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Spatial and temporal variation in the demography of early-stage juvenile Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) from Australia's Great Barrier Reef

PhD thesis submitted by

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For Jacob and Werner

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JW, MP, AH, VM conceptualised the scope of the chapter. CC, Z-LC, BL compiled data in relation to pre-settlement processes, CC analysed this data and produced associated tables and figures (Figure 1.1, Table 1.1). JW compiled and analysed data in relation to settlement and post-settlement mortality rates and produced associated tables and figures (Table 1.2, 1.3; Figure 1.2, 1.3, 1.4, 1.5). JW wrote the original draft manuscript, which was then edited and added to by AH, MP and BL.

Chapter 2: Habitat associations of early-stage juvenile crown-of-thorns starfish on Australia's Great Barrier Reef

JW, MP conceptualised the scope of the chapter. JW, DS collected field data. MP, VM organised the charter vessel and drove the tender. JW analysed the data and produced figures. JW wrote the manuscript, with contributions from AH and MP.

Chapter 3: Modelling growth of early-stage juvenile crown-of-thorns starfish on the Northern Great Barrier Reef

JW, MP conceptualised the scope of the chapter. JW, DS collected field data. JW, SM analysed the data and JW produced figures. JW wrote the manuscript, with contributions from SM, AH, VM and MP.

Chapter 4: Contrasting size and fate of early-stage juvenile crown-of-thorns starfish linked to ontogenetic diet shifts

JW, MP conceptualised the scope of the chapter. JW, DS collected field data. JW analysed the data and produced figures. JW wrote the manuscript, with contributions from AH and MP.

Chapter 5: Incidence and severity of injuries among early-stage juvenile crown-of-thorns starfish on Australia's Great Barrier Reef

JW, MP, AH conceptualised the scope of the chapter. JW collected size measurement data for the study. JW analysed the data and produced figures. JW wrote the manuscript, with contributions from AH, VM and MP.

Chapter 6: General discussion

JW wrote the discussion.

Abstract

The coral-feeding crown-of-thorns starfish (CoTS, *Acanthaster* spp.[1]) is a native of Indo-Pacific coral reefs, and renowned for its ongoing contribution to global coral loss and associated reef degradation. Causes of population outbreaks of CoTS have been debated for decades and a lack of key demographic rates has undermined consensus. In particular, there persists a lack of field-based estimates of demographic rates for early life history stages, which greatly hinders our understanding of fundamental aspects of CoTS biology and population dynamics. The overall objective of this research was therefore to specifically provide field-based estimates of demographic rates for early-stage juvenile Pacific CoTS, *Acanthaster* cf. *solaris*. The focus was on small individuals (<70 mm diameter), presumed to have settled as larvae within the last year, to i) better understand how early post-settlement processes influence the incidence and severity of outbreaks, and ii) to provide critical rates for demographic modelling studies that inform management actions. This research is presented as a series of six chapters including a formative review of existing knowledge on the relative influence of pre- versus early post-settlement processes on population dynamics of CoTS (see Chapter 1).

For Chapter 2, I conducted extensive sampling of early-stage juvenile CoTS at 42 sites around the circumference of three distinct mid-shelf reefs (at 1–18 m depths) of Australia's Great Barrier Reef (GBR), during active outbreaks. I then related the occurrence and densities of early-stage juvenile starfish (2–65 mm diameter) to distinct habitat features. Thereby, I provided the first estimates for recruitment rates of early-stage juvenile CoTS to shallow waters (<20 m depth) of the GBR. Overall, 140 juvenile starfish (134 were 2–14 mm in diameter) were detected across 1,242 quadrats (1 m^2). At the scale of individual reefs, juveniles were recorded from 31 out of 42 sites (73.8%) at densities of 0–0.77 starfish m^{-2}, and occurred most frequently in south-western and northern fore reef habitats. Both estimated densities and the likelihood of occurrence of juvenile starfish within quadrats increased overall with the proportion of coral rubble (and dead intact corals), were greatest at intermediate depths (8–14 m), but decreased with the proportion of live hard coral.

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[1] *Acanthaster* spp. solely refers herein to the *Acanthaster planci* species complex, without consideration given to *A. brevispinus*.

For Chapter 3 and 4, I used extensive data on the size (diameter) of early-stage juvenile CoTS (*n* = 3,532) – collected during extensive surveys at 64 reefs across the northern GBR in 2015. For every juvenile, I recorded whether it was found feeding on coralline algae or hard coral, based on the presence of conspicuous feeding scars on coralline algae and coral respectively. In Chapter 3, I fitted an exponential growth model to the size measurement data to estimate monthly ranges of growth rates for juvenile starfish, presumed to be in their first year of life. Estimated growth rates varied considerably and increased with age (e.g., 0.028–0.041 $\mathrm{mm \cdot day^{-1}}$ for one-month-old juveniles versus 0.108–0.216 $\mathrm{mm \cdot day^{-1}}$ for twelve-month-old juveniles).

In Chapter 4, I provided field-based empirical evidence of a strong link between a fitness component (i.e., growth) of juvenile CoTS and the availability of coral prey. I showed that the increasing variation in body size with age among juvenile CoTS is linked to a size-related ontogenetic shift in diet (and microhabitat use) from coralline algae to live coral. The transition to a corallivorous diet leads to exponential growth in juveniles and is essential for individuals to reach reproductive size, whereas growth is stunted in individuals that remain on an algal diet. As mortality is generally size-related, with smaller individuals experiencing higher mortality than larger ones, the ontogenetic shift to corallivory will not only lead to accelerated growth and maturity, but also enhanced survivorship. I suggest that juvenile CoTS that shift their diet from coralline algae to coral early, experience enhanced growth rates for longer, and therefore ultimately reach a larger body size, with important consequences on individual lifetime fitness and population dynamics. Variability in the timing of ontogenetic shifts in diet is therefore likely to drive variability in individual fitness and resulting population replenishment of CoTS, and thereby contribute to, if not cause, the hypothesised de-phased coupled oscillations between the crown-of-thorns starfish and its coral prey.

In Chapter 5, I examined whether vulnerability to predation of early-stage juvenile CoTS is related to body size, microhabitat and fisheries regulation. I used the incidence and severity of sublethal injuries in field-collected juvenile starfish (5–45 mm diameter) as a proxy for predation risk. The majority (180 out of 200) of juvenile starfish had conspicuous injuries, presumably caused by predation. The incidence of injuries in juvenile starfish was negatively related to body size, but links between body size and severity of injuries was only evident in individuals collected from dead coral microhabitats (mostly coral rubble). Small (3 mm radius) starfish from dead coral microhabitats had injuries to 68.06% of arms, compared to 12.00% of arms in larger (12 mm radius) starfish from the same microhabitat. Juvenile starfish associated with dead coral habitats had a higher incidence (95% versus 87% respectively) and severity (i.e., the percentage of injured arms; 21% versus 6%) of injuries, compared to those associated with live corals. Interestingly, there was no difference in the incidence or severity of injuries between areas that are open versus closed to fishing.

By providing field-based empirical evidence of a strong link between a fitness component (i.e., growth) of juvenile CoTS and the availability of coral prey, this research adds greatly to increasing evidence that human-induced environmental changes are not a prerequisite for the initiation of outbreaks. However, it is important to acknowledge that anthropogenic activities may, nonetheless, enhance the severity and incidence of outbreaks. Aside from highlighting the importance of the early juvenile growth phase to CoTS population dynamics, this research also shed light on the microhabitat and habitat of early-stage juvenile CoTS, as well as on their relative abundance and vulnerability to injury potentially caused by predation within these habitats. Importantly, the detection of 3,160 small (2–20 mm diameter) algal-feeding juvenile CoTS demonstrates that this early life history stage can be detected and studied in shallow waters (<20 m) of the GBR. Although spatial patterns in the abundance of visually detectable algal-feeding juvenile CoTS may not necessarily reflect patterns in settlement, the findings of this thesis raise doubt about the assumption that settlement and/or recruitment of CoTS predominantly occurs in deeper reef habitats on the GBR (*aka* deep-water recruitment hypothesis). The improved knowledge about the microhabitat and habitat associations of early-stage juvenile CoTS, also offers an opportunity to inform the design of laboratory and field experimental studies on settlement and early post-settlement survivorship, and to concentrate future field-based research on early life history stages of CoTS in these habitats.

Measuring annual changes in the relative abundance of visually-detectable herbivorous juvenile starfish has the potential to provide a measure for annual recruitment strength. This does not only provide an opportunity to greatly enhance our understanding of the relative importance of anthropogenic activities in the incidence and severity of outbreaks, but also provides a potentially viable option for an early warning system of future outbreaks. It is important therefore, to quantify changes in the abundance of herbivorous juvenile starfish over time across different reef habitats — beginning early following settlement — to establish i) whether and at what rate different year-class cohorts of visually-detectable herbivorous starfish may accumulate within settlement areas, and to quantify ii) the rate at which coral-feeding juvenile starfish populations build-up thereafter. Changes in the abundance of juvenile starfish also need to be related to benthic assemblages, such as coral prey, to explicitly examine how the size, structure and composition of coral communities constrains population replenishment of CoTS. Along with field and laboratory experimental studies, this could greatly enhance our understanding of the CoTS-coral interaction and its overall importance to the functioning of coral reef systems.

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— **Chapter 1** —

General introduction - Contributions of pre- versus post-settlement processes to fluctuating abundance of crown-of-thorns starfishes (*Acanthaster* spp.)

Chapter 1: General introduction - Contributions of pre- versus post-settlement processes to fluctuating abundance of crown-of-thorns starfishes (*Acanthaster* spp.)

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1.1 Abstract

Numerous hypotheses have been put forward to account for population outbreaks of crown-of-thorns starfishes (CoTS, *Acanthaster* spp.), which place specific importance on either pre- or post-settlement mechanisms. The purpose of this review is to specifically assess the contributions of pre- versus post-settlement processes in the population dynamics of CoTS. Given the immense reproductive potential of CoTS (>100 million eggs per female), persistent high densities would appear inevitable unless there are significant constraints on larval development, settlement success, and/or early post-settlement growth and survival. In terms of population constraints, pre- and post-settlement processes are both important and have additive effects to suppress densities of juvenile and adult CoTS within reef ecosystems. It is difficult, however, to assess the relative contributions of pre- versus post-settlement processes to population outbreaks, especially given limited data on settlement rates, as well as early post-settlement growth and mortality. Prioritising this research is important to resolve potential effects of anthropogenic activities (e.g., fishing) and habitat degradation on changing population dynamics of CoTS, and will also improve management effectiveness.

1.2 Introduction

Crown-of-thorns starfishes (*Acanthaster* spp.; CoTS) are native inhabitants of coral reefs throughout the Indo-Pacific (Birkeland and Lucas, 1990). Although formerly regarded as a single widespread species, *Acanthaster planci* [Linnaeus, 1758], throughout its geographical range, genetic analyses (using microsatellite markers) have revealed there are at least four different species of CoTS with distinct, but overlapping, geographic ranges (Vogler et al., 2008; Haszprunar and Spies, 2014; Haszprunar et al., 2017). In the Indian Ocean there are two nominal species; *A. planci* [Linnaeus, 1758] which occurs throughout the northern Indian Ocean from the Sea of Oman to North Sumatra, and *A. mauritiensis* [de Loriol, 1885], found mainly in the western Indian Ocean, but also Chagos and Christmas Island (Vogler et al., 2012). There is also a third distinct, and currently undescribed species from the Red Sea, which is purported to have fewer arms and may also have comparatively limited toxicity (Haszprunar et al., 2017). In the Pacific, there appears to be a single species (Vogler et al., 2008), for which the most likely valid name is *Acanthaster solaris* [Schreber, 1795] (Haszprunar et al., 2017).

Despite genotypic and phenotypic differences, there are no obvious dissimilarities in the biology of coral reef CoTS, and all four nominal species have been reported to undergo population outbreaks (Haszprunar et al., 2017). Adult CoTS feed on scleractinian corals (e.g., Ormond et al., 1976; Glynn, 1988; De'ath and Moran, 1998; Pratchett, 2007) and at low densities (<10 starfish per hectare) have negligible impact on the abundance of prey corals and associated reef processes (e.g., Glynn, 1973; Zann et al., 1990). However, CoTS outbreaks (defined herein as pronounced increases in the abundance of CoTS to levels that cannot be sustained by pre-existing levels of coral prey) are a major contributor to ongoing coral loss and associated degradation of coral reef ecosystems (e.g., De'ath et al., 2012; Kayal et al., 2012; Baird et al., 2013; Pisapia et al., 2016). In extreme cases, outbreak densities of CoTS can exceed 100,000 starfish ha^{-1} and cause significant and widespread depletion of reef-building corals (e.g., Chesher, 1969; Kayal et al., 2012), with concomitant effects on the biodiversity, productivity, structure and functioning of coral reef ecosystems (Pratchett et al., 2014; 2017a).

When outbreaks of CoTS were studied in the 1960s, it was assumed that they represented new and unprecedented phenomena linked to sustained and ongoing exploitation of marine species (Endean, 1977) or inputs of excess nutrients or pollutants to coastal waterways (Chesher, 1969). It is possible, however, that outbreaks of CoTS occur naturally (e.g., Vine, 1973; Caballes and Pratchett, 2017), due to variation in key demographic rates linked to environmental fluctuations or inherent stochasticity. Fundamentally, disruption to (or natural variability in) any of the mechanisms that typically regulate population size has the potential to lead to pronounced changes in local abundance (e.g., Andrewartha and Birch, 1954). However, species with high intrinsic rates of population growth are predisposed to very large fluctuations in abundance (e.g., Uthicke et al., 2009) and CoTS have extremely high reproductive potential (Endean, 1982; Conand, 1984; Babcock et al., 2016a), combined with early maturation and relatively rapid somatic growth (Yamaguchi, 1974; Lucas, 1984; Moran, 1986).

Numerous hypotheses have been put forward regarding the explicit causes or triggers of CoTS outbreaks (reviewed by Moran, 1986; Birkeland and Lucas, 1990; Pratchett et al., 2014). These hypotheses place specific importance on either i) factors affecting pre-settlement life stages and processes (e.g., *larval recruitment hypothesis*, Lucas, 1973; *terrestrial run-off hypothesis*, Birkeland 1982) or ii) changes in the behaviour and survivorship of post-settlement individuals (e.g., *predator removal hypothesis*, Endean, 1969; *adult aggregation hypothesis*, Dana et al., 1972; *prey-threshold hypothesis*, Antonelli and Kazarinoff, 1984). While ultimate causes of outbreaks may be many and varied (e.g., Babcock et al., 2016b), the relative importance of pre-settlement processes in initiating primary outbreaks continues to be debated (Johnson, 1992; Pratchett et al., 2014; 2017a; Rogers et al., 2017). Larval supply to individual reefs will undoubtedly be constrained by production, growth, survival, and dispersal of larvae, but post-settlement processes may alter the patterns established at settlement and ultimately limit the number of CoTS that actually grow, survive, and ultimately feed on reef-building corals. Consequently, biological and physical processes that occur during and after settlement may be just as important, if not more important, in regulating population size and conversely, initiating outbreaks (Keesing and Halford, 1992b).

Despite the potential importance of early post-settlement processes in structuring the dynamics of CoTS populations, this phase of the life history has received remarkably limited scientific attention. This is due, at least in part, to difficulties in detecting early-stage juvenile CoTS in natural environments, especially on the Great Barrier Reef (Doherty and Davidson, 1988; Johnson et al., 1992). However, emerging technologies (Uthicke et al., 2015; Doyle et al., 2017) and existing protocols (Keesing et al., 1993; Chapter 3) provide opportunities to effectively sample and study CoTS at various stages throughout their early life history, from planktonic larvae, through settlement, and during the formative period (first 12 months) immediately following settlement (Chapter 3). The purpose of this review, therefore, is to critically evaluate the relative contributions of pre- versus post-settlement processes in regulating the abundance and initiating population outbreaks of CoTS. Where possible, data on demographic rates during distinct life history phases will be presented and summarised. The specific focus on pre- versus post-settlement processes (and particularly, early post-settlement processes) differentiates this review from other major reviews on CoTS (e.g., Moran, 1986;

Birkeland and Lucas, 1990; Caballes and Pratchett, 2014; Pratchett et al., 2014; 2017a), which tend to provide a broad overview of the specific biology of CoTS and/or consider predominant hypotheses put forward to account for population outbreaks and corresponding management actions.

