1970s, it was concluded that COTS did not pose an overall threat to GBR's reef communities (Walsh et al. 1971; Westcott et al. 2016). Regardless, the vast Indo-Pacific plagues that followed later in the decade, drove conservationists to conclude that they could not possibly be intended by Nature, and must be manmade (Birkeland & Lucas 1990, cited in Pratchett et al. 2014; Brodie et al. 2017), where temperatures of less than 25°C curb the development of bipinnaria (Henderson & Lucas 1971; Lucas 1973).

Fig. 11. A marine fireworm, *Hermodice carunculata* (Errantia: Amphinomidae) on a sea fan with a conspicuous anterior caruncle [Ca] which discerns this taxon (McCaulley 2016).

Endean postulated the predator removal hypothesis (Endean 1969). Countless giant triton snails (*Charonia tritonis*) were plundered by shell collectors from the 1960s (Endean & Stablum 1973; Burchett & Dando 1996), which was followed by the capture of numerous carnivorous fish (Sweatman 2008; Cowan et al. 2017) that seemed to coincide with increased incidences (Fig. 8.; Fabricius et al. 2010). Previously implicated in keeping COTS in check, *Charonia tritonis* exert little impact on overall echinoderm communities (Burchett & Dando 1996). However, the safeguarded ecosystems of GBR with a "no take" policy have lower populations and fewer outbreaks than unprotected areas (Sweatman 2008; Westcott et al. 2020). Computer-based analyses of the datasets from historic surveys are indicative of 21 to 38 percent increased stability, a 30 percent lower response to disturbances, and a 20 percent faster recovery of reefs in marine protected areas (MPAs; Mellin et al. 2016), whereas reports of COTS sustaining sublethal injuries are highest in younger sea stars on reefs where fishing is prohibited (Messmer et al. 2017; Budden et al. 2019). Gonad development and thus fecundity was significantly diminished in limb-damaged COTS (Budden et al. 2019) as they develop on their undersides at the base of these appendages (Fig. 9.; Pratchett et al. 2014). Their camouflage, venomous spines that inject the potentially lethal liver (hepto)toxin plancitoxin-1 (Motokawa 1986; Shiomi et al. 2004), saponin-enriched eggs (Lucas et al. 1979; Barnett et al. 1988), and the predation avoidance of both larvae and adults (Cowan et al. 2016; Hall et al. 2017) together with their competency for rolling into a ball to protect their soft ventrums (Devaney & Randall 1973; Deaker et al. 2021) lend credence to this idea. The saponin content of three-day-old starfish is twice that of adults (Lucas et al. 1979; Barnett et al. 1988). Numerous fish seem indifferent to the eggs of COTS, where sightings of wild predation are limited to a handful of teleosts (Pratchett et al. 2014): ovum-eating scissortail sergeant (*Abudefduf sexfasciatus*) and staghorn damsel (*Amblyglyphidodon curacao*), and extraordinary sperm-eating oriental butterflyfish (*Chaetodon auripes*). Tropical ecosystems with decidedly diverse assemblages of teleosts including sizeable carnivores and sustained oligotrophy supplemented with "spikes" of ammonium, tend to support healthier and resilient communities of reef-building corals (Kroon et al. 2020). The overfishing of large piscivores leads to sizeable populations of their prey, in particular, small to

moderate-sized wrasse (Sweatman 2008) which likely hunt on rubble fields for invertebrates that would otherwise consume the early life stages of COTS (Keesing & Halford 1992), yet unless their saponins make them unpalatable (Lucas et al. 1979; Barnett et al. 1988), it is just as likely that these fish will prey upon nascently-settled and newly-formed juveniles (Sweatman 2008). Conversely, sizeable dogfaced pufferfish of the genus *Arothron* are recognised predators of adults that are not overfished on GBR (Fig. 12.; Cowan et al. 2017). Nevertheless, proficient teleostean bioremediatory heavyweights remained elusive in 2015 (Miller et al. 2015). See: Control.

Despite established management protocols (Westcott et al. 2016) it is challenging to devise effective strategies without knowing why outbreaks occur (Lane 2012; Pratchett et al. 2014; Miller et al. 2015). Undoubtedly, outcomes are influenced, significantly or otherwise, by larval survival and predation (Deaker & Byrne 2022).

Ocean currents (Miller et al. 2015) and post-settlement development (Keesing & Halford 1992; Deaker et al. 2020) appear to contribute to the rapidity of population growth in a single, or the accumulation of individuals over multiple spawning years (Stump 1996; Pratchett 2005; Pratchett et al. 2014). The early life stages of numerous broadcast-spawning invertebrates remain particularly vulnerable (Gosselin & Qian 1997; Hunt & Scheibling 1997) whilst the varying degrees of reproductive success observed in echinoderms, epitomise “boom and bust” dynamics (Uthicke et al. 2009). However, this gives the impression of a “flash in the pan”, yet epizootics can last for years (Potts 1981, cited in Pratchett et al. 2014) while conceivably, species of *Acanthaster* constitute an unremitting pandemic (Cowan et al. 2018). Embryo to juvenile development is thought a key outbreak determinant, whilst they do not occur in subregions devoid of corals (Deaker & Byrne 2022).