1.3 Pre-settlement processes

Many of the hypotheses put forward to explain the initiation of CoTS outbreaks (e.g., *larval starvation* and *terrestrial runoff* hypotheses; Birkeland, 1982; Lucas, 1982; Brodie, 1992; Brodie et al., 2005) emphasise factors affecting larval production, development and survival. Importantly, it is often assumed that there are major natural constraints on larval development and survival, meaning that settlement rates are normally very low despite potentially very high fecundity and reproductive potential (Cheney, 1974). Anthropogenic factors (e.g., eutrophication of coastal ecosystems) that relax normal constraints on larval development and survival may therefore represent important causes or triggers of population outbreaks (Birkeland and Lucas, 1990). Alternatively, outbreaks of CoTS may represent a natural and inherent manifestation of population instabilities associated with their extreme fecundity and reproductive potential (e.g., Vine, 1973; Uthicke et al., 2009). However, CoTS outbreaks do not necessarily arise due to sudden and dramatic increases in larval supply and mass settlement of planktonic larvae, though this has been documented in some locations (Yokochi and Ogura, 1987; Zann et al., 1987). Elsewhere, CoTS outbreaks may arise from progressive accumulation of individuals over multiple successive recruitment events (e.g., Pearson and Endean, 1969; Pratchett, 2005).

When considering factors that may cause or contribute to population outbreaks, it is important to distinguish between primary versus secondary outbreaks. Primary outbreaks arise independently (Endean, 1973), caused by inherent changes in demography at one or more stages in the life cycle, which may lead to either subtle and sustained increases in local population size (i.e., population build-up; Pratchett, 2005) or sudden and dramatic spikes in local population densities (i.e., population irruptions; Zann et al., 1987). Understanding the factors that contribute to initiation of primary outbreaks is fundamental to effective long-term management (Pratchett et al., 2014). Secondary outbreaks, by contrast, are an almost inevitable outcome resulting from marked increases in larval supply following increases in abundance of adult/reproductive CoTS on nearby or upstream reefs, and simply reflect the inevitable spread of primary outbreaks (Harrison et al., 2017).

Fecundity

Crown-of-thorns starfishes are purported to have exceptional fecundity (Conand, 1984; Babcock et al., 2016a), which provides for very high reproductive potential. However, the phenomenal reproductive capacity of CoTS is largely inferred based on the mass of ripe gonads, while relying on very preliminary estimates of oocyte concentrations (90,000 oocytes gm^{-1}) estimated by Conand (1984) from limited sampling ($n = 10$) of a single population of *A.* cf. *solaris*. By combining the estimates of oocyte concentrations with measures of total mass of ovarian tissues, Conand (1984) estimated that each female CoTS was capable of producing up to 60 million eggs. By extrapolating to larger bodied CoTS based on known relationships between diameter and gonad weight, Babcock et al. (2016a) extended the upper estimates of fecundity for *A.* cf. *solaris* to >100 million oocytes, which may be as high as 200 million for the largest reported CoTS (62 cm diameter) in Pratchett (2005). Fecundity of female CoTS increases exponentially with body size, due partly to allometric increases in weight relative to diameter, though larger females also invest disproportionately in gametogenesis (Kettle and Lucas, 1987; Caballes and Pratchett, 2014; Babcock et al., 2016a).

Aside from the size of adult CoTS, the fecundity and reproductive potential of *A.* cf. *solaris* is also dependent upon their recent feeding history and physiological condition (Caballes et al., 2016; Caballes et al., 2017a). Caballes et al. (2016) showed that CoTS with unfettered access to *Acropora* corals during the final stages of gametogenesis had >25% larger gonads (standardised for body size) compared to starved individuals. CoTS fed on *Acropora* also had 10% larger gonads compared to individuals restricted to feeding on *Porites* corals, potentially highlighting the importance of coral composition rather than overall coral cover. These differences in reproductive investment also translated into significant increases in the development rate, survival and size of the progeny (Caballes et al., 2016; Caballes et al., 2017a). Overall, well-fed female CoTS produce larger oocytes that develop faster and into bigger bipinnaria/early brachiolaria stage larvae (Caballes et al., 2016). Conversely, the reproductive potential of CoTS populations will decline as they deplete local coral resources, especially preferred coral species (Caballes et al., 2016), thereby dampening population growth during active outbreaks.

Fertilisation

The widespread occurrence and persistent low densities of CoTS in some locations (e.g., Birkeland and Lucas, 1990) suggests that their exceptional reproductive potential is rarely realised, or that there are other regulatory factors that limit reproductive success. Notably, CoTS have separate sexes and fertilisation rates depend upon synchronous spawning of male and female individuals within reasonably close proximity (Babcock et al., 1994; Rogers et al., 2017). For broadcast spawning marine organisms, the first and foremost bottleneck to reproductive success may occur at fertilisation (e.g., Lasker et al., 1996), which may be greatly constrained by sperm dilution (but see Yund, 2000). Experimental studies of fertilisation success for CoTS do reveal some evidence of sperm limitation (Benzie and Dixon, 1994), though fertilisation rates for CoTS are much higher than for other echinoderms, especially at large distances between male and female individuals (Pratchett et al., 2014). For isolated and low-density populations, however, the limited proximity of spawning CoTS may represent critical constraints on reproductive success (Babcock et al., 1994; Caballes and Pratchett, 2017; Rogers et al., 2017), though these limitations may be offset if CoTS actively aggregate immediately before or during spawning. Cheney (1974) reported that CoTS in aggregations exhibited higher investment in gametogenesis than those in non-aggregated populations, though aggregations themselves may be catalysed by non-reproductive factors (e.g., chemo-sensory attractants produced by actively feeding conspecifics). Regardless of the cause, active aggregation of CoTS would, at the scale of a reef, result in marked increases in fertilisation rates (Babcock et al., 1994; Rogers et al., 2017), thereby contributing to greatly increased larval production.

Fertilisation success is also dependent on environmental conditions, which influence both spawning synchrony (Caballes and Pratchett, 2017) as well as the concentration of gametes (Babcock et al., 1994). Caballes and Pratchett (2017) showed that spawning by male CoTS, but not females, may be induced by abrupt changes in temperature. However, both male and female CoTS were induced to spawn by addition of freshly collected sperm (Caballes and Pratchett, 2017). These findings suggest that environmental cues may induce preliminary spawning by male CoTS, which in turn triggers a hormonal cascade and the synchronised spawning of male and female CoTS. Given the critical temporal linkages between the timing of spawning and fertilisation events, variability in the extent and synchrony of spawning will significantly influence reproductive success and may account for interannual variation in population replenishment and the occurrence of outbreaks.

Larval development

The pelagic larval phase of CoTS is often considered key to understanding the initiation of population outbreaks (e.g., Lucas, 1982; Birkeland, 1982), whereby anthropogenic eutrophication of coastal waters is considered to be one of the foremost triggers of primary outbreaks. There has been a long history of experimental studies suggesting that larval survivorship may be highly constrained by nutrient concentrations and food availability (Lucas, 1982; Fabricius et al., 2010; Wolfe et al., 2017). Most notably, Lucas (1982) suggested that the amount of phytoplankton required to maintain larvae in aquaria was much higher than generally occurs in the wild. Thereafter, Birkeland (1982) proposed that enhanced nutrient supply caused by heavy rainfall and runoff, especially in areas of intensive agriculture, enhances food availability and survival of CoTS larvae. Spatial and temporal coincidence between flood events and CoTS outbreaks is considered to be further evidence for the role of nutrient enhancement in initiating outbreaks (Fabricius et al., 2010); however, elevated nutrient concentrations do not in and of themselves necessarily cause outbreaks (Wooldridge and Brodie, 2015; Roche et al., 2015; Suzuki et al., 2016).

Research increasingly suggests that CoTS larvae may actually be resilient to low nutrient conditions, partly relying on endogenous energy sources (Caballes et al., 2016; 2017a) or exploiting alternative food sources (e.g., Olson, 1987; Hoegh-Guldberg, 1994; Okaji, 1996; Nakajima et al., 2016) when phytoplankton is in limited supply. The quantity and quality of food does, however, influence developmental rates of CoTS larvae (Wolfe et al., 2015; 2017), which may translate into important differences in larval survivorship in the wild. Importantly, delayed development and prolonged planktonic larval duration (PLD) increases exposure to predation, and is likely to result in elevated mortality in the field (as per the *stage-duration hypothesis* for fishes; Leggett and Deblois, 1994), which will greatly exacerbate apparent differences in larval survivorship recorded during laboratory studies (e.g., Pratchett et al., 2017b). It is also apparent that very high nutrient concentrations and food availability may adversely affect larval survivorship, as high food concentrations can block the alimentary canal of larvae, reducing their feeding efficiency (Wolfe et al., 2015; 2017; Pratchett et al., 2017b). Moderate increases in nutrient concentrations and food availability could therefore, play a role in exacerbating CoTS outbreaks or contributing to their spread (Brodie et al., 2017), but it is unlikely that low nutrient conditions would sufficiently constrain larval survival to prevent the initiation of outbreaks.

Understanding purported links between nutrient enrichment, increases in phytoplankton abundance or changes in phytoplankton composition, and the increased survivorship and settlement of CoTS is constrained by the lack of any field-based sampling to explicitly relate the nutritional condition of CoTS larvae to local environmental and biological conditions (Pratchett et al., 2017a). The extent to which elevated nutrients will lead to increases in the local availability of suitable food for CoTS larvae also requires explicit examination (Brodie et al., 2017). Overall, there is definitive need for improved data on rates of pre-settlement mortality in the wild, for all larval stages, and for both outbreak and non-outbreak populations. This information will be critical in understanding the range of factors that may contribute to increased survival, thereby leading to population outbreaks (**Figure 1.1**).

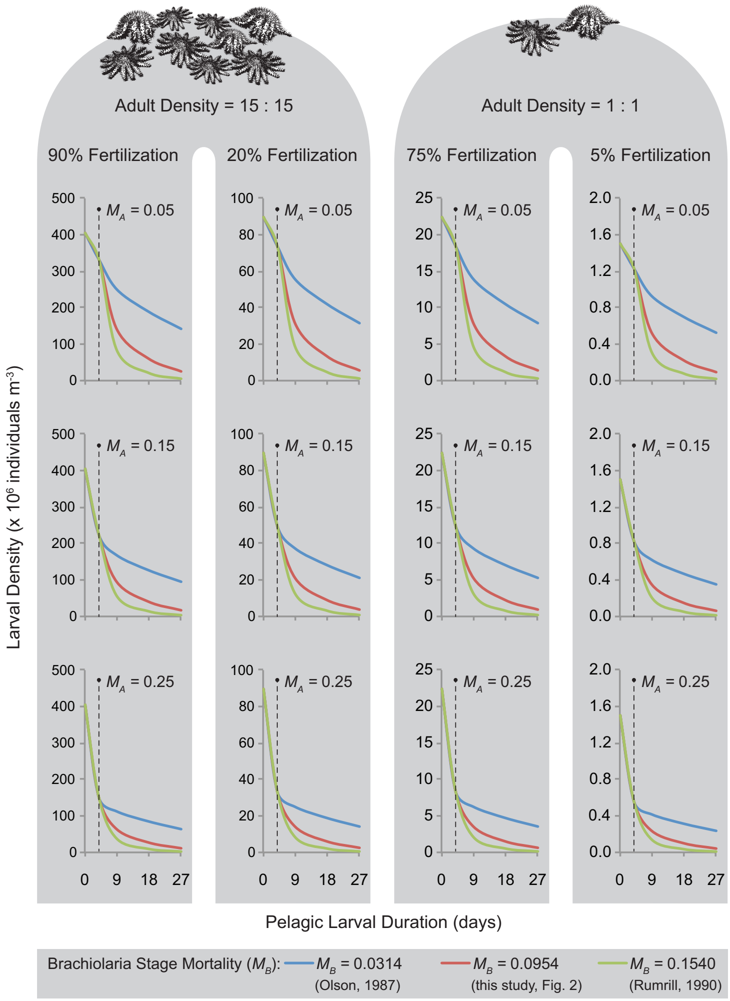


Figure 1. 1 Estimates of larval and settlement density calculated using the instantaneous rate model: $N_t = N_0 e^{-Mt}$ (Rumrill, 1990); where N_t is the larval or settlement density, N_0 is the initial zygote or larval density, *e* is the Naperian constant, *M* is the mortality rate, *t* is the pelagic larval duration. Initial differences in the density of reproductively mature starfish (30 CoTS ha^{-1} versus one breeding pair) and fertilisation rates (Babcock et al., 1994) will influence larval density, even when sex ratio (1:1) and fecundity (30 x 10^6 eggs per female starfish) are kept constant. A 10% change in hypothetical mortality (M_A) during the early larval stages (first 4 days) — potentially driven by environmental factors, larval predation, and exogenous/endogenous nutrition — will have pronounced effects on larval density. Variability in mortality rates (M_B) presumably due to predation and in *t* due to environmental factors and food availability will also have a significant effect on the ultimate density of settled larvae.

Mortality and predation

Constraints on success and survival during the pelagic (pre-settlement) phase may occur due to many different factors, including food limitation, environmental factors (e.g. temperature, salinity, pH), predation, and larval transport to unfavourable settlement substrata (**Table 1.1**). Importantly, constraints imposed throughout the pre-settlement phase, from spawning to settlement, may ultimately limit the number of larvae that successfully settle (**Figure 1.1**). Measuring mortality rates between intervening stages of the life cycle of CoTS — including intervals between reproduction and larval density, larval density and settlement density, settlement and recruitment rates, and recruitment and reproduction — will be critical in understanding population dynamics. However, pre-settlement survivorship is very challenging to measure (Hines, 1986) and natural mortality rates at distinct pre-settlement stages (i.e., gametes, zygotes and planktotrophic larvae) have never been quantified for CoTS. In the absence of direct measures, estimates of pre-settlement mortality may be derived by i) relating estimates of reproductive potential and settlement rates and assuming a fixed rate of larval mortality (Rumrill, 1990), ii) laboratory tests of larval responses to changing conditions of food availability, predation risk, or environmental constraints (e.g., Pratchett et al., 2017b; Sparks et al., 2017), or iii) modelling of population dynamics to explicitly derive estimates for specific demographic rates (e.g., Chen et al., 2017).

These estimates are illustrated in **Figure 1.1**, where larval supply trajectories were calculated from a hypothetical outbreak population (30 CoTS ha^{-1}) and a low-density population comprising one breeding pair. When sex ratio (1:1) and reproductive output (30 x 10^6 eggs per female; Babcock et al., 2016a) were held constant, the influence of initial differences in the density of breeding adults and fertilisation rates (**Table 1.1**; Babcock et al., 1994) persisted throughout settlement. For example, a breeding population of 15 aggregated females spawning synchronously can achieve high fertilisation rates (90%; Babcock et al., 1994) resulting in a zygote density of 405 x 10^6. Even when relatively high mortality rates were used for early and late larval stages (25% and 15.4%, respectively), the predicted density of pre-settlement larvae (22 days after fertilisation) was 9 x 10^6, which is twice that of the highest larval densities measured from field samples (Uthicke et al., 2015a; Doyle et al., 2017; Suzuki et al., 2016). Larval mortality during the early stages of development (bipinnaria stage: four days post-fertilisation) also has disproportionate effects on larval supply such that a 10% increase in hypothetical mortality resulted in a 50% decrease in the density of early brachiolaria larvae. Furthermore, larval mortality and time spent in the plankton during the late larval stages have pronounced interactive effects on the ultimate abundance of recruits. For example, the settlement density for a larval population experiencing low mortality (3.14%) and early settlement (13 days post-fertilisation) is predicted to be 48 times higher compared to a population with a high mortality rate (15.4%) and long pelagic larval duration (31 days post-fertilisation). This demonstrates that small differences in the density of breeding populations and fertilisation rates, coupled with small changes in mortality and development rates, will have pronounced effects on settlement density and subsequent recruitment; although the relative importance of each source of potential bottlenecks at specific stages of larval development will most likely vary spatially and temporally.