Pocillopora damicornis voraciously consume zooplanktonic COTS (Yamaguchi 1974) alongside planktivorous fish and other filter feeders, and likewise, crabs, shrimp, or small wrasse (Yamaguchi 1973; Cowan et al. 2016a; Cowan et al. 2017; Deaker & Byrne 2022), and dragonettes, may devour rubble-dwelling juveniles. Planktivorous fish significantly lessen the numbers of bipinnaria (Hamner et al. 1988). For instance, *challenging to satiate* humbug damselfish, *Dascyllus aruanus* (Fig. 14.; Cowan et al. 2017), yet these kinds of fish decline after starfish-instigated phase shifts (Yamaguchi 1973; Cowan et al. 2016a; Deaker & Byrne 2022) where rubble wastelands remain ideal for settlement and early nurture (Chesher 1969).

Fig. 12. Black-spotted dogface pufferfish (*Arothron nigropunctatus*; Tetraodontidae) can ingest species of *Acanthaster* (Cowan et al. 2017).

Control

Corallimorpharian anemones, *Pseudocorynactis hoplites* (Anthozoa; Hexacorallia) are known ambush predators of ~25-centimetre adults, that favour the shaded undersides of ledges or the kinds of fissures within which these starfish hide. However, these nooks and crannies tend to be exploited by covertly-foraging juveniles which probably constitute their usual diet (Bos et al. 2008). Still, 17-centimetre examples have ingested 34-centimetre COTS (Bos et al. 2011). Exquisitely ornamental harlequin shrimp (*Hymenocera picta*) consume several starfish of the class Asteroidea including cushion starfish of the genus *Asterina* (Fig. 13.; Aslett 2024), yet their size limits them to smaller juveniles (Glynn 1984). The lined fireworm, *Pherecardia striata* proved meaningfully bioremediatory (Glynn 1977; Glynn 1982; Glynn 1984), albeit remarkably, despite the presence of what was likely *A. ellisii* (Glynn 1973), significant communities of these two predators seemed responsible for prohibiting outbreaks and / or elevated numbers in Panama up to 2017 (Cowan et al. 2017). Bristle worms are significantly less injurious to the spats and first polyps of corals (Nakamura et al. 2015). Excluding marine fireworms (*Hermodice carunculata*; Toren et al. 1998; Banin et al. 2000; Shimek 2003; Sussman et al. 2003; Rosenberg & Falkovitz 2004; McCaulley 2016) which bear conspicuous anterior caruncles (Fig. 11.; Shimek 2003; McCaulley 2016),

most bristle worms are non-corallivorous detritivore ecoengineers which augment benthic-pelagic coupling insofar as they create small burrows in substrate to deliver dissolved oxygen and nitrate-laden water to deep euxinic zones (Dornhoffer 2014). Nonetheless, the majority of fireworms do not devour or harm corals (McCaulley 2016). COTS remain consistently low where there are buoyant populations of *Paracorynactis hoplites* (Bos et al. 2011), harlequin shrimp, and lined fireworms (Glynn 1982; Cowan et al. 2017), where 100 percent of COTS died that were attacked by both shrimp and polychaete (Glynn 1982). Small predators are scarce in Okinawa's benthic fauna (Keesing et al. 1995).