While there is very limited data on settlement rates for CoTS (discussed later), comparisons of the reproductive potential of CoTS relative to realised densities of juvenile and adult CoTS (even during population outbreaks) intuitively suggest that there must be extensive constraints on population replenishment, affected through either low rates of reproductive success, settlement, or post-settlement survivorship (**Figure 1.2**). Larval supply will almost certainly be influenced by a combination of biotic and abiotic factors including (but not limited to) gamete production, fertilisation success, food availability, predation, and environmental variability (**Figure 1.1**). Estimating mortality at different larval stages and partitioning mortality from these various sources, as well as understanding inherent variation within each source, will greatly enhance understanding of potential causes of CoTS outbreaks. Discounting constraints due to fertilisation (discussed previously; see also Chen et al., 2017), very high rates of mortality during the planktonic larval phase (e.g., Pratchett et al., 2017b) are likely to represent an important population bottleneck. For example, assuming fixed mortality rates of 15.4% day^{-1} throughout the pre-settlement phase (*sensu* Rumrill, 1990) and a PLD of ≥ 21 days (Pratchett et al., 2017b), only 3.5% of fertilised zygotes will survive to settlement (**Figure 1.2**).

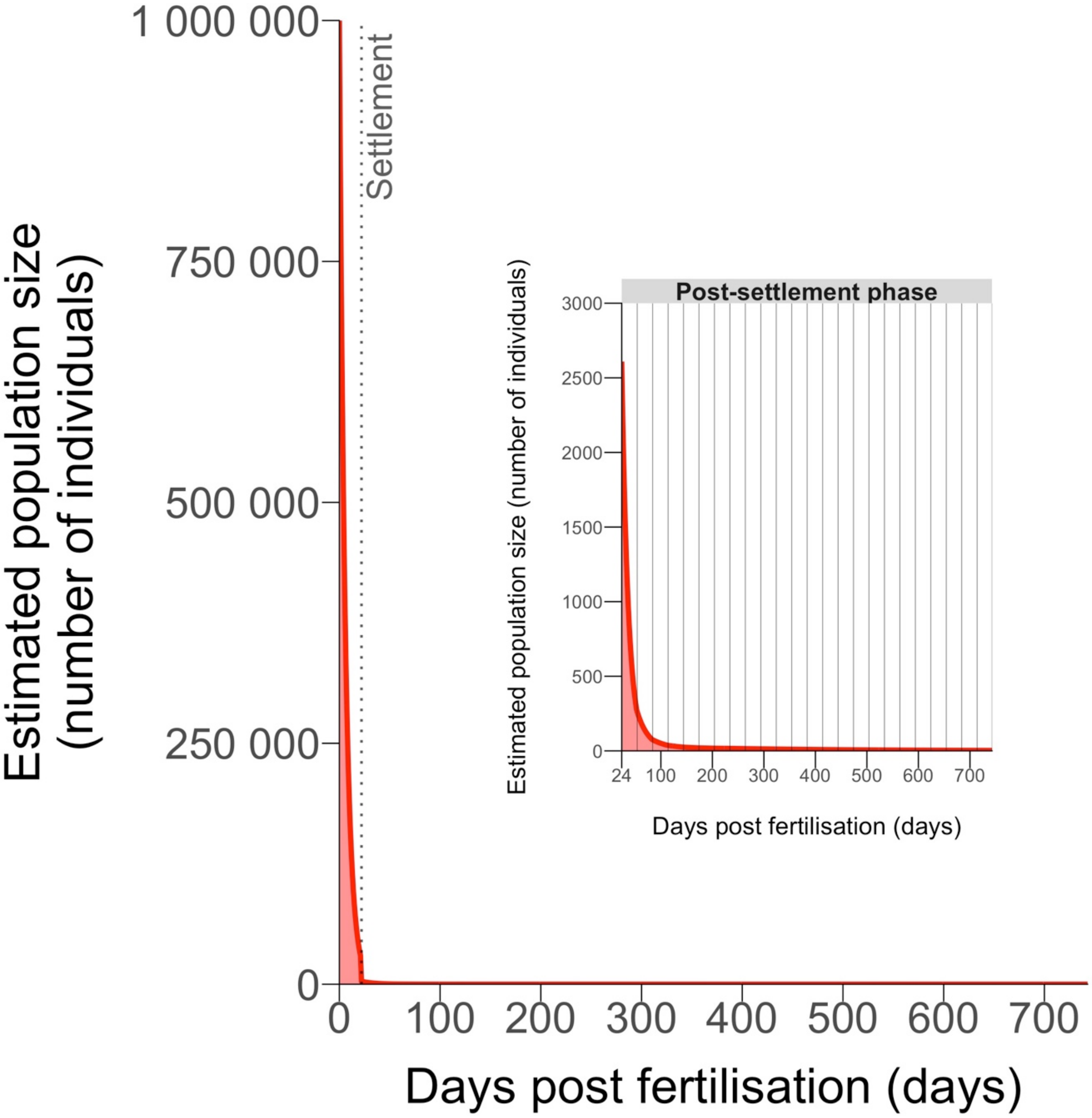


Figure 1. 2 Survivorship curve (Type III) for theoretical cohort of crown-of-thorns starfish, based on a pelagic phase of 21 days at a daily mortality rate of 15.4% (*sensu* Rumrill, 1990). Thereafter, only 9.54% effectively settle (see Figure 1.3). The subsequent post-settlement phase (expanded in the inset to improve resolution) shows further exponential declines in abundance based on high rates of early post-settlement mortality (6.49% day^{-1} for up to 1-month post-settlement), which is further explored in Figure 1.5.

Larval culture experiments (e.g., Pratchett et al., 2017b) invariably report high levels of pre-settlement mortality for CoTS, up to 8.5% day^{-1} (**Table 1.1**), which are likely to be further exacerbated in the field, due to additional effects of environmental variation and predation. In particular, predation on larval CoTS is expected to be very high, especially during the late brachiolaria stage, when larvae come within the vicinity of reefs environments (Cowan et al., 2017a). Despite apparent chemical defences (e.g., saponins) that are particularly concentrated in larval stages, CoTS larvae are readily consumed by planktivorous fishes and often in preference to other asteroid larvae (Cowan et al., 2016a; 2017a; 2020). Moreover, CoTS larvae may also be consumed by corals (Chesher, 1969; Yamaguchi, 1973). It is possible therefore, that spatial variation in the abundance of planktivores and corresponding differences in predation on CoTS larvae may influence the severity, if not occurrence of outbreaks.

The extent to which planktonic predators can or cannot effectively suppress larval densities of CoTS and constrain settlement success will depend on the density and distribution of the larvae (Cowan et al., 2017a). Horizontal plankton tows conducted in Okinawa, Japan, indicate that maximum densities of advanced-stage brachiolaria larvae are 0.05 larvae l^{-1} (53.3 larvae m^{-3}) in near reef waters (Suzuki et al., 2016). On the Great Barrier Reef, the maximum larval densities recorded during active outbreaks in 2014 were only 0.04 larvae l^{-1} (36.9 larvae per m^{-3}), with negligible densities recorded in most locations (Doyle et al., 2017). In experimental studies, individual damselfishes were capable of consuming up to 90% of CoTS larvae provided at densities of 10 larvae l^{-1}, at feeding rates of up to 158 larvae h^{-1} (Cowan et al., 2016a). Damselfishes and other planktivores could therefore, exact considerable toll on the eggs and larvae of CoTS (Cowan et al., 2016a; 2017a). However, protracted exposure to high larval densities may swamp the consumption capacity of planktivorous reef fishes, especially in areas with naturally low or suppressed densities of planktivores (Cowan et al., 2016a).

Table 1. 1 Stage-specific constraints on reproductive success and larval survivorship during the pre-settlement phase for crown-of-thorns starfish.

Ontogenetic Stage	Possible Constraints	Key Metrics	Source
1.Spawning Adults	Gametogenesis - Size	*Fecundity* 2 x 10^6 (~20 cm diameter) to 100 x 10^6 (~40 cm diameter) per female starfish per spawning season	Conand, 1984 (New Caledonia); Kettle and Lucas, 1987; Babcock et al., 2016a (Australia – GBR)
	Spawning - Proximity	*Fertilisation rate* 90% fertilisation when one female was next to one male; 20% if 60 m apart	Babcock and Mundy, 1992a; Babcock et al., 1994 (Australia – GBR)
	- Sex ratios	16% less fertilisation success when one female and one male spawn compared to when five males spawn with one female	Babcock et al., 1994 (Australia – GBR)
	- Timing	Fertilising capacity of sperm decreased by 40% after two hours from spawning and fertilisation rates are 20 to 30% higher when gametes are released earlier compared to later in the breeding season	Babcock and Mundy, 1992b; Benzie and Dixon, 1994 (Australia – GBR)
	- Hydrodynamics	78–99% lower fertilisation when female is upstream of spawning male compared to when spawning female is downstream at the same distance from the male starfish	Babcock et al., 1994 (Australia – GBR)
	Environmental factors - Temperature	*Fertilisation rate* 99% at 28°C; >89% from 24°C to 32°C; <20% at below 24°C and above 34°C	Caballes et al. 2017b (Micronesia – Guam)
	- Salinity	98% at 32 psu; >80% from ambient (34 psu) down to 26 psu	Caballes et al. 2017b (Micronesia – Guam); Allen et al., 2017 (Australia – GBR)
	- pH	94% at pH 8.2; >88% from pH7.6 to pH 8.2; reduction of fertilisation by 25% at pH 7.7	Caballes et al., 2017b (Micronesia – Guam); Uthicke et al., 2013 (Australia – GBR)

2.Gamete	Maternal investment	*Egg size* Eggs from starved female starfish 12% smaller than eggs from well-fed females (Relationship between egg size and fecundity not known for CoTS, but egg size may have flow-on effects on larval development)	Caballes et al., 2016 (Micronesia – Guam)
	Environmental factors - Temperature	*Sperm motility* >50% between 24 and 36°C; 69% at ambient conditions (28°C); peaked at 75% in 34°C treatment	Caballes et al., 2017b (Micronesia – Guam)
	- Salinity	72% at ambient salinity (34 psu) and >50% down to 24 psu *Egg osmotic balance* Salinities below 26 psu were deleterious to ova	Caballes et al., 2017b (Micronesia – Guam)
	- pH	*Sperm motility* 70% at ambient pH (8.1–8.2) and significant decrease in the proportion of motile sperm below pH 7.6 (<50%)	Caballes et al., 2017b (Micronesia – Guam); Uthicke et al., 2013 (Australia – GBR)
	Predation	*Consumption rate* Some planktivorous reef fish species consumed >50% of food pellets containing 100% CoTS egg extracts or up to 1 x 10^{-3} parts of saponin extract wet weights	Cowan et al., 2017a; Lucas et al., 1979 (Australia – GBR)
3.Zygote	Environmental factors - Temperature	*Cleavage rate* 87% at 28°C; >80% between 26°C and 30°C; <50% below 24°C and above 33°C	Lamare et al., 2014; Sparks et al., 2017 (Australia – GBR); Caballes et al., 2017b (Micronesia – Guam)
		Gastrulation rate 83% at 28°C; >80% between 26°C and 30°C; ~20–40% decrease below 24°C and above 31°C	Lamare et al., 2014; Sparks et al., 2017 (Australia – GBR); Caballes et al., 2017b (Micronesia – Guam)
		Proportion of normally developing embryos >70% at 27–28°C; no development below 20°C and above 33°C	Lamare et al., 2014 (Australia – GBR)
		Development rate Embryonic period 31 hrs at 20°C; 11 hrs at 32°C	Habe et al., 1989 (Japan – Ryukyu Islands)
	- Salinity	*Cleavage rate* 88% at 34 psu; >80% between 30 and 34 psu	Caballes et al., 2017b (Micronesia – Guam)

		Gastrulation rate 87% at 34 psu; >80% between 30 and 34 psu	Caballes et al., 2017b (Micronesia – Guam)
		Proportion of normally developing embryos >75% between 29 and 34 psu; <60% below 27 psu	Allen et al., 2017 (Australia – GBR)
	- pH	*Cleavage rate* 91% at pH 8.2; >80% between pH 7.8 and pH 8.2	Caballes et al., 2017b (Micronesia – Guam)
		Gastrulation rate 91% at pH 8.2; >80% between pH 8.0 and pH 8.2	Caballes et al., 2017b (Micronesia – Guam)
	Predation	*Consumption rate* No data; but most likely comparable to consumption rates for eggs or larvae	Cowan et al., 2016a; 2017a (Australia – GBR)
4.Swimming larvae	Environmental factors - Temperature	*Mortality rate* ~40% between 25°C and 32°C 45% at 28°C; 60% at 24°C; 99% at 32°C 7% daily mortality rate (24 days) across temperature treatments (28–30°C)	Lamare et al., 2014 Lucas, 1973 Uthicke et al., 2015b (Australia – GBR)
		Proportion of competent larvae >50% of larvae normally developing at 26–28°C; 0% at 30°C after 10 days; Temperature had initial (10 days after fertilisation) accelerating effect with only <5% larvae competent to settle at 28°C compared to ~10% competent at 30°C	Kamya et al., 2014 (Australia – GBR); Uthicke et al., 2015b (Australia – GBR)
	- Salinity	*Mortality rate* 50% at 30 psu; 75% at 35 psu	Lucas, 1973 (Australia – GBR)
	- pH	*Proportion of normally developing larvae* ~70% at pH 8.1; <50% at pH 7.6	Uthicke et al., 2013; Kamya et al., 2014 (Australia – GBR)
		Larval Growth 20% larger at pH 8.1 compared to pH 7.6 and pH 7.8 treatments	Uthicke et al., 2013 (Australia – GBR)
	Maternal provisioning	*Mortality Rate* 30–50% for larvae from well-fed starfish; 40–70% for larvae from starved starfish	Caballes et al., 2016 (Micronesia – Guam); 2017a (Australia – GBR)

	Proportion of competent larvae 47% for larvae from well-fed starfish; 5% for larvae from starved starfish	Caballes et al., 2016 (Micronesia – Guam); 2017a (Australia – GBR)
	Larval growth Larvae from fed starfish were 30% bigger than larvae from starved starfish	Caballes et al., 2016 (Micronesia – Guam); 2017a (Australia – GBR)
Food availability	*Mortality rate* 50% for well-fed larvae; 70% for starved larvae 16 days after fertilisation; ~50% higher mortality for larvae in low (0.1 μgL^{-1} chl-*a*) and high (10 μgL^{-1} chl-*a*) compared to intermediate food (1 μgL^{-1} chl-*a*) treatment after 22 days; Mortality ~30–40% for larvae in 0 to 1 μgL^{-1} chl-*a* treatment and 19% in 10 μgL^{-1} chl-*a* after 10 days	Caballes et al., 2017a; Pratchett et al., 2017b (Australia – GBR); Wolfe et al., 2015 (Australia – GBR)
	Proportion of competent larvae larvae complete development 8-fold with every doubling of chlorophyll concentration up to 4; μgL^{-1}; ~50% competent larvae at 9800 algal cells ml^{-1} and ~10% at 1,100 algal cells ml^{-1}	Fabricius et al., 2010 (Australia – GBR); Uthicke et al., 2015b (Australia – GBR)
Planktonic predation	*Consumption rate* Depending on the planktivorous fish species, 15–75% of larvae (density = 10 larvae L^{-1}) were consumed	Cowan et al., 2016a (Australia – GBR)

1.4 Post-settlement processes

While the distribution and abundance of benthic marine organisms is fundamentally constrained by patterns of larval supply (Gaines and Roughgarden, 1985; Hughes, 1990), spatial and temporal variation in settlement and post-settlement processes may effectively obscure any relationship between larval supply and adult abundance. For example, variation in rates of settlement of corals to experimental substrata (assumed to reflect variability in larval supply) often shows little or no relation to patterns of adult abundance (e.g., Hughes et al., 1999). As such, there is increasing interest in the extent to which early post-settlement mortality, which may be very high (Babcock, 1985), but also variable (Mundy and Babcock, 2000), may structure coral populations and communities (Vermeij and Sandin, 2008; Penin et al., 2010; Trapon et al., 2013). For CoTS, research on settlement and early post-settlement processes has been largely restricted to laboratory-based experimental studies (**Table 1.2; Table 1.3**) because early-stage juvenile CoTS are notoriously difficult to detect and effectively sample in the wild (Doherty and Davidson, 1988; Johnson et al., 1992). It is increasingly apparent, however, that like corals and other marine organisms, constraints on settlement and early post-settlement survival may be critically important in understanding the population dynamics of CoTS (Zann et al., 1987; Keesing and Halford, 1992b; Chapter 3). In particular, resource requirements, growth and vulnerability to predation of juvenile CoTS may vary spatially and temporally, and have a critical influence on the incidence of outbreaks (Keesing and Halford, 1992b).