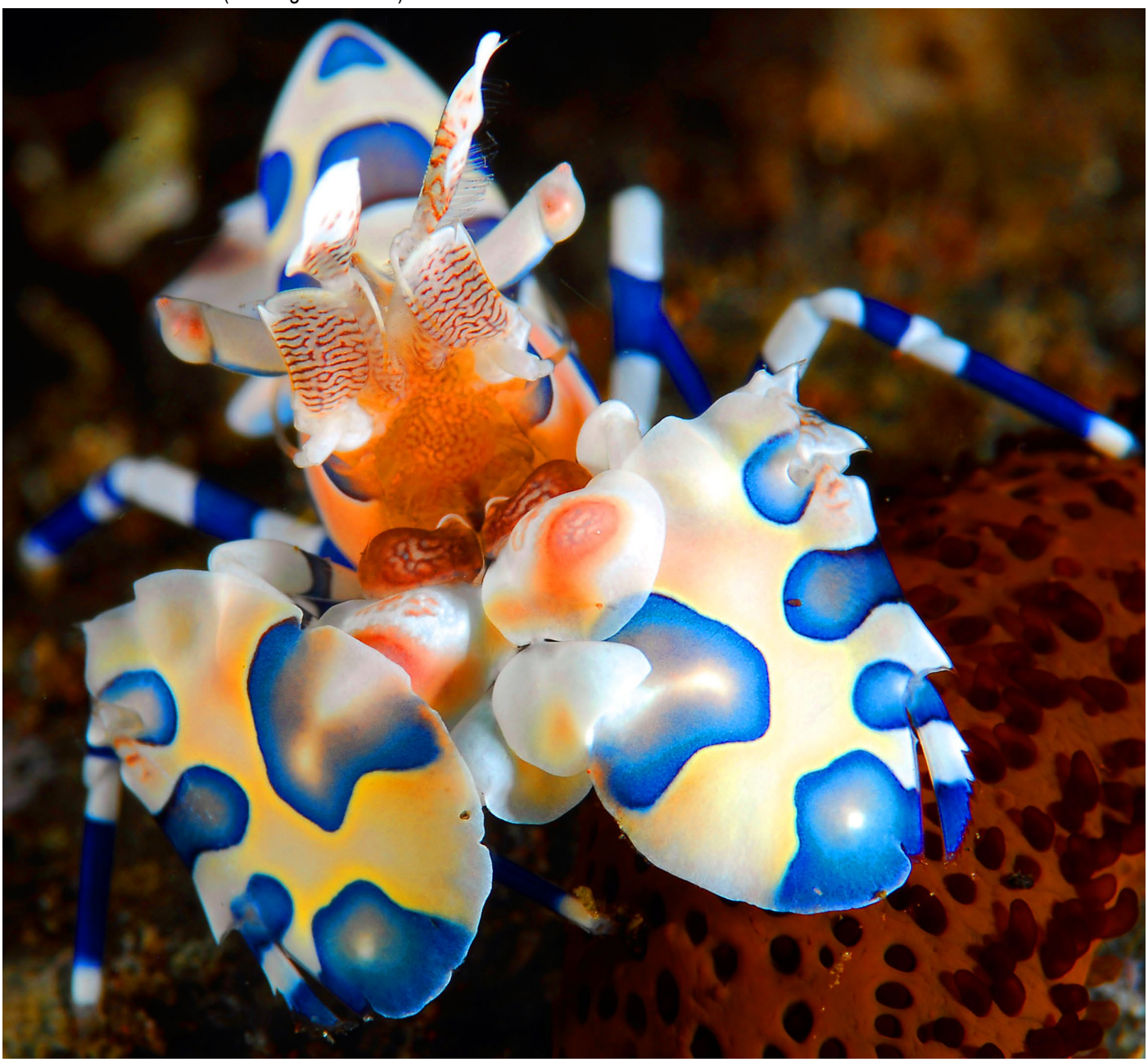


Fig. 13. A magnified photograph of a harlequin shrimp (*Hymenocera picta*; Multicrustacea: Palaemonidae) that bioremediate herbivorous juvenile crown-of-thorns starfish (Glynn 1984).

Potts made the eminent deduction that the abundance of predators was unlikely to have a significant impact unless this kind of starfish were their main source of nourishment (Potts 1981). Regardless, their diet must be generalist enough to sustain populations when sea stars are scarce (McCallum 1987), which is not the case for harlequin shrimp (Aslett 2024).

Mariculturists are more than capable of intensively procreating and rearing a range of potentially bioremediatory animals which may be inoculated onto rubble during the COTS breeding season from December to February on GBR, yet the ability of brachiolaria to avoid settling where these animals are, will likely nullify efficacy. Alternatively, local populations could be inoculated with Lucas's 1984 captive bread *A. planci* and *A. brevispinus* F_1 hybrids, which should lead to widespread procreative failure. However, prudent researchers like Cowan and allies remind us that it is unwise to exploit any approach other than those commensurate with the paradigm of "no regrets" (Lucas 1984; Cowan et al. 2017).

24-hour surveys of predation on adult *Acanthaster solaris* were carried out on the northern and central territories of The Great Barrier Reef's Marine Park (GBRMP) dominated by Lizard Island and Townsville whose protection comprised green, yellow, and blue zones ratified as reefs of the Marine National Park with no-fishing and -take policies, those of the Conservation Park with restricted fishing and recreational boating and diving, and finally, habitat protection areas where fishing is permitted (Doll et al. 2025).

Schools of spangled emperor (*Lethrinus nebulosus*) and / or starry puffer (*Arothron stellatus*) or spangled emperor and titan

triggerfish (*Balistoides viridescens*) were responsible for 55, 35, and 6.1 percent of teleostean predation, whereas ostensibly effective *Charonia tritonis* and humphead wrasse (*Cheilinus undulatus*) barely impacted populations (Doll et al. 2025).

Adult COTS were 3.6 and 2.8 times more likely to be eaten in green and yellow zones as opposed to those in blue, where comparable rates were evident in the northern and central subregions of the GBRMP. COTS were 55, 54, and 36 percent more likely to be killed and entirely consumed in zones rated green, yellow, and blue, whilst frequencies of half-eaten sublethally-injured COTS were 56, 36, and 22 percent higher in respective blue, yellow, and green. Proficient bioremediatory schools of spangled emperor were 2.5 times more abundant in green (Fig. 18.; Doll et al. 2025) which offers fresh support for Endean's predator removal hypothesis (Endean 1969).

Fig. 14. Two known predators of zooplanktonic COTS, juvenile humbug damselfish (*Dascyllus aruanus*; Cowan et al. 2017) sheltering around a head of *Pocillopora damicornis* (Yamaguchi 1974) in Egypt's Red Sea.

Remarkably, these sea stars avoid traversing tidal surge-exposed granulated substrate like sand, which obstructs their tube feet when they can be overturned, yet unfortunately, such channels remain no barrier in calmer waters (Chesher 1969).

Although conservationists recognise the importance of ongoing measures to curb wild populations, they are ever mindful of their shortcomings in the face of recurrent epizootics (Pratchett & Cumming 2019; Deaker & Byrne 2022). Uthicke and allies developed laboratory procedures for extracting, amplifying, and enumerating the mitochondrial DNA of the early life stages of waterborne COTS. ~10^{10} zooplankton reside in the water column throughout outbreaks of approximately a million benthic sea stars which highlights the futility of manual control (Uthicke et al. 2015). Fortunately, estimations of the effectiveness of repeated culls appear significantly favourable (Westcott et al. 2020). Methods include collection and lethal injection (Fig. 7.; Pratchett et al. 2019; Hewitt & Campbell 2020) where an estimated eighteen million COTS have been taken from the wild since the 1950s (Westcott et al. 2016; Pratchett et al. 2019). Multiple jabs of copper sulphate, sodium bisulphate, lime juice, or white wine vinegar were originally used to elicit lethal effect (Rivera Posada et al. 2013; Moutardier et al. 2015) where death from the latter two was more likely to occur from acidic shock rather than bacteriological disease (Moutardier et al. 2015). However, an injection of oxbile, peptone, or thiosulfate-citrate-bile-sucrose agar (TCBS) appears to encourage the proliferation of species of *Vibrio* that overwhelm starfish to induce 100 percent mortality within 24 hours (Rivera Posada 2012; Rivera Posada et al. 2013). TCBS pathologically-destabilises starfish holobionts by supressing gram positive bacteria including coliforms whilst it stimulates the proliferation of Vibrionaceae (Rivera Posada 2012). This approach has a knock-on effect where the disease is transmitted to nearby healthy COTS (Pratchett 1999; Rivera Posada 2012) whilst the illness does not affect corals, benthic fauna, or vestige-devouring housekeeping fish (Rivera Posada et al. 2014). Presumably bile from other animals will suffice, yet field and ex situ trials are advised to appraise their lethality. 84 manual control programs were operational in the Indo-Pacific in 2014, where killing conspicuous sizeable, fecund, and destructive sea stars on the first visit, usually shrinks populations to within the sustainability of the site. Coral cover increases in proportion to the frequency of recurrent culls (Westcott et al. 2020) which may require iteration every 12th day (Hewitt & Campbell 2020). The ongoing capture of juveniles together with surveys and prediction analyses assist the anticipation of imminent outbreaks (Wilmes et al. 2017; Miller et al. 2019; Babcock et al. 2020; Pláganyi et al. 2020), whilst contemporary analyses of oceanic environmental (e)DNA alert conservationists insofar as detection is attuned to outbreak densities (Uthicke et al. 2018; Kwong et al. 2021). More DNA is liberated into the environment by voraciously-feeding adults (Kwong et al. 2021).

Fig. 15. What appears to be a brown variant of *Acanthaster solaris* with sky blue thorns with peach-coloured tips. Courtesy of Wescott et al. 2016, Csiro, and The Creative Commons Attribution 4.0 Australian Licence.

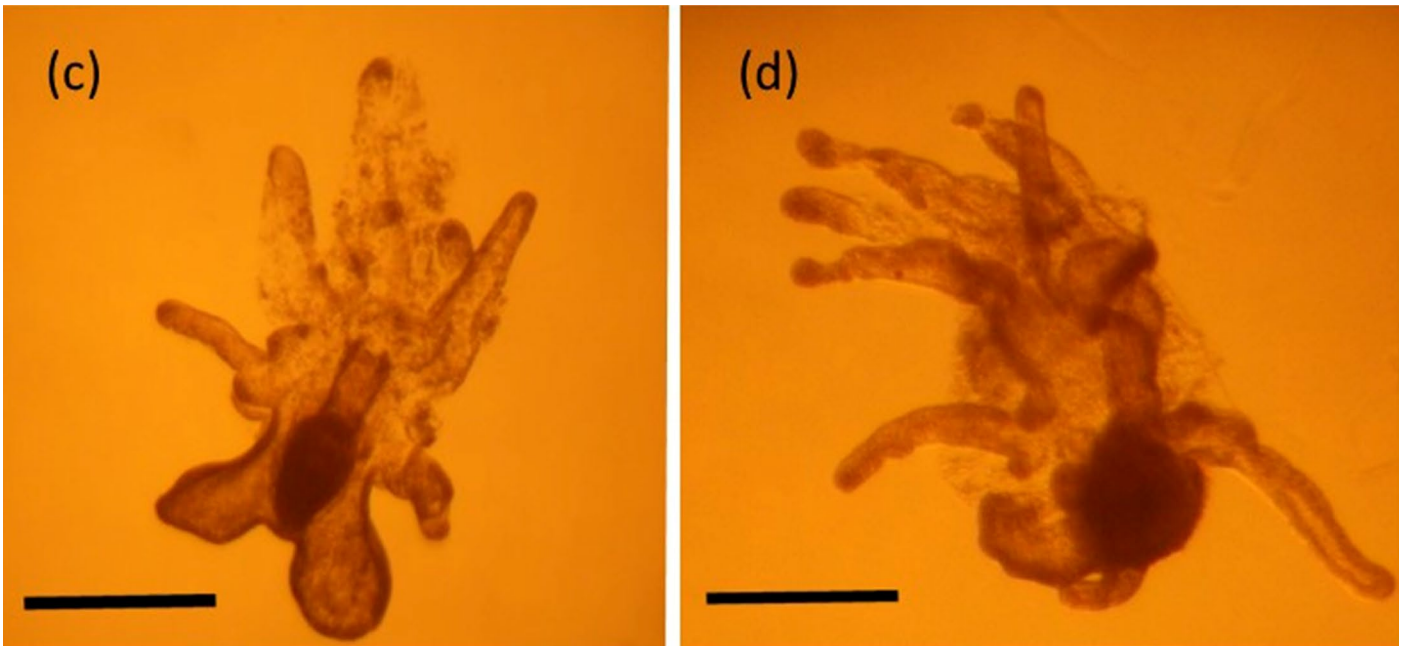


Fig. 16. Micrographs of mid- [c] and late brachiolaria with 200-micron (µm) scale bars (Fig. 1. F): [d] with an engorged darkened primordium consistent with Birkeland from 1989. Courtesy of Suzuki et al. 2016, Diversity, and The Creative Commons Attribution Licence.