Settlement rates and preferences

Natural settlement rates of CoTS are yet to be quantified, though there are estimates of proportional settlement derived from laboratory-based studies (Yamaguchi, 1973; Johnson et al., 1991; Pratchett et al., 2017b; Uthicke et al., 2018; **Table 1.2**). These aquarium studies indicate that settlement success is generally low (median settlement rate of 9.45%), but also highly variable, ranging from 0–52.50% (**Figure 1.3**). Despite protracted periods of competency, settlement success peaks at 14–21 days and then declines with increasing larval duration (**Figure 1.3**). Settlement success is therefore, likely to be even more constrained in the wild due to the limited window of opportunity for CoTS larvae to encounter suitable settlement substrates. Settling larvae are also exposed to a wide range of potential predators, including sessile plankton feeders (Chesher, 1969), that will further reduce settlement success. Accordingly, settlement may constitute a major bottleneck phase in the CoTS life cycle, as has been shown for other coral reef organisms (Doherty et al., 2004; Chong-Seng et al., 2014).

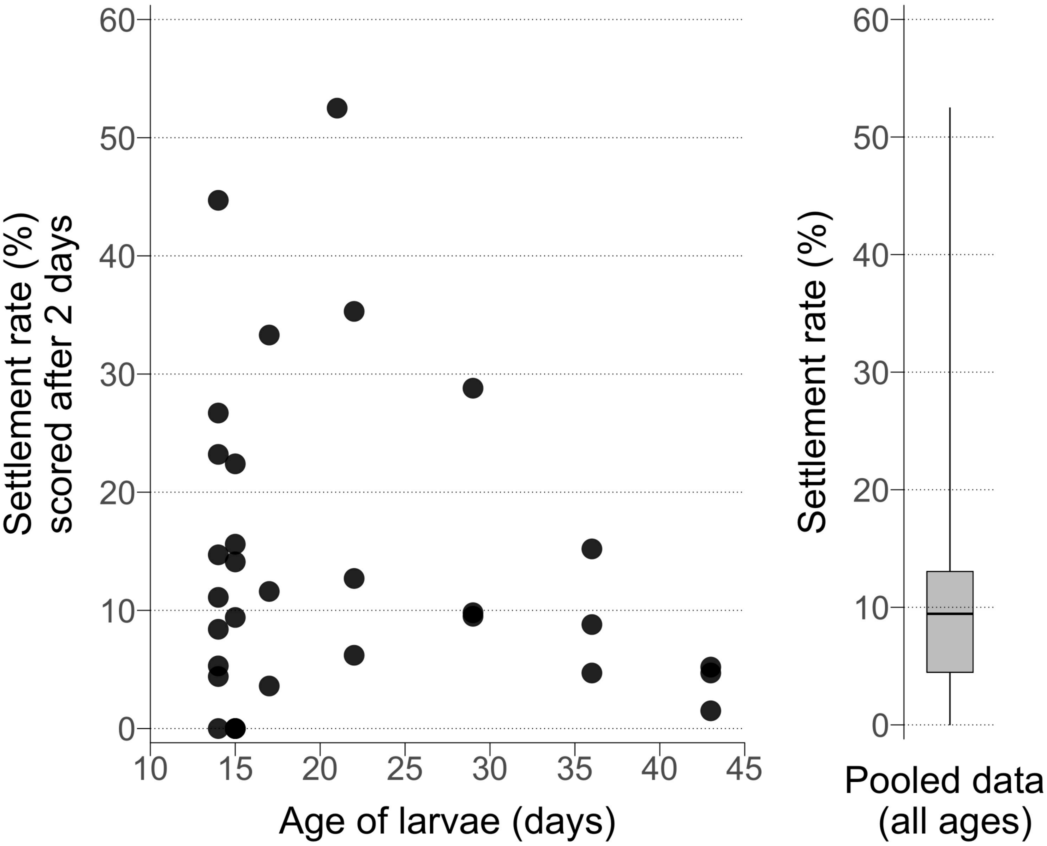


Figure 1. 3 Settlement rates of *A*. cf. *solaris* based on proportion of late-stage brachiolaria larvae that initiated or fully metamorphosed into five-armed juvenile starfish between 14 and 44 days post-fertilisation when exposed to settlement cues (e.g., coral rubble encrusted with crustose coralline algae). Data sources: Yamaguchi, 1973; Johnson et al., 1991; Pratchett et al., 2017b; Uthicke et al., 2018. Individual records (1A) were compiled to estimate the median (horizontal line, 9.45%), lower and upper quartile (rectangle, 4.47–15.50%), and minimum and maximum (vertical line, 0–52.50%) settlement rates (1B).

Settlement rates of CoTS are likely to be constrained, at least in part, by the availability of suitable settlement substrate (*sensu* Johnson et al., 1991), though their specific settlement requirements are equivocal. If settling CoTS do exhibit marked preferences for certain types of benthic substrates, which in turn promote high rates of post-settlement survival, then outbreaks would be expected to originate in those reef habitats where preferred settlement substrates are abundant. Laboratory reared CoTS larvae settle preferentially on coral rubble encrusted with crustose coralline algae (CCA) (Johnson et al., 1991; Cowan et al., 2016b) reflecting a combination of both biological and physical habitat features that promote settlement (Ormond and Campbell, 1974). However, the range of substrates used in these experiments was limited (**Table 1.2**) and not entirely representative of the full range of potential settlement substrates encountered in the field. CoTS larvae have also been observed to preferentially settle on undersides of highly inductive CCA fragments (Johnson et al., 1991), indicating an inherent preference for cryptic or shaded microhabitats (Keesing, 1995) and showed preferences for specific species of CCA (Johnson et al., 1991). However, early-stage juvenile CoTS in the field have often been recorded feeding on *Porolithon onkodes* (Yokochi and Ogura, 1987; Zann et al., 1987), though settlement rates on *P. onkodes* were low compared to those on other CCA, such as *Lithothamnium pseudosorum*, *Neogoniolithon fosleii* and *Peysonellia* spp. (Johnson et al., 1991). More rigorous field and laboratory experimental studies will therefore, be needed to evaluate settlement rates and post-settlement survival across different natural habitats, as well as environmental and larval density gradients.

Settling CoTS respond to chemical stimuli (Johnson et al., 1991; Cowan et al., 2016b) and competent larvae have the capacity to detect chemical cues in the water column (e.g., adult conspecifics and potential predators) and to actively swim towards or away from these cues, at least under low current flow conditions (Cowan et al., 2016b). It is still unknown, however, whether CoTS can effectively respond to chemical stimuli under field conditions and thereby actively influence their patterns of settlement. It is perhaps more likely that CoTS larvae that are passively distributed across a broad range of settlement habitats and simply defer settling in the absence of relevant settlement cues, or are subject to elevated mortality when forced to settle in marginal habitats. Laboratory-based settlement assays revealed that CoTS larvae are able to detect predators (i.e., polychaetes and trapeziid crabs) in potential settlement substrates and where possible, will preferentially settle in microhabitats without predators (Cowan et al., 2016b). However, larvae did not necessarily defer settlement in the presence of predators, though there were fewer settlers that actually persisted in the presence of predators (Cowan et al., 2016b). This suggests that settlement of CoTS may be very sensitive to changes in the abundance of benthic predators (Keesing and Halford, 1992b), and maintaining intact assemblages of cryptic infauna may be critically important in regulating abundance and moderating settlement success of CoTS (Cowan et al., 2016b).

Predation

Mortality rates of early-stage juvenile CoTS has been shown to be very high (Keesing and Halford, 1992a), even within seemingly preferred settlement habitats (coral rubble; Johnson et al., 1991). Mortality rates are particularly high in the 1-month immediately after settlement (6.49% day^{-1}; Keesing and Halford, 1992a) but decline rapidly with increasing size and age of early-stage juvenile CoTS (**Figure 1.4**). While susceptibility to predation likely declines with growth even throughout the first month after settlement, sustained mortality at 6.49% day^{-1} will reduce the effective population size by >90% in just 30 days post-settlement (**Figure 1.5**). Early post-settlement mortality is largely attributed to epibenthic predators (e.g., polychaetes and crustaceans) living within the coral rubble (Keesing and Halford, 1992a; Keesing et al., 1995; Cowan et al., 2016b), which are known to be very abundant (Keesing and Halford, 1992a) though there is no information regarding their predilection for CoTS or potential satiation limits. Benthic feeding fishes, meanwhile, appear to contribute very little to early post-settlement mortality (Sweatman, 1995). Nonetheless, the highly cryptic and predominantly nocturnal behaviour of juvenile CoTS, is considered to be a behavioural adaptation to reduce vulnerability to diurnally active visual predators, such as fishes (Keesing, 1995).

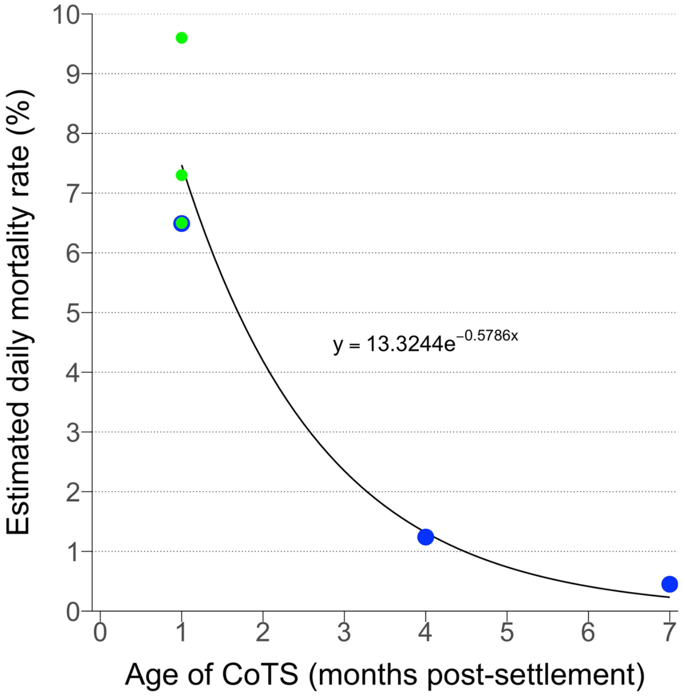


Figure 1. 4 Age-specific mortality rates for early-stage juvenile *A*. cf. *solaris*, based on experimental studies conducted on the Great Barrier Reef (Keesing and Halford, 1992a; Keesing et al., 1996). Laboratory reared individuals were subject to natural mortality/ predation in the field at 1, 4 and 7 months of age (Table 1.2). The fitted line shows the exponential growth equation fitted to reflect these estimated mortality rates.

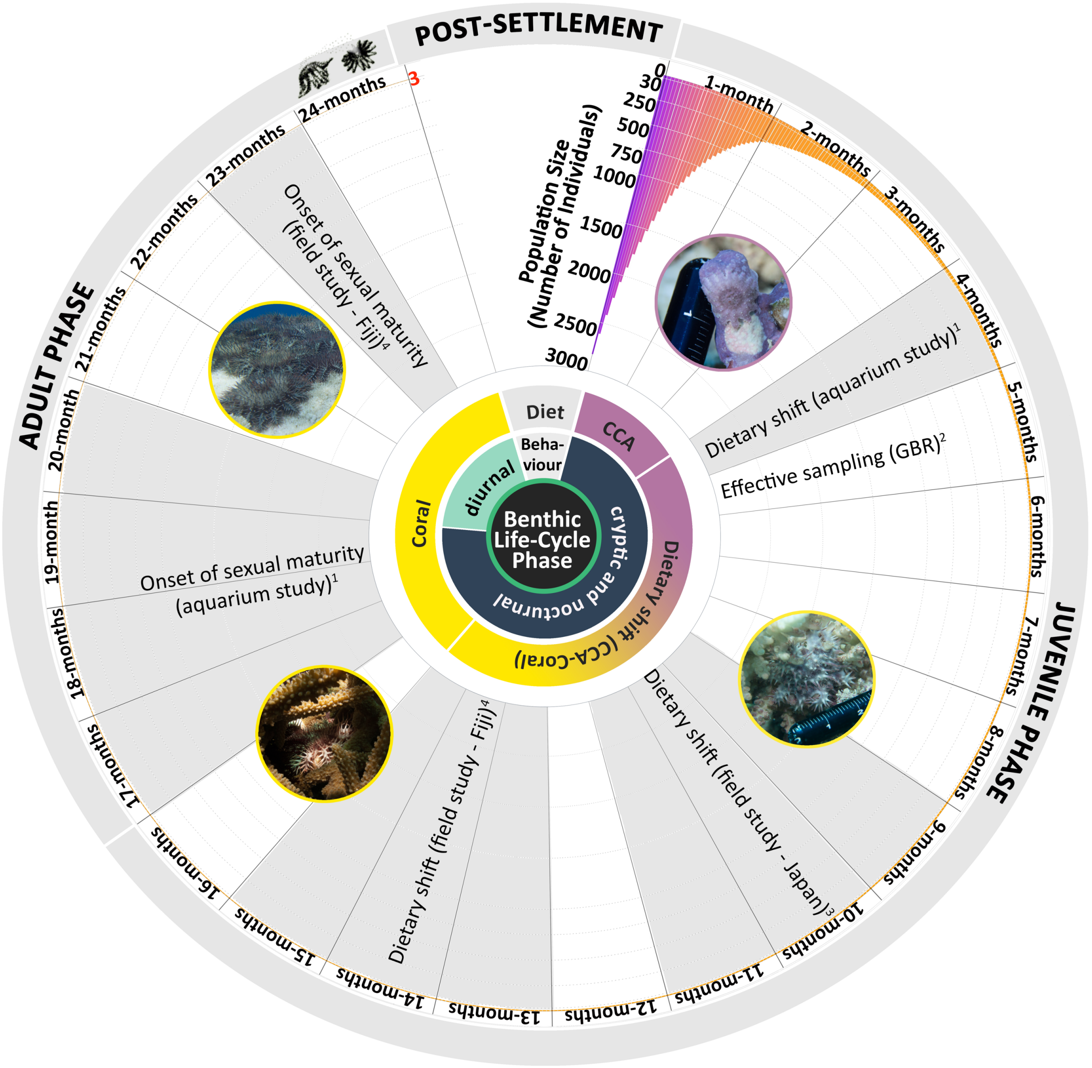


Figure 1. 5 Post-settlement survivorship for a theoretical cohort of CoTS (see inset of Figure 1. 2), showing population size as a function of age (in months after settlement), and key stages in the benthic phase. Each bar represents the estimated population size at daily time increments. Survivorship curves are based on daily mortality rates recorded up to 7 months post-settlement (Figure 1. 4). Due to the lack of age-specific mortality rates, rates for ages 8–24 months post-settlement are based on field estimates for juvenile starfish (Table 1. 2). According to this model, only 0.1% of settling CoTS will survive the first 24-months after settlement (i.e., 3 out of 3,000), though actual survivorship may vary spatially and temporally. Images show examples, from start to end, of algal- and coral-feeding juvenile stages, and sub-adult and adult stages of CoTS. Citations: [1]Yamaguchi, 1973; [2]Chapter 3; [3]Habe et al., 1989; [4]Zann et al., 1987.