Manual control is currently the only available strategy, yet when and where, and for how long remain critical considerations, as efficacy relies upon strategic implementation, where integrated pest management (IPM) decision tools clarify uncertainties (Westcott et al. 2016; Pláganyi et al. 2020). Countering the putative outbreak inducers of eutrophication (Birkeland 1982) and overfishing (Endean 1969) would go a long way to making GBR's reef communities less susceptible to numerous a- and -biotic disturbances including bleaching and coral disease (Voss & Richardson 2006; Cunning & Baker 2013; Ho 2013; Vega Thurber et al. 2014). However, terrestrial management requires cooperation and realistic *over the horizon* objectives, whilst zoning is far from straightforward (Westcott et al. 2016).

Maritime zoning spatially separates potentially-clashing usages whilst it enforces safeguarding. Intentions are advertised in the public domain to invite contributions from existing users and stakeholders whose rights are considered and validated. An open debate

facilitates an overall appreciation of current practices whilst it accommodates reasonable requirements and provides a forum for resolving conflicts. A final draft of a zoning proposal is once again openly publicised so that all parties have a last opportunity to air their views and defend prerogatives that remain unconsidered. Concluding amendments then precede its ratification as a legally-binding agreement. All territories of GBR's Marine Park were zoned in the late 1980s (Zann 1987a).

The seminal study of Hall and collaborators identified the molecular cues and their receptors that enable these animals to communicate, aggregate (Beach et al. 1975; Campbell et al. 2001), locate prey, avoid predators, and spawn (Dale 1999; Heinzeller & Welsch 2001) which implicated proteins that could be used for biocontrol insofar as attractants that encourage aggregations would make them easier to capture or inject (Hall et al. 2017).