The vulnerability of CoTS to different types of predators is likely to change as they grow (Keesing, 1995). In support of this, the proportion of CoTS with conspicuous injuries, presumed to be caused by sublethal predation from fishes, is low (<25%) for small (<10 cm diameter) individuals, but approaches 80% among starfish that are 11–20 cm diameter (Rivera-Posada et al., 2014). This suggests that CoTS are much more susceptible to fish predation once they reach 10 cm diameter (Rivera-Posada et al., 2014) which coincides with the size at which juvenile starfish become diurnally active and much less cryptic (Keesing, 1995). This does not, however, necessarily mean that smaller starfish are less susceptible to predation. Rather, predation on smaller starfish may be more likely to be lethal, rather than causing injuries. Adult CoTS may also be subject to lethal predation (Cowan et al., 2017b) albeit at lower rates for increasingly large individuals (**Table 1.3**).

Table 1. 2 Settlement rates estimated for Pacific CoTS (*A.* cf. *solaris*) at 14–43 days post-fertilisation, based on experimental studies that used differential settlement substrates as well as varying densities of larvae in settlement assays. "*" indicates comparable values used to estimate overall settlement rates (Figure 1.3).

Study type	**Settlement substrate**	**Age (days)**	**Density at settlement**	**Estimated settlement rate**	**Reference**
Laboratory study	Field collected small pieces of dead coral covered with coralline algae (presumably not cleaned)	21	-	52.5% in 2 days*	Yamaguchi, 1973
Laboratory reared larvae deployed in the field in flow-through chambers for 2 days at 2 m depth	*Porolithon onkodes* fragment (ca. 1 cm^2)	14	42 larvae l^{-1}	0% in 2 days*	Johnson et al., 1991
	Neogoniolithon fosleii fragment (ca. 1 cm^2)	14	42 larvae l^{-1}	8.4% (sd = 7.6%) in 2 days*	
	Lithothamnium pseudosorum fragment (ca. 1 cm^2)	14	42 larvae l^{-1}	11.1% (sd = 4.9%) in 2 days*	
	Peysonellia sp. fragment (ca. 1 cm^2)	14	42 larvae l^{-1}	4.4% (sd = 4.1%) in 2 days*	
	Coral rubble fragment (ca. 1 cm^2)	14	42 larvae l^{-1}	23.2% (sd = 4.7%) in 2 days*	
	Fresh *L. pseudosorum* shards	14	133–167 larvae l^{-1}	44.7% (sd = 7.6%) in 2 days *	
	Fresh *L. pseudosorum* shards separated from larvae at a distance of 15 to 30 mm by 100 micrometre mesh	14	133–167 larvae l^{-1}	26.7% (sd = 32.2%) in 2 days *	
	Plexiglas beneath mesh, as a control	14	133–167 larvae l^{-1}	0% in 2 days	
	L. pseudosorum shards boiled for 15 min	14	133–167 larvae l^{-1}	0% in 2 days	
	Dialysis tubing (10 000 Daltons pore size) containing *L. pseudosorum* shards	14	133–167 larvae l^{-1}	0% in 2 days	
	Dried coral (*Porites* sp.) blocks perfused with ethanol or chloroform or aqueous (distilled water) extracts of *L. pseudosorum*	14	133–167 larvae l^{-1}	0% in 2 days	
	Shards of *P. onkodes* from high light environments	14	133–167 larvae l^{-1}	5.3% (sd = 4.2%) in 2 days*	
	Shards of *P. onkodes* from shaded habitats	14	133–167 larvae l^{-1}	14.7% (sd = 11.7%) in 2 days*	
Laboratory study	Fresh L. pseudosorum shards	-	250 larvae l^{-1}	Lp1 40.2% (sd = 38%); Lp2 16.2% (sd = 16.4%) in 4 days	

Study type	Settlement substrate	Age (days)	Density at settlement	Estimated settlement rate	Reference
Laboratory study	Coralline algae (*Lithothamnion sp.*) carefully cleaned of epifauna	-	-	15% in 2 days	Keesing and Halford, 1992b
Laboratory study (larvae reared under three chlorophyll concentrations: 0.1,1.0 and 10.0 μg·$l^{-1)}$	Polycarbonate plate encrusted with a 1 cm^2 crustose coralline algae (CCA)	17	2500 larvae l^{-1}, 10 larvae cm^{-2}	3.6% in 2 days (0.1 μg· l^{-1}); 33.3% in 2 days (1.0 μg· l^{-1}); 11.6% in 2 days (10 μg· l^{-1})*	Pratchett et al., 2017b
		22	2500 larvae l^{-1}, 10 larvae cm^{-2}	6.2% in 2 days (0.1 μg· l^{-1}); 35.3% in 2 days (1.0 μg· l^{-1}); 12.7% in 2 days (10 μg· l^{-1})*	
		29	2500 larvae l^{-1}, 10 larvae cm^{-2}	9.5% in 2 days (0.1 μg·L−1); 28.8% in 2 days (1.0 μg·L−1); 9.8% in 2 days (10 μg·L−1)*	
		36	2500 larvae l^{-1}, 10 larvae cm^{-2}	8.8% in 2 days (0.1 μg·L−1); 15.2% in 2 days (1.0 μg·L−1); 4.7% in 2 days (10 μg·L−1)*	
		43	2500 larvae l^{-1}, 10 larvae cm^{-2}	5.2% in 2 days (0.1 μg· l^{-1}); 4.7% in 2 days (1.0 μg l^{-1}); 1.5% in 2 days (10 μg l^{-1})*	
Laboratory study (larvae reared under five chlorophyll concentrations: 0.1, 0.5, 0.8, 1.0 and 5.0 μg·l^{-1})	A small fragment (~1 cm^2) of crustose coralline algae (CCA)	16	10 larvae ml^{-1}	23–26% in 3 days (<0.8 μg· l^{-1}); 30% in 3 days (1.0 and 5.0 μg·l^{-1}).	Wolfe et al., 2017

Study type	Settlement substrate	Age (days)	Density at settlement	Estimated settlement rate	Reference
Laboratory study (larvae reared under three chlorophyll concentrations: 890–1030 algae ml^{-1}, 300–480 algae ml^{-1}, 760–1070 algae ml^{-1}; and three nominal densities: 0.5,1,2 larvae m^{-1})	Small chips of the crustose red algae *L. pseudosorum*	15	-	0% in 2 days (890–1030 algae ml^{-1}, nominal density = 2); 9.4% in 2 days (890–1030 algae ml^{-1}, nominal density = 1); 22.4% in 2 days (890–1030 algae ml^{-1}, nominal density = 0.5)*	Uthicke et al., 2018
		15	-	0% in 2 days (300–480 algae ml^{-1}, nominal density = 2); 0% in 2 days (300–480 algae ml^{-1}, nominal density = 1); 0% in 2 days (300–480 algae ml^{-1}, nominal density = 0.5)*	
		15	-	0% in 2 days (760–1070 algae ml^{-1}, nominal density = 2); 14.1% in 2 days (760–1070 algae ml^{-1}, nominal density = 1); 15.6% in 2 days (760–1070 algae ml^{-1}, nominal density = 0.5)*	

Table 1. 3 Post-settlement mortality rates estimated for Pacific CoTS (*A.* cf. *solaris*) accounting for the age (time since settlement), size (diameter) and densities of CoTS. Unless specified, the mortality rate is the overall mortality rate for the specific study period or age range of the CoTS studied. "*" indicates comparable values used to model early post-settlement mortality **(Figure 1.4).**

Study type	**Time post-settlement**	**Diameter (mm)**	**Density/relative abundance**	**Estimated mortality rate**	**Reference**
Laboratory study	2 weeks	-	-	0%	Yamaguchi, 1973
Field study – mortality rates inferred from changes in densities between estimated ages of 8 and 23 months	Estimated age: 8–23 months	Estimated age 8 months (0+ year old starfish): 24 mm (mean size); estimated age 23 months (1+ year old starfish): 140 mm (mean size)	8.8–0.06 ind. m^{-2}	99.3%	Zann et al., 1987
Field study – mortality rates inferred from changes in densities between estimated ages of 22 and 34 months	Estimated age: 22–34 months	Estimated age 22 months (i.e., 1+ year old starfish): 98 mm (mean size); estimated age 34 months (i.e., 2 + year cohort): 180–300 mm (dominant size group)	-	ca. <77%	Doherty and Davidson, 1988
Field study – Estimates based on monitoring changes in density of the 1987 starfish cohort from 1988 to 1989 at Suva Reef – Fiji	1–2 years	-	-	75%	Zann et al., 1990
Field study – Estimates based on monitoring changes in density of the 1977 starfish cohort from 1979 to 1985 at Suva Reef – Fiji	2–3 years	mode: 270 mm	5 480 ind. m^{-2}	42%	
	3–4 years	-	3 170 ind. m^{-2}	47%	
	4–5 years	-	1 687 ind. m^{-2}	44%	
	5–6 years	-	943 ind. m^{-2}	45%	
	6–7 years	-	519 ind. m^{-2}	51%	
	7–8 years	-	256 ind. m^{-2}	93%	
	8+ year	-	17 ind. m^{-2}	-	

Laboratory reared individuals deployed *in situ* within boxes containing coral rubble from deployment sites (12–15 m)	1-month	Size range (after recovery): 0.6–1.7 mm	2 137 ind. m^{-2}	6.49% day^{-1} (5.05% day^{-1} attributed to predation)*	Keesing and Halford, 1992a
	4-months	Size range (after recovery): 0.7–4.7 mm	748 ind. m^{-2}	1.24% day^{-1} (0.85% day^{-1} attributed to predation)*	
	7-months	Size range (after recovery): 1.4–6.0 mm	110 ind. m^{-2}	0.45% day^{-1} *	
	16-months	Size range (after recovery): 9–23 mm	114 ind. m^{-2}	No juveniles recovered, uncertain whether individuals moved out of boxes or were predated	
Laboratory reared individuals deployed *in situ* within boxes containing coral rubble from deployment sites	1-month	Size range: 1–1.6 mm	1 068 ind. m^{-2}	9.6% day^{-1} (deployed at 2 m on reef flat)*	Keesing et al., 1996
	1-month	Size range: 1–1.6 mm	1 068 ind. m^{-2}	6.5% day^{-1} (deployed at 12 m on back reef lagoon)*	
	1-month	Size range: 1–1.6 mm	1 068 ind. m^{-2}	7.3% day^{-1} (deployed at 15 m on front reef slope)*	
Laboratory reared individuals deployed *in situ* within artificially constructed units of microhabitats containing concrete building blocks, coral rubble, large dead coral plates and live pieces of at least 3 staghorn and corymbose *Acropora* spp. and one or two small colonies of *Seriatopora histrix*	Not given (estimate: majority <1 year)	Size range: 15–79 mm (48% <25 mm and 80% <50 mm)	99 ind. m^{-2}	0.34% day^{-1} (0.13%/day due to predation)$^{+}$	Sweatman, 1995
Laboratory reared individuals deployed *in situ* within boxes containing coral rubble from deployment sites	3-months	3 mm	109 ind. m^{-2}	2.60% day^{-1} (73.0% attributed to predation)	Keesing et al., 2018
	15-months	13 mm	109 ind. m^{-2}	0.82% day^{-1} (deployed at average depth of 10 m at 6 sites in back reef at Davies Reef)	

Growth

As for much of the demographic information pertaining to CoTS, initial estimates of juvenile growth were derived from laboratory reared animals (e.g., Lucas, 1984), though field-based estimates have been obtained by recording temporal changes in the size structure of specific localised cohorts (Zann et al., 1987). More recently, growth of juvenile CoTS on the Great Barrier Reef (*A*. cf. *solaris*) was modelled based on opportunistic collections of 3,532 starfish, presumed to be in their first year post-settlement (Chapter 3). As for other asteroids and echinoderms (Lawrence and Lane, 1982), growth of early-stage juvenile *A*. cf. *solaris* is characterised by an initial phase of slow growth followed by rapid growth during the remaining juvenile phase (Yamaguchi, 1973; 1974; Lucas, 1984). For captive-reared CoTS, this accelerated growth has been shown to coincide with dietary shifts from CCA to corals (Yamaguchi, 1973; 1974; Lucas, 1984), and in field populations this has been suggested to occur at approximately 9 to 13 months post-settlement (Zann et al., 1987; Habe et al., 1989). Indeed, growth rates during the phase of rapid growth appear remarkably consistent between laboratory reared individuals and field populations (Chapter 3).

The microhabitat preferences and resource requirements of juvenile CoTS are likely to be very different depending upon their reliance on CCA versus coral prey (Zann et al., 1987). As a result, each growth phase (i.e., coralline algae versus coral feeding) is likely to be characterised by its own set of limiting biotic (e.g., inter- and intraspecific competition, predation and prey availability) and abiotic factors (e.g., structural complexity which may provide shelter from predators, temperature and salinity) that influence growth and survival. While CCA is fairly ubiquitous in shallow reef environments, growth (and survival) of juvenile CoTS may be very sensitive to availability and accessibility of coral prey. Importantly, there does not appear to be significant constraints on realised growth rates of early-stage juvenile CoTS based on abundance or composition of CCA (Keesing and Halford, 1992b; Caballes and Pratchett, 2014; Pratchett et al., 2014). In contrast, early-stage juvenile CoTS that have limited access to coral prey fail to grow beyond 20 mm in diameter (Lucas, 1984; Keesing and Halford, 1992b). These stunted juvenile CoTS will be more susceptible to predation and disease (Lucas, 1984). Therefore, marginal reef environments with low coral cover, especially of preferred coral species, are likely to limit the prospects of outbreaks occurring, and may explain the natural demise of population outbreaks and protracted periods of low densities following local coral depletion caused by major population outbreaks (Pratchett et al., 2014). However, there have not been any explicit tests of the role of local coral cover and composition in determining the growth and survival of early-stage juvenile CoTS.

The ontogenetic diet shift of CoTS from CCA to live coral (Zann et al., 1987; Habe et al., 1989) may under certain circumstances lead to shifts in habitat use. For example, Zann et al. (1987) observed that the distribution of juvenile starfish shifted markedly at an estimated age of 10 to 11 months, when the population moved 5 to 10 m through a coral rubble and rock dominated reef flat area (coral cover <0.1%) towards the reef crest. At 19 months of age, most juveniles had left the coral rubble dominated area and moved 30–50 m to the adjacent reef crest where they were preying on sparse coral (ca. 5% coral cover) (Zann et al., 1987). Accordingly, even where there was limited availability of coral prey (0.1–5% local coral cover) 19-month old juvenile starfish remained close to the area where they were first detected (i.e., 30–50 m) and where they most likely settled. The starfish population only started migrating over larger distances, at a speed of ca. 3–5 m month^{-1}, at an estimated age of 23 months, when over 50% of sampled starfish had developed gonads (Zann et al., 1987). Taken together, these results suggest that individual starfish cohorts remain close to where they first settle in the initial 19 months post-settlement and that larger scale movements only occur as a result of limited food availability (Ling et al., 2020) that may be caused by and increased feeding activity of starfish leading up to the spawning season (Keesing and Lucas, 1992). Juvenile coral-feeding CoTS are therefore, likely to be found within 100 m from where they first settled (Yamaguchi, 1974).