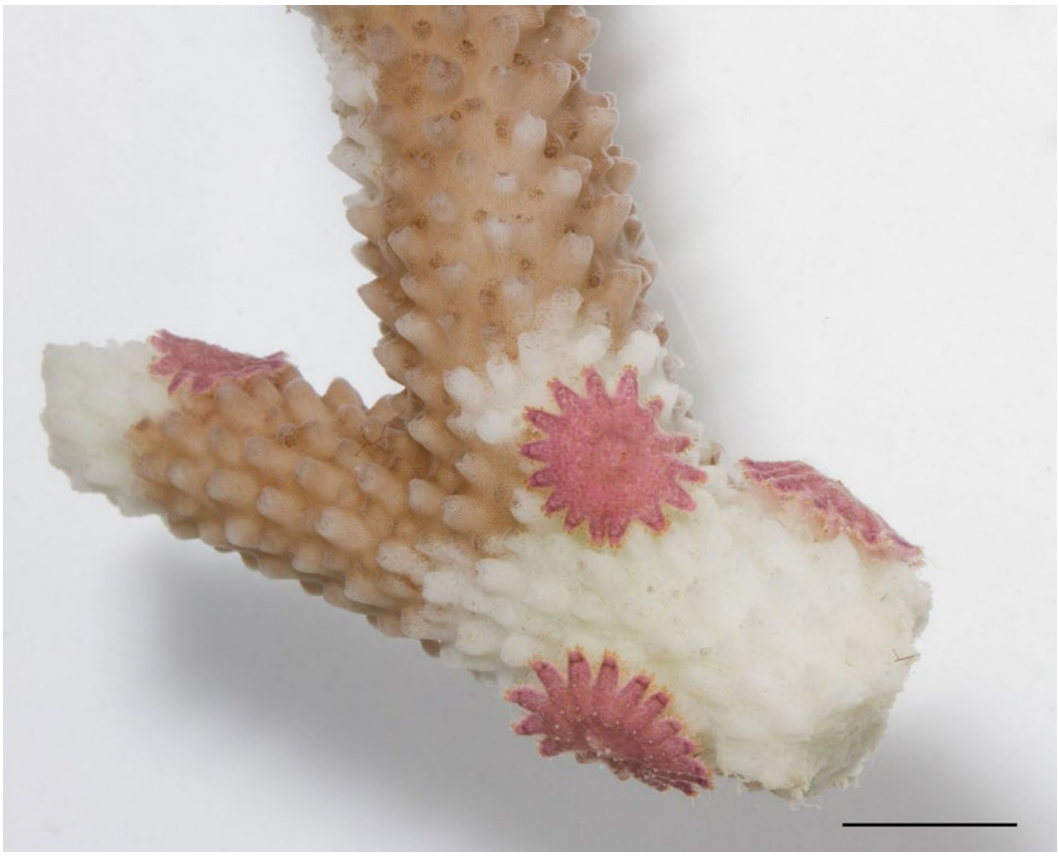


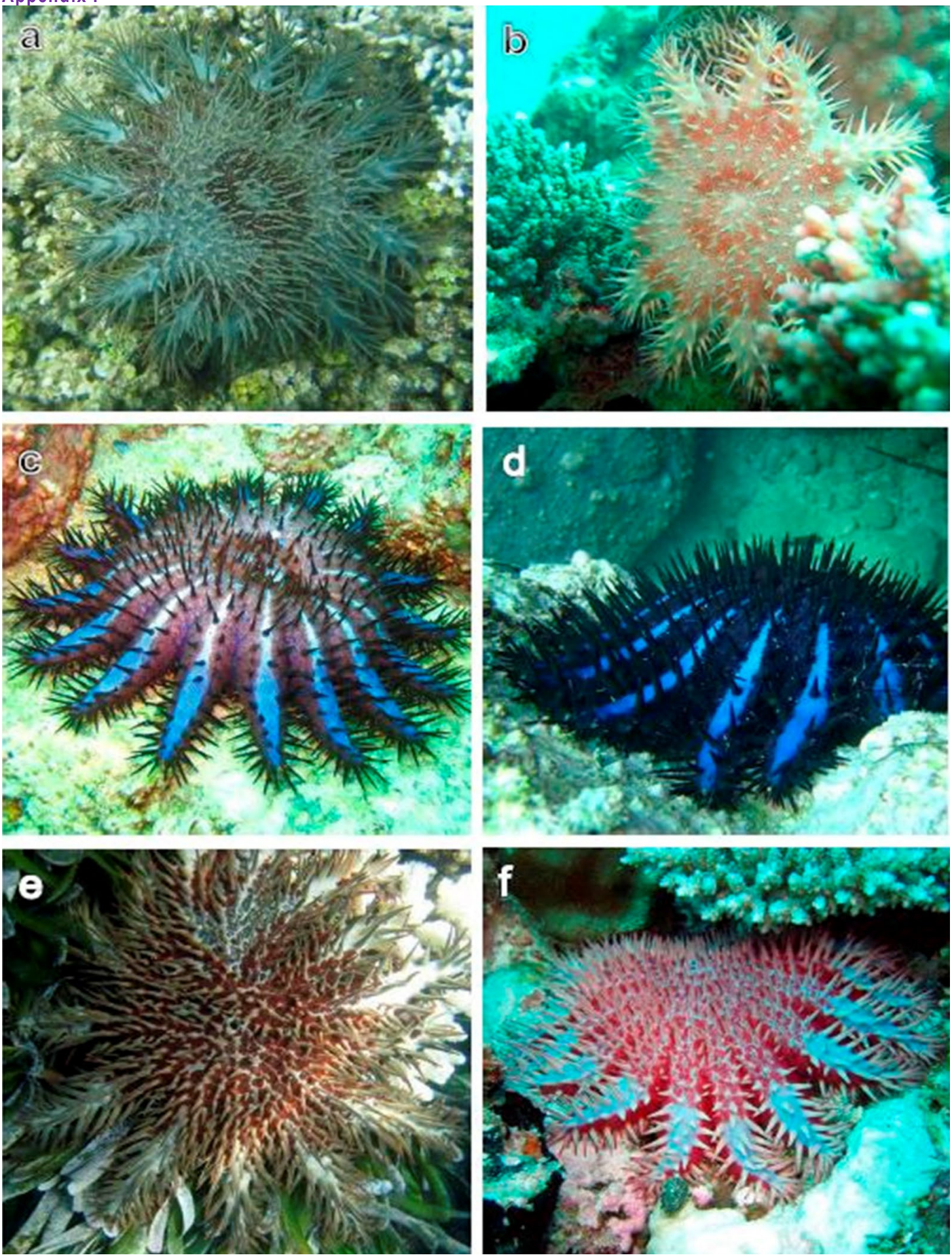
Fig. 17. With permission, captive six-month to one-year-old corallivorous juveniles digesting *Acropora formosa* with a 1-centimetre scale bar, Phil Mercurio © the Australian Institute of Marine Science (AIMS).

The entire genomes of two regional COTS from northeastern Australia's GBR and Japan's Okinawa were sequenced and BLAST searched for homologues. *A. planci* and *A. solaris* were thus confirmed as ostensibly genotypically alike and descendants of those from the Pleistocene which recommended they be classified within the same complex. 71 and 12 respective signal proteins were excreted from aggregating and alarmed COTS, whereas 23 were found to be liberated from those experiencing both. Y-maze-confined quiescent starfish exposed to dilutions of putative waterborne attractants became active and moved towards the source, whilst seawater previously exposed to giant triton snails caused alarm and avoidance. Such exoproteins are expressed in the cells of the body wall, mouth, and those associated with their spines (Hall et al. 2017). Over 83 percent, or 48 exudates are enzymes, 40 of which are hydrolases including a type II DNase present in thorn venom, plancitoxin-1 (Shiomi et al. 2004), which is injected by a mere minority of dorsal spines (Lawrence, unpublished data, cited in Lawrence & Moran 1992). An additional 73 are encoded by recognised homologues whose products are signal and structural proteins comprising 15 ependymin-related (EPDRs), five likely adherence-facilitating lectin receptors, and four deleted in malignant brain tumours 1. The former are implicated in species-specific communications between aggregating sea stars, whilst an additional 11 EPDRs were excreted from the peripheral cells of organs and tissues. Excluding conserved disulphide bridge-forming fold-stabilising cysteine residues, each one of these 26 proteins is structurally diverse which infers they are used to elicit a different response. Despite the widespread usage of EPDRs by most members of the animal kingdom, vertebrates use ependymin peptides as signalling molecules (Shashoua 1991; Suárez-Castillo & García-Arrarás 2007), whilst genes encoding this protein family have undergone developmental expansion in members of the class Asteroidea. Hence over eight groups of recognised pathway-integral orthologues are exploited by two of its largest monophyletic lineages. These exoproteins thus remain strong candidates for molecular mimicry (mimetics) as it is likely that one of them will stimulate congeneric aggregations (Hall et al. 2017).