1.5 Conclusions

Crown-of-thorns starfishes appear predisposed to major population fluctuations due to their considerable reproductive potential and the multitude of factors (e.g., maternal condition, spawning synchrony, local environmental constraints on fertilisation success, larval development and settlement success) that may influence whether this reproductive potential is actually realised (**Figure 1.1**). Even with significant constraints on larval survival (3.52%; **Figure 1.2**), settlement success (9.45%; **Figure 1.3**) and post-settlement survival (0.1%; **Figure 1.5**), the intrinsic rate of population growth (r = 1.5, assuming each female produces 1 million eggs, while also imposing 40% annual mortality among adult CoTS) approximates that documented by Pratchett (2005) and may be sufficient to initiate a primary outbreak. Moreover, small and subtle changes in stage-specific rates of survivorship or transitions among life history phases (i.e., pre-settlement, settlement and post-settlement phases) could lead to substantial changes in densities of juvenile and adult CoTS within reef environments. This in turn means that there are a multitude of potential scenarios under which outbreaks might arise (Babcock et al., 2016b), and quite possibly, different types of population outbreaks; primary outbreaks may arise from either subtle and sustained increases in local population size of CoTS through successive recruitment events (i.e., population build-up; Pratchett, 2005) or sudden and dramatic spikes in local recruitment (i.e., population irruptions; Zann et al., 1987).

This systematic review of demographic data for CoTS reveals that there are potentially important population bottlenecks during pre-settlement (**Table 1.1**), settlement (**Table 1.2**) and post-settlement phases (**Table 1.3**). Application of these data to assess whether it is pre- or post-settlement processes that are most likely to initiate population outbreaks of CoTS, is however, hampered by our lack of knowledge regarding variability in key processes (and the extent to which these processes may or may not be influenced by anthropogenic activities or degradation of reef ecosystems) and corresponding influences on population dynamics. At least in terms of inherent population constraints, pre- and post-settlement processes are both important and have additive effects to suppress densities of juvenile and adult CoTS within reef ecosystems (**Figure 1.2**). While not tested, it is also likely that increased levels of larval production and survivorship would overwhelm normal regulatory processes that operate during the post-settlement phase (e.g., swamping the consumptive capacity of benthic predators), such that relaxation of population constraints during either pre- or post-settlement phases would invariably lead to elevated densities of juvenile and adult CoTS, thereby contributing to population outbreaks.

The majority of recent research on the population dynamics of CoTS has focused on demography and behaviour of adult starfishes (e.g., Kayal et al., 2012; Babcock et al., 2016a), or the nutritional ecology and development of CoTS larvae (Wolfe et al., 2015; Pratchett et al., 2017b), building on well-established fields of CoTS research (reviewed by Moran, 1986; Birkeland and Lucas, 1990; Pratchett et al., 2014). There has been comparatively little research on settlement and early post-settlement stages, other than preliminary experimental studies on settlement rates and preferences (Johnson et al., 1991; Keesing et al., 1993), post-settlement predation (Keesing and Halford, 1992a, b; Sweatman, 1995) and growth (Yamaguchi, 1974; Lucas, 1982). However, settlement and early post-settlement stages are widely recognised as being critically important in understanding stock-recruit relationships and the dynamics of CoTS populations (Moran, 1986; Pratchett et al., 2017b). Quantifying rates of settlement for CoTS, as well as early post-settlement growth, survival and resulting rates of recruitment (and variation therein), is therefore a foremost priority for CoTS research. Herein, I specifically quantify rates of post-settlement growth and recruitment (and variation therein) for early-stage juvenile *A*. cf. *solaris* from Australia's Great Barrier Reef to better understand how variation in these demographic rates shapes the dynamics of CoTS populations, and I explore the underlying mechanisms (namely predation and coral prey availability) that are most likely to drive variability in the demography of juvenile CoTS populations.

1.6 Thesis outline

My thesis consists of four published data chapters (Chapters 2–5), which provide critical demographic rates and insights into the biology and ecology of early-stage juvenile *A*. cf *solaris*, with a strong focus on the elusive algal-feeding stage. All data chapters are based on field data that was collected from Australia's Great Barrier Reef. Each chapter makes an important independent contribution to better understanding how processes that occur during the early post-settlement phase influence CoTS population dynamics and the incidence of outbreaks, as outlined below.

In ***Chapter 2****: Habitat associations of early-stage juvenile crown-of-thorns starfish on Australia's Great Barrier Reef*, I describe the habitat of early-stage juvenile *A*. cf *solaris*, at different spatial scales. Specifically, I examine how the occurrence and density of early-stage juvenile CoTS (n = 140) varies in relation to exposure (reef aspect), depth and benthic substrate composition (e.g., proportion of coral rubble and live coral). This chapter provides the first field-based estimates of recruitment (and variation therein) for early-stage juvenile CoTS in the midst of active outbreaks on the Great Barrier Reef, and demonstrates that substantial settlement of early-stage juvenile starfish occurs in relatively shallow water habitats (<18 m) on mid-shelf reefs of the Great Barrier Reef.

In ***Chapter 3****: Modelling growth of early-stage juvenile crown-of-thorns starfish on the Northern Great Barrier Reef*, I model growth of juvenile *A*. cf *solaris* (n = 3,532) in their first year following settlement to provide the first field-based estimates of monthly ranges of body size and growth rates for early-stage juvenile CoTS from the Great Barrier Reef. I then compare these modelled growth rates to those of previous field studies that were conducted in Japan and Fiji, and to those of an experimental study conducted on the Great Barrier Reef – in which laboratory reared early-stage juvenile CoTS were deployed in the field and recovered afterwards.

In ***Chapter 4****: Contrasting size and fate of juvenile crown-of-thorns starfish linked to ontogenetic diet shifts*, I model growth of algal- and coral-feeding early-stage juvenile *A*. cf *solaris* (n = 3,532) separately to test whether their growth trajectories differ *in situ*, and test whether there is a critical size threshold below which early-stage *A*. cf *solaris* do not seem to shift their diet and microhabitat (i.e., dead coral substratum encrusted with coralline algae versus live coral). I then use the proportion of algal-feeding juvenile CoTS in samples as a proxy to model the timing of ontogenetic shifts in diet. Finally, I compare my findings with those of previous field and tank-based studies that followed growth of CoTS since settlement or the early post-settlement period, and discuss the importance of the ontogenetic shift in diet to population dynamics and the incidence of outbreaks.

In **Chapter 5***: Incidence and severity of injuries among early-stage juvenile crown-of-thorns starfish on Australia's Great Barrier Reef*, I quantify the incidence and severity of sublethal injuries in 200 early-stage juvenile *A*. cf *solaris* to examine whether and how their vulnerability to predation varies with size and between microhabitats (i.e., dead coral substratum versus live coral). I then test whether the incidence and severity of sublethal injuries in early-stage juvenile *A*. cf *solaris* differs between individuals that were collected from protected (i.e., no-take) versus fished reefs of the Great Barrier Reef.

Finally, in ***Chapter 6****: General discussion,* I summarise the most important findings of my thesis, discuss the relevance of these new insights to the ecology and management of CoTS populations, and identify avenues for future research.

— Chapter 2 —

Habitat associations of early-stage juvenile crown-of-thorns starfish on Australia's Great Barrier Reef

Chapter 2: Habitat associations of early-stage juvenile crown-of-thorns starfish on Australia's Great Barrier Reef

Adapted from: Wilmes JC, Schultz DJ, Hoey AS, Messmer V, Pratchett MS. 2020a Habitat associations of settlement-stage crown-of-thorns starfish on Australia's Great Barrier Reef. *Coral Reefs* 39, 1163-1174 (doi:10.1007/s00338-020-01950-6).

2.1 Abstract

Outbreaks of crown-of-thorns starfish (*Acanthaster* spp.) contribute greatly to the degradation of coral reefs throughout the Indo-Pacific. Effective management of outbreaks is limited, in part, by incomplete knowledge of their early life history. Importantly, there is very limited data on the distribution and abundance of early-stage juvenile crown-of-thorns starfish (in their first year since settlement). Extensive sampling was conducted around the circumference of three distinct mid-shelf reefs (at 1–18 m depths) in the central Great Barrier Reef (GBR), during active outbreaks, in May–June 2017 to quantify the occurrence and densities of early-stage juvenile starfish (2–65 mm diameter), and relate patterns of abundance to distinct habitat features at the scale of individual reefs. Overall, 140 early-stage juvenile starfish were detected across 1,242 quadrats (1 m^2). Early-stage juvenile starfish were recorded from 31 out of 42 sites (73.8%) at densities of 0–0.77 starfish m^{-2}. Both estimated densities and the likelihood of occurrence of early-stage juvenile starfish within quadrats increased overall with the proportion of coral rubble (and dead intact corals), were greatest at intermediate depths (8–14 m), but decreased with the proportion of live hard coral. At the scale of individual reefs, early-stage juvenile starfish occurred most frequently in south-western and northern fore reef habitats. Our results suggest that settlement and/or post-settlement survival of crown-of-thorns starfish is greatest in relatively shallow waters of obliquely exposed fore reef habitats where there is high cover of coral rubble. The specific occurrence of these habitat types (within spur and groove systems and rubble slips) provides an opportunity to concentrate searches and increase effective sampling of early-stage juvenile starfish, though these habitats are relatively widespread and unlikely to constrain the population replenishment or outbreaks of crown-of-thorns starfish on the GBR.

2.2 Introduction

While climate-induced coral bleaching is emerging as the foremost threat to coral reefs globally (Hughes et al., 2018), outbreaks of coral-eating crown-of-thorns starfish (*Acanthaster* spp.) continue to occur and contribute to reef degradation throughout the Indo west-Pacific (e.g., De'ath et al., 2012; Baird et al., 2013; Mellin et al., 2019). On Australia's Great Barrier Reef (GBR), for example, recurrent outbreaks of the Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*), along with severe tropical storms, account for much of the sustained coral loss recorded on shallow reef slopes throughout the last 35 years (De'ath et al., 2012; Mellin et al., 2019), which has now been exacerbated by recurrent mass coral bleaching episodes (Hughes et al., 2017). Causes of crown-of-thorns starfish outbreaks have been debated for decades, and largely focus on factors that influence reproduction, settlement and recruitment (Pratchett et al., 2014; Babcock et al., 2016b; Chapter 1). Empirical data on early life history stages of crown-of-thorns starfish is, however, scarce and hinders our ability to fully understand and predict spatial and temporal fluctuations in the abundance of adult starfish within and among reefs. While variation in larval supply and settlement have been shown to be decoupled from the size and structure of local adult populations for some Asteroidea (e.g., *Asterias forbesi* – Loosanoff, 1964; Ebert, 1983), such relationships are yet to be established for *Acanthaster* spp.

Although large-scale patterns in the distribution of crown-of-thorns starfish and the predominantly south-ward progression of outbreaks have been well documented on the GBR (e.g., Reichelt et al., 1990a; Hock et al., 2014; Vanhatalo et al., 2016), it remains unknown to what extent larval supply, settlement and recruitment dictate variability in the abundance of adult starfish among and within reefs. Ultimately, reefs with very high adult abundance are likely to have experienced high levels of larval settlement, but high levels of settlement may not always result in outbreaks if there are local constraints on growth and survival of early-stage juvenile starfish (Chapter 1). Understanding the factors that influence patterns of settlement and establishment (recruitment) of high densities of crown-of-thorns starfish is important in developing strategies towards effectively managing outbreaks (Chapter 4; Pratchett and Cumming, 2019). Numerous and varied factors are likely to influence settlement and abundances of early-stage juvenile starfish. These factors include: i) reproductive output of various source populations (e.g., Caballes et al., 2016; Babcock et al., 2016a; Rogers et al., 2017), ii) hydrodynamic conditions encountered during the pelagic larval phase (e.g., Black and Moran, 1991; Hock et al., 2014), iii) predation- and food-related larval survival (e.g., Cowan et al. 2016a, 2020; Pratchett et al. 2017b), iv) substrate availability- and predation related-settlement success (Johnson et al., 1991; Cowan et al., 2016b) and v) early post-settlement survivorship (Keesing and Halford, 1992a; Keesing et al. 1996, 2018; Chapter 5). However, our knowledge about the extent to which these factors dictate spatial variability in settlement and abundances of early-stage juvenile starfish *in situ*, among and within reefs, remains limited.

Growth of asteroids can be highly plastic, often in response to food availability, potentially obscuring the relationship between size and age (Mead, 1900; Nauen and Böhm, 1979; Deaker et al., 2020a). Importantly, Deaker et al. (2020a) showed that juvenile *A.* cf. *solaris* maintained in captivity and deprived of coral prey reached an asymptotic size of 16–18 mm and did not grow for 6.5 years. This suggests that early-stage juvenile crown-of-thorns starfish may represent starfish from several successive cohorts, ranging in age from <1 to several years (Deaker et al., 2020a). However, early-stage juvenile crown-of-thorns starfish sampled in the field do tend to have distinct and highly constrained size ranges, suggesting that the majority of individuals are from a single cohort (Habe et al., 1989; Chapter 3). Moreover, distinct cohorts of early-stage juvenile *A.* cf. *solaris* have been tracked over months to years (Zann et al., 1987; 1990; Okaji, 1996; Habe et al., 1989), and while they do exhibit expected patterns of somatic growth (*ibid*) there is also often an apparent increase in size variation over time within these cohorts (e.g., Habe et al., 1989). This increased variation in size may reflect disparity in the timing of ontogenetic shifts in diet (from coralline algae to hard horal) that lead to marked changes in the rate of growth (Chapter 4). Similarly, Nauen (1978) showed that juveniles of *Asterias rubens* may exhibit periods of negligible growth before switching their diet, in this case from detritus to macrobenthic invertebrates. Even so, distinct cohorts of early-stage juvenile *A. rubens* have been tracked in the field for at least one year post-settlement (Barker and Nichols, 1983; Nichols and Barker, 1984; Guillou et al., 2012). In field settings, survivorship of small starfish is very low (Keesing and Halford, 1992a; Keesing et al., 1996, 2018), such that any delays in diet shifts and corresponding constraints on growth will impact on individual survival (Chapter 5), and early-stage juveniles are likely to be dominated by cohorts of individuals that transition rapidly through ontogenetic stages to maximise growth (Chapter 4).

Regardless of the actual age of early-stage juvenile starfish, effective sampling of very small individuals has been difficult, due in part to their low detectability (Johnson, 1992; Johnson et al., 1992; MacNeil et al., 2016). This has greatly hindered our understanding and research into the mechanisms that influence settlement, recruitment and population dynamics of *Acanthaster* spp. Importantly, the distribution and abundance of early-stage juvenile crown-of-thorns starfish have rarely been measured in the field (but see Habe et al., 1989; Zann et al., 1987, 1990; Chapter 3), and are mostly inferred from patterns of abundance for larger, more motile, starfish (e.g., Laxton, 1974; Moran et al., 1985). For example, Laxton (1974) suggested settlement of *A.* cf. *solaris* on mid-shelf reefs of the GBR mainly occurred in shallow fore reef habitats (<3 m), and some back reef habitats due to high densities of small size classes of starfish (mostly 100–150 mm) in these habitats. This is supported by other studies that have reported the greatest numbers of smaller starfish (<100 mm) in these habitats (sheltered back reef: Pearson and Endean, 1969; Pratchett, 2005; shallow fore reef: Moran et al., 1985; Engelhardt et al., 1999). However, the absence of and/ or difficulty of detecting recently-settled and early-stage juvenile starfish in these habitats has led to suggestions that settlement occurs in deep inter-reefal habitats (at 30–60 m depth), after which individual starfish move up exposed reef fronts to recruit to adult populations in shallow coral-rich habitats; *sensu* the deep-water recruitment hypothesis (Johnson et al., 1991). The deep-water recruitment hypothesis was further supported by experimental studies of settlement, whereby the coralline algae (*Lithothamnium pseudosorum*) that was most effective in inducing settlement of *A.* cf. *solaris*, was believed to be mainly restricted to deep reef habitats (Johnson et al., 1991). Differentiating between these two hypotheses has been hampered by difficulties in detecting recently-settled and early-stage juvenile starfish *in situ*, however, recent studies have shown that early-stage juvenile starfish can be reliably detected using systematic searches of reef habitat (Chapter 3, 4, 5).

Current knowledge about spatial patterns in the abundance of early-stage juvenile crown-of-thorns starfish is mostly derived from studies of *A.* cf. *solaris* conducted in the 1980s at fringing reefs off Iriomote Island, Japan (Yokochi and Ogura, 1987; Habe et al., 1989) and Viti Levu, Fiji (Zann et al., 1987; 1990). In these studies, very small individuals (up to 70 mm diameter) were recorded at high densities (up to 8.3 individuals m^{-2}) within coral rubble or dead coral rock habitats, as opposed to coral-rich habitats, and mainly within very shallow (<10 m depth) reef environments (Yokochi and Ogura, 1987; Zann et al., 1987; 1990; Habe et al., 1989). Similarly, extensive and targeted field sampling on the GBR detected early-stage juvenile starfish across a wide range of reefs (n = 64) in <15 m depth (Chapter 3, 4, 5), though specific densities and habitat associations of early-stage juveniles were not recorded. The purpose of this study was to i) explicitly quantify densities of early-stage juvenile starfish (defined herein as individuals that are <70 mm diameter) across a range of habitats at distinct reefs in the central GBR, and ii) characterise specific habitat features (e.g., substrate type) that influence the occurrence and density of early-stage juvenile crown-of-thorns starfish.

2.3 Methods

Field surveys

Field surveys were conducted on three mid-shelf reefs in the central GBR; Walker Reef, Lodestone Reef and Rib Reef (**Figure 2.1**), off Townsville in May and June 2017. The timing of surveys (> 5 months after predicted spawning and settlement; Uthicke et al., 2019) represents a necessary trade-off between detectability and post-settlement mortality, as early-stage juvenile starfish are difficult to visually detect <5 months post-settlement due to their extremely small size (Chapter 3, 4). It was important, however, to begin surveys as early as possible to minimise the extent to which differential post-settlement mortality, as well as ontogenetic shifts in habitat use, may moderate habitat associations of early-stage juvenile starfish (Chapter 4). The study reefs (**Figure 2.1**) were selected based on reports of high densities of adult starfish at the time of the surveys, and were comparable in terms of their distance offshore (46–58 km) and subject to the same fisheries regulation (i.e., habitat protection zone; open to most forms of fishing, except trawling). At each reef, surveys were conducted at randomly selected locations approximately equidistant around the circumference of the reef. At Walker Reef, however, back reef habitats were characterised by narrow depth ranges and a predominance of sandy substrate, such that surveys were mostly restricted to fore reef habitats. A total of 42 sites were surveyed across the three reefs; 16 sites at Walker Reef, 14 sites at Rib Reef and 12 sites at Lodestone Reef (**Figure 2.1**). All study sites had a relatively steep reef slope, enabling sampling of multiple depths (up to a maximum of 18 m depth) within close proximity (<30 m between the furthest separated quadrats).

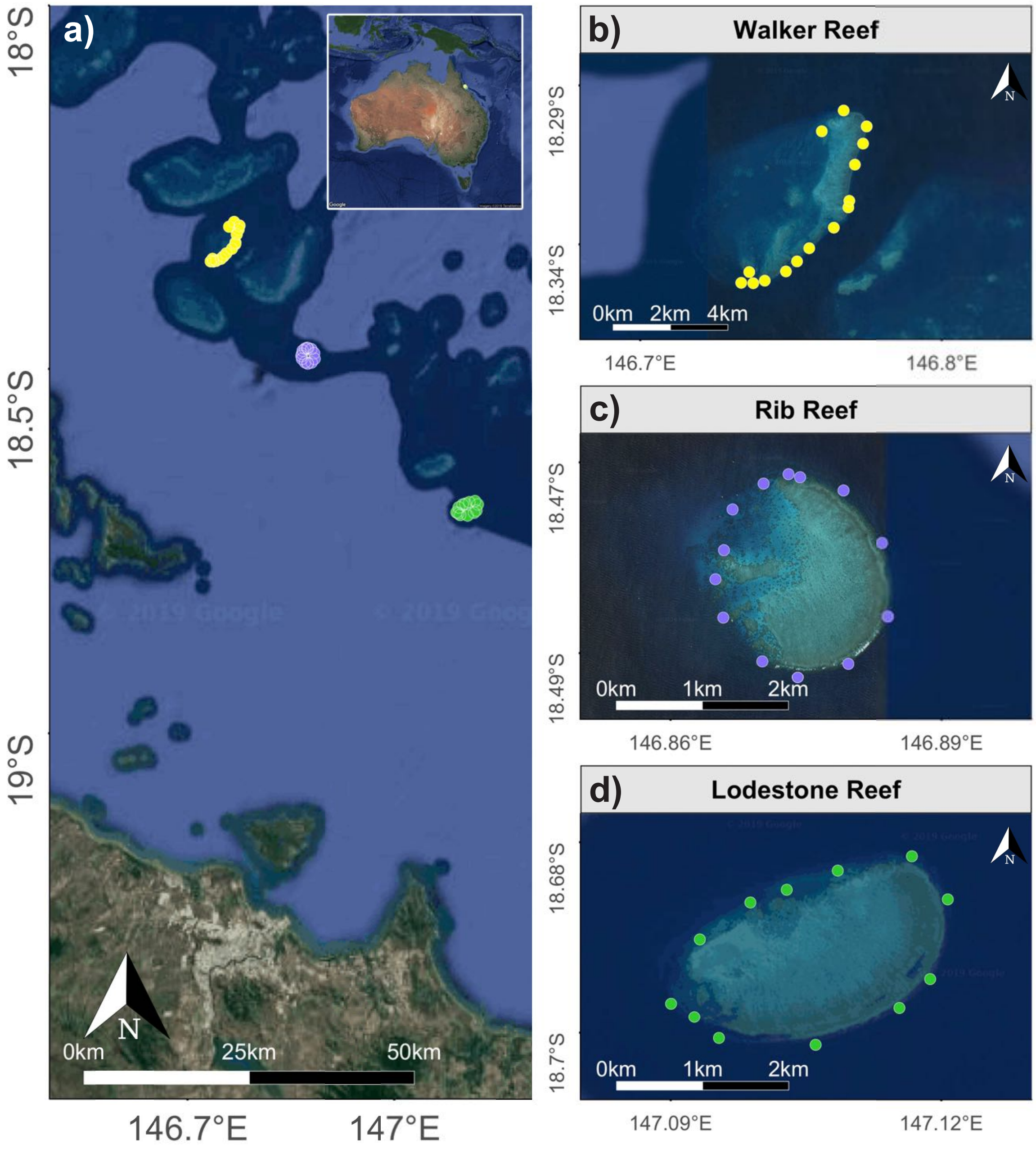


Figure 2. 1 a) Survey sites in relation to the mainland (three reefs located off Townsville, Australia). Survey sites on individual reefs, from north to south b), Walker Reef, c) Rib Reef and d) Lodestone Reef (Map data©2018 Google).

Local densities of early-stage juvenile starfish were quantified using 1m × 1m quadrats (n = 30), placed haphazardly within sites. Sampling was conducted from the bottom of the reef slope (maximum 18 m depth) on areas where crustose coralline algae was observed and avoiding areas comprised mostly or entirely of sand. Each quadrat was divided into quadrants, and each quadrant was thoroughly searched for early-stage juvenile starfish by carefully inspecting individual pieces of unconsolidated substrate for early-stage juvenile starfish or conspicuous feeding marks on coralline algae or live coral. Where feeding marks were observed, individual starfish were tracked down by following these marks. Each quadrat was photographed and the total number of early-stage juvenile starfish sampled per quadrat was recorded. Depth (m), slope angle (0–90º, where 0º is horizontal and 90º is vertical) and habitat complexity (estimated visually on a five-point scale, following a modified version of Wilson et al., 2007) were recorded for each quadrat. For each individual starfish detected, the size (maximum diameter to the nearest mm), diet (coral genera and growth form – Veron, 2000; coralline algae growth form – Littler and Littler, 2013) and substrate (e.g., coral rubble, intact dead coral skeleton, coral rock) were recorded *in situ*.

We typically refer to early-stage juvenile starfish as either coralline algal-eating (herbivorous) or coral-eating (corallivorous) starfish, based on whether we find them feeding and/or in proximity to recent feeding marks (in the present study, mostly <10 cm away), on either coralline algae or live hard coral, respectively. Herbivorous starfish, especially early stages, are typically extremely small (diameter <8 mm), range in colour from purple to pink, and are characterised by short arms, fan-shaped marginal spines and nodules on the aboral body side that will later develop into spines (Chapter 4). Corallivorous early-stage juvenile starfish are larger (diameter >8 mm) and have brown-yellow bodies, longer arms, well developed spines, madreporites, papulae and more closely resemble adult starfish (Chapter 4). Later stages of coral-eating juvenile starfish often display a conspicuous dark circle on their aboral side, which is also referred to as a “juvenile ring” (Yamaguchi, 1974). Both life history stages of early-stage juvenile starfish are extremely cryptic. Herbivorous starfish typically occupy the underside or interstices of coral rubble or dead coral skeleton, whereas corallivorous individuals generally occupy the base or underside of live hard coral colonies and are often found associated with branching forms of *Acropora* spp., such as “bottlebrush” growth forms (Chapter 3, 4).

Reef aspect was calculated as the bearing of each study site (n = 42) from the centre point of the reef using ArcGIS (in GDA_1994_MGA_Zone_55), and allowed exposure of sites to the prevailing south-easterly wind direction to be compared. Benthic composition was assessed for each quadrat by visually identifying major benthic categories (i.e., live hard coral, intact dead coral skeleton, coral rubble, coral rock, sand, soft coral and macroalgae) under a 5 by 5-point image overlay. For each quadrat, the proportion of a given benthic category was estimated as the ratio between the count of points falling on a given category and the total number of points used for the image analysis (n = 25).

Data analyses

Patterns in the occurrence and densities of early-stage juvenile starfish at the quadrat level

Boosted trees (BTs, see Leathwick et al., 2006; De'ath, 2007; Elith et al., 2008; Buston and Elith, 2011) were used to relate the occurrence (presence/absence) and density (individuals.m^{-2}) of early-stage juvenile starfish to 13 predictor variables (**Table 2.1**). Boosted tree analysis was chosen over a multiple regression analysis to avoid issues related to collinearity among predictor variables. All BTs were fitted in R (R Core Team, 2018) using the *gbm.step()* function from the *dismo* package (Hijmans et al., 2017), which automatically computes the optimal number of boosting trees via k-fold cross validation (CV, here k = 10). During this process, the data is divided into 10 random subsets that are used to generate 10 training data sets, each of which omits one of the 10 subsets (i.e., the left-out data set or test data). BTs of progressively increasing tree size are then fitted to each one of the 10 training data sets, and their predictive performance is evaluated on their respective left-out data set. The optimum number of trees is then selected as the one at which the mean deviance (relative to the left-out data) is minimised. For the development of BTs, we specified "Bernouilli" (for presence/absence data) and "Poisson" (for density data) distributions as family, an out-of-bag fraction of 0.5, and trialled different learning rates (0.001, 0.0001) and tree complexities (1–5). The final two BTs were selected based on one or two measures of performance: the predictive deviance expressed as a percentage of the null deviance and for BTs with presence/absence as response, the area under the receiver operator characteristic curve (AUC). The BT's ability to explain the observed data and to predict new data is evaluated based on the predictive deviance of the training (mean total deviance – mean residual deviance/mean total deviance) and left-out data (mean total deviance – mean CV deviance/mean total deviance) respectively.

Major determinants of the occurrence and densities of early-stage juvenile starfish were ultimately identified based on the computed relative influence (%) of BTs, which reflects the number of times a predictor variable is selected for splitting and the improvement to the model as a result of the selection. Patterns in the occurrence and densities of early-stage juvenile starfish along predictor variables were then visualised with partial dependence plots, showing the effect of the focal predictor on the response after accounting for the average effects of all other variables in the model.

Table 2. 1 Variables used to model the occurrence (presence/absence) and density (individuals.m^{-2}) of early-stage juvenile crown-of-thorns starfish.

Predictor variable	**Description**	**Mean, range**
Reef scale predictor		
Reef	Reef name (Walker Reef, Rib Reef, Lodestone Reef)	N/A (categorical variable)
Site scale predictor		
Reef aspect	Bearing as calculated from the centre point of each reef (0° & 360° = north)	171.1, 8.1–355.4
Quadrat scale predictor		
Observer	Observer (A and B)	N/A (categorical variable)
Quadrat depth	Quadrat depth (m)	7.6, 1.1–18.2
Slope	Estimated slope angle (0–90°), 0° = flat surface, 90° = perpendicular surface	17.6, 0.0–90.0
Habitat complexity	Estimated habitat complexity (1–5), 1 = low complexity (e.g., pavement) and 5 = high complexity (e.g., diverse branching coral)	N/A (categorical variable)
Proportion coral rubble	Estimated proportion of coral rubble	0.3, 0.0–1.0
Proportion live hard coral	Estimated proportion of live hard coral	0.1, 0.0–0.9
Proportion intact dead coral skeleton	Estimated proportion of intact dead coral skeleton (growth form of hard coral colony can still be identified)	0.2, 0.0–1.0
Proportion coral rock	Estimated proportion of coral rock (pavement or consolidated coral)	0.3, 0.0–1.0
Proportion sand	Estimated proportion of sand	0.00, 0.0–0.4
Proportion soft coral	Estimated proportion of soft coral	0.00, 0.0–0.6
Proportion macroalgae	Estimated proportion of macroalgae	0.00, 0.0–0.4

Patterns in the occurrence of early-stage juvenile starfish at the site level

A generalised linear mixed effects model was used to test whether the occurrence of early-stage juvenile starfish at sites (n = 42) was related to local cover of coral rubble. To this end, we modelled the proportion of quadrats with juveniles present against the mean proportion of coral rubble in quadrats (averaged by site) using the *glmmTMB()* function from the glmmTMB package (Brooks et al., 2017), with a binomial error distribution and zero-inflation. A zero-inflation model was chosen over a hurdle model, as zeros (26.2%) in our data could have been false sampling zeroes. The fitted zero-inflated binomial model is divided into two models: a conditional model that fits a binomial model to the proportion of quadrats with early-stage juvenile starfish present, and a zero-inflation model that fits a binomial model to presence/absence of early-stage juvenile starfish. The zero-inflation model thereby provides an estimate for the rate of false zero identification. Reef was added as random effect in the model to account for variation at the reef level. Given the limited number of site replicates (n = 2–6) within different levels of bearing (i.e., 0–90°, 90–180°, 180–270°, 270–360°) of each reef, we could not statistically test whether early-stage juvenile starfish occurred more frequently in exposed north-eastern (0–90°) and south-western (180–270°) fore reef habitats. Results have nonetheless been visualised in relation to the mean proportion of coral rubble and reef aspect.

2.4 Results

A total of 140 early-stage juvenile *A.* cf. *solaris* (diameter <70 mm) were sampled in May and June 2017 across 1,242 quadrats from 42 sites, corresponding to a mean density of 0.11 starfish m^{-2} (range = 0–5 starfish m^{-2}). Individuals ranged in size from 2–65 mm in diameter (**Figure 2.2**), with most individuals (134 out of 140) being smaller herbivorous starfish, which measured between 2 and 14 mm in diameter (mean ± 1sd = 7.33 ± 2.58 mm). These herbivorous starfish were predominantly found attached to coral rubble (67.16%) and to a lesser extent to intact dead coral skeleton (20.15%) and coral rock (12.69%) (**Figure 2.2a**). Most herbivorous early-stage juvenile starfish were feeding on crustose coralline algae (92.54%); a small percentage was found feeding on knob-forming (5.22%), articulated (1.49%) and shelf-forming (0.75%) types of coralline algae (**Figure 2.2b**). The few coral-eating starfish (n = 6) were at least twice the diameter of herbivorous individuals and ranged in size between 28 and 65 mm (mean ± 1sd = 52.33 ± 14.95 mm), of which half were found attached to live hard coral (50.00%), with the remainder being found on coral rubble (33.33%) and coral rock (16.67%). Coral-eating starfish were found feeding on four different coral genera/ growth form combinations: bushy *Acropora* spp. (n = 2), bottlebrush *Acropora* spp. (n = 1), bushy *Seriatopora* spp. (n = 1) and foliose *Montipora* spp. (n = 1). The diet of one individual (64 mm) could not be identified due to a lack of any feeding marks within the immediate proximity of the starfish. However, the individual was presumed to be feeding on live hard coral given its large size and distinct morphology.