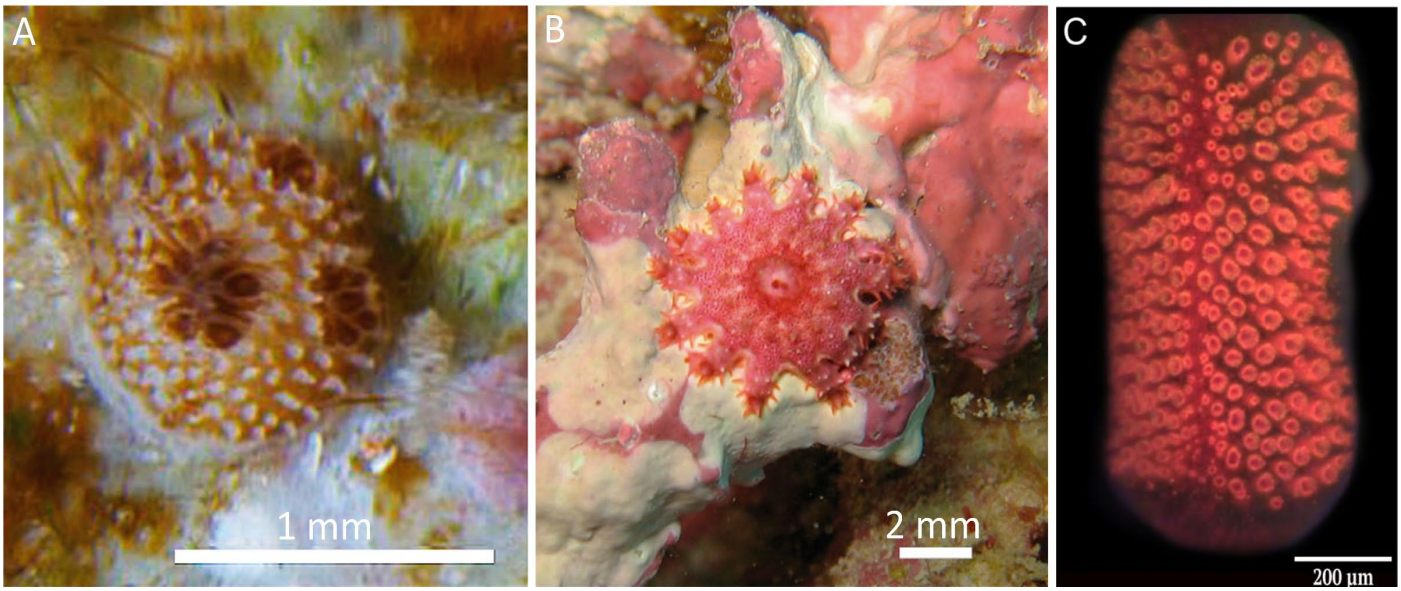
Fig. 18. A photograph of a spangled emperor, *Lethrinus nebulosus* courtesy of Kroon et al. 2020 and The Creative Commons Attribution Licence 4.0 (CC BY).

Most aspects of their natural history and behaviour for which we appear to have a comprehensive appreciation, are likely to act synergistically to expedite outbreaks. All the same, incongruity and a lack of substantiation advocate caution when interpreting causality. Versed in what we perceive as the complexities and fundamentals of Nature, one tries to rationalise how the "boom and bust" population dynamics and destructiveness of COTS could possibly contribute to reef communities over evolutionary timescales, whilst the developmental trials and tribulations of these defensible animals remain contextualised.

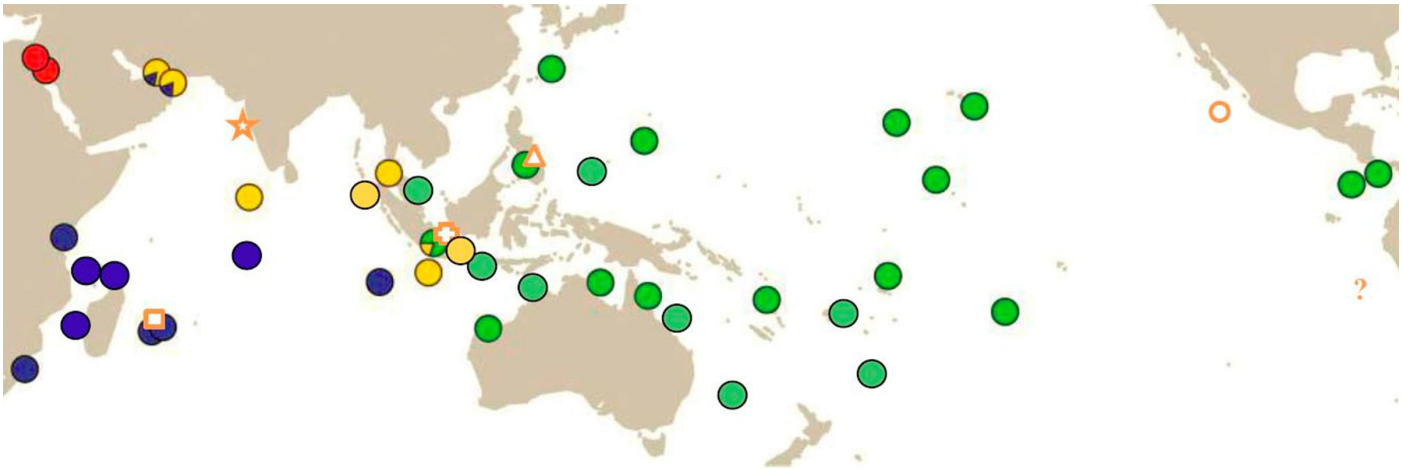
Appendix I



The colour morphs of global COTS: [a] putatively *Acanthaster solaris* Schreber 1793 off Fiji; Nina Yasuda ©; [b] the *yet to be named* Red Sea variant with fewer arms; Jessica Bouwmeester ©; [c & d] the northern Indian Ocean's *Acanthaster planci* Linnaeus 1758 off the United Arab Emirates and Oman respectively; [c] Maral Shuriqi ©; [d] David Mothershaw ©; and [e & f] the southern Indian Ocean's *Acanthaster mauritiensis* de Loriol 1885 off respective Kenya and Chagos; [e] Kevin Ransom ©; [f] Anne Sheppard ©. Courtesy of Haszprunar et al. 2017 and The Creative Commons Attribution Licence.



Magnified photography of a multipolyp juvenile coral of the family Acroporidae [A] and an herbivorous juvenile crown-of-thorns starfish (COTS; *Acanthaster solaris*) digesting crustose coralline algae (CCA) [B]. [C] a micrograph of a COTS compound eye otherwise known as a red optic cushion with roughly 250 ommatidia which multiply to enhance spatial awareness as starfish grow. [A] Masako Nakamura © and [B] Kei Ogasawara © courtesy of Nakamura et al. 2015 and the Creative Commons Attribution Licence. [C] courtesy of Korsvig-Nielsen et al. 2019 and the Creative Commons Attribution Licence.



The geographic distributions (coloured circles) and type localities (orange symbols) of species of COTS. [●] currently unnamed species inhabiting the Red Sea; [●] the southern Indian Ocean's occurrence of *A. mauritiensis*; [●] the northern Indian Ocean's domain of *A. planci*, and [●] the Pacific Ocean's dispersal of *A. solaris*. The original description's type locality: [★] *A. planci* Linnaeus 1758, off Goa; [✚] *A. echinites* Ellis & Solander in Watt 1786 (*incertae sedis*) likely a junior synonym of *A. planci* consistent with Haszprunar & Spies 2014, off Indonesia's Jakarta (formerly: Batavia) within the range of *A. planci* and *A. solaris*; [△] *A. solaris* Schreber 1793 (*incertae sedis*), ostensibly off Cebu in the Philippines; [□] *A. mauritiensis* de Loriol 1885, off Mauritius Island; [○] *A. ellisii pseudoplanci* Caso 1962 (*incertae sedis*), off Socorro Island in the Mexican Pacific, and [?] *A. ellisii* Gray 1840 (*incertae sedis*) within the South American waters of the eastern Pacific. Consistent with the findings of Vogler et al. 2008; Vogler et al. 2012, cited in Haszprunar et al. 2017; Vogler et al. 2013; Haszprunar & Spies 2014, and Haszprunar et al. 2017. Courtesy of Haszprunar et al. 2017 and The Creative Commons Attribution Licence.

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Chris Aslett

As the principal director of Reef Ranch Publishing Ltd (https://reefranch.co.uk/) and author of The Complete Reef Aquarist—A Conservation Manual (https://reefranch.co.uk/reef-aquarium-guide/), Chris has over 55 years of experience keeping aquatic animals with 47 of them nurturing marine species. His innate passion for system dynamics drove him from the laboratory to university where he gained a greater appreciation of biochemistry, biotechnology, epidemiology, genetics, histology, inorganic and organic chemistry, mariculture, molecular and microbiology, saltwater zoology, and the diagnosis and treatment of aquatic diseases. His dedicated marine livestock supplier, The Reef Ranch™, demanded he devise, streamline, and establish protocols for combined acclimation and prophylactic pest/parasite clearance, and innovate system design, optimisation, maintenance, and husbandry in the face of incessant influxes of hundreds of delicate marine animals. With exceptional, uncompromising, and likely the UK's most disease-free reef and fish-only facilities, losses were less than one resident every six months. 20 years hence, he has refined his expertise for digesting, authoring, editing, and publishing reef conservation-driven scientific literature (https://reefranch.co.uk/reef-research-and-aquarium-advice/), to an end of diminishing the impact the tropical marine ornamental industry exerts in the wild.

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