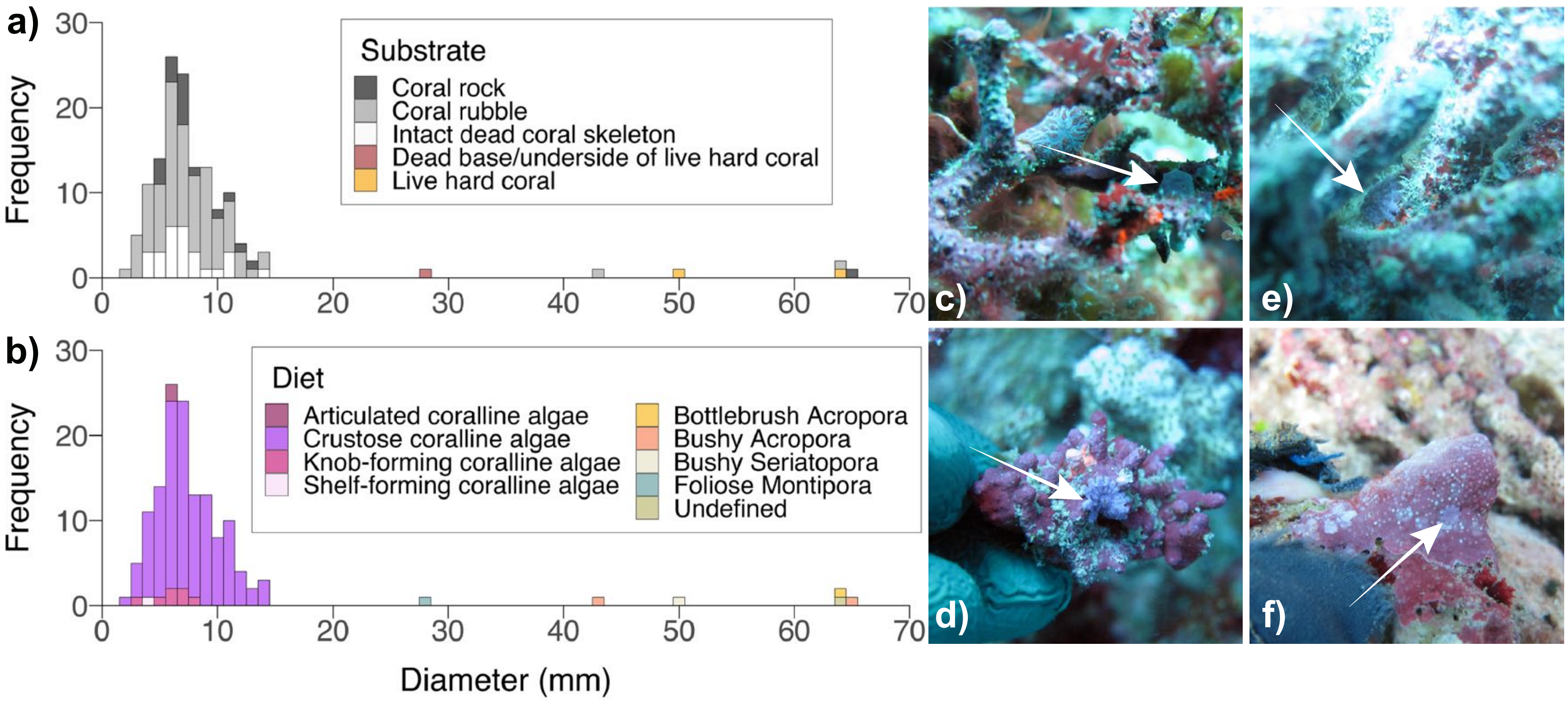


Figure 2. 2 Size frequency distribution of early-stage juvenile crown-of-thorns starfish (n = 140, diameter <70 mm) by (a) substrate and (b) diet. Examples of herbivorous early-stage juvenile starfish (diameter = 3–10 mm) on different types of substrate and diet; c) on intact dead coral skeleton feeding on crustose coralline algae, d), on coral rubble feeding on knob-forming coralline algae e), on intact dead coral skeleton feeding on crustose coralline algae f), on coral rubble feeding on crustose coralline algae.

Overall, early-stage juvenile starfish occurred in just 108 out of 1,242 quadrats (8.7%). Six predictor variables were identified as important determinants (as defined by a relative influence >5%, **Figure 2.3**) for the occurrence of early-stage juvenile starfish in quadrats: i) reef aspect (21.62%), ii) depth (20.14%) and iii) proportion of coral rubble (18.65%), and to a lesser extent iv) proportion of intact dead coral skeleton (8.73%), v) slope (6.09%), and vi) reef (5.40%). The model explained 31% of the deviance using training data (explanation of the observed data) and 12% of the deviance using CV (prediction of left-out data). The AUC was 0.91 in training and 0.75 in CV data. Three predictor variables were identified as important determinants (relative influence >5%, **Figure 2.3**) for densities of early-stage juvenile starfish: i) proportion of coral rubble (38.02%), ii) reef aspect (31.60%) and iii) depth (16.32%). The model explained 34% of the deviance using training data (explanation of the observed data) and 17% of the deviance using CV (prediction of left-out data).

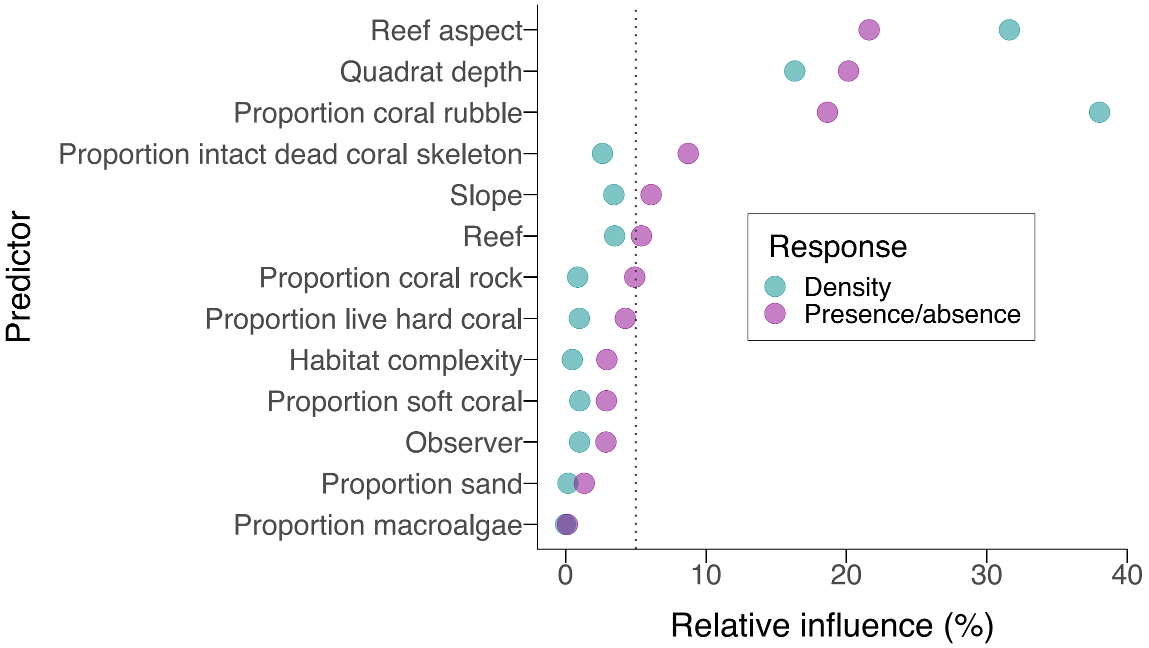


Figure 2. 3 Summary of the relative influence (%) of predictor variables for boosted tree models for the occurrence (presence/absence, in purple) and density (individuals.m^{-2}, in turquoise) of early-stage juvenile starfish, developed via cross validation on data from 1,242 quadrats. Dotted vertical line delimits 5% relative influence.

Depth-related patterns in the occurrence and densities of early-stage juvenile starfish were prominent (**Figure 2.4**). The estimated likelihood of occurrence of starfish was greatest at a depth of 14.2 m (0.1). Estimated mean densities of starfish also increased with depth, but levelled off around 8.5 m (0.063 ind. m^{-2}) before reaching a peak at 11.6 m (0.07 ind. m^{-2}). Partial dependence plots showed that the estimated likelihood of occurrence and mean densities of early-stage juvenile starfish increased overall with the proportion of coral rubble and intact dead coral skeleton and decreased with an increasing proportion of live hard coral (see Supplementary material Figure 2.1, 2.2).

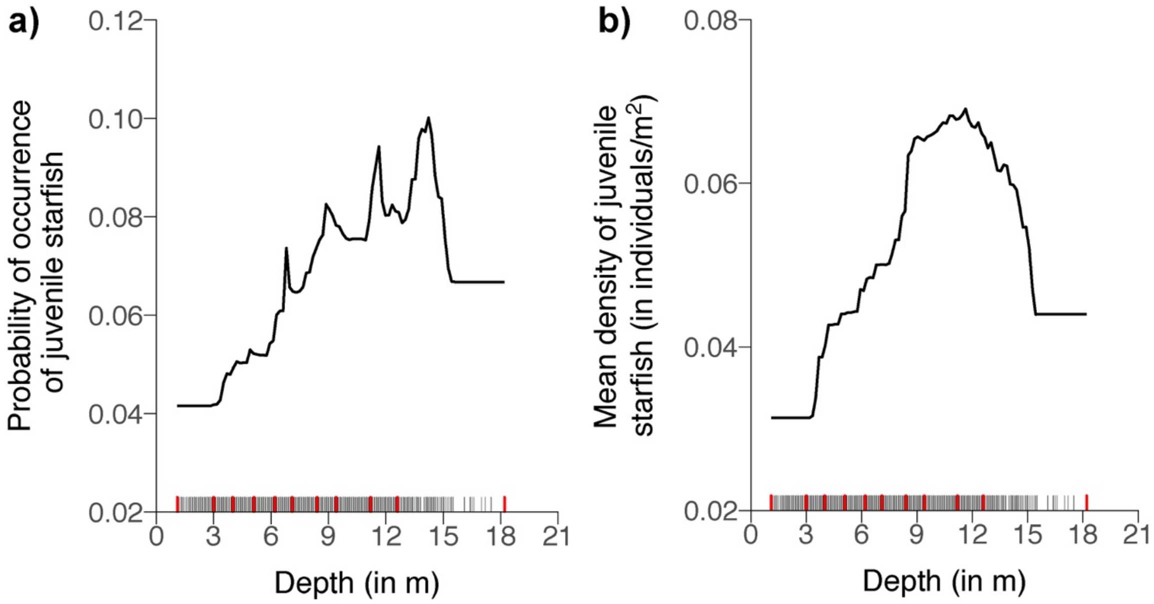


Figure 2. 4 Partial dependence plots for depth in the boosted tree models for a) the occurrence and b) the density (individuals.m^{-2}) of early-stage juvenile starfish in quadrats. Rug plots show individual (in black) and deciles (in red) of replicate quadrats across sampled depth range.

Among sites, early-stage juvenile crown-of-thorns starfish were recorded at 31 out of 42 (73.8%) sites, with a maximum site-level density of 0.77 starfish m^{-2} (mean = 0.11 starfish m^{-2}, median = 0.07 starfish m^{-2}, IQR = 0.01–0.13 starfish m^{-2}). The proportion of quadrats with early-stage juvenile starfish present within each site varied between 0 and 0.43 (mean = 0.09, median = 0.07, IQR = 0.01–0.1) (**Figure 2.5** and **2.6**) and was positively related to the mean proportion of coral rubble (estimate ± se = 1.8711 ± 0.7727, Pr (> |z|) <0.05). The rate of false zeroes, as given by the rate of change in the zero-inflation model (estimate ± se = -1.7200 ± 0.6055, Pr (> |z|) <0.05), was estimated to be 15.19% at the site level. While patterns in the occurrence relative to aspect could not be statistically tested at the site level, the proportion of quadrats with early-stage juvenile starfish present peaked consistently in obliquely exposed south-western reef areas, between 180° and 240° (**Figure 2.6**). Overall, early-stage juvenile starfish occurred most frequently at a south-western site of Walker Reef, where they were detected in 13 out of 30 surveyed quadrats (43%). Comparatively high frequencies of starfish were also observed in the exposed north-eastern region of Walker Reef, between 30° and 60°, where early-stage juvenile starfish were detected in 11 out of 30 quadrats (37%, **Figure 2.6**).

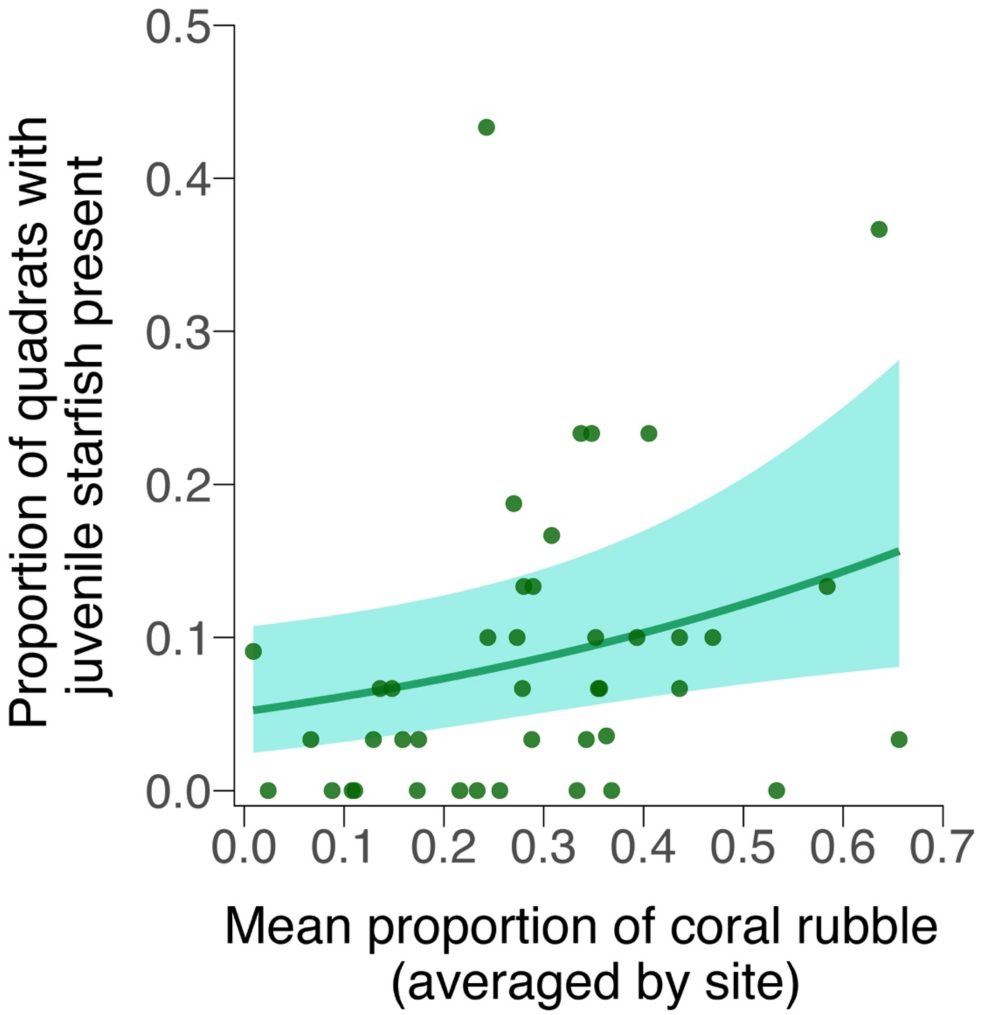


Figure 2. 5 Modelled proportion of quadrats with early-stage juvenile starfish present against mean proportion of coral rubble (averaged by site). Points represent individual observations by survey site (n = 42).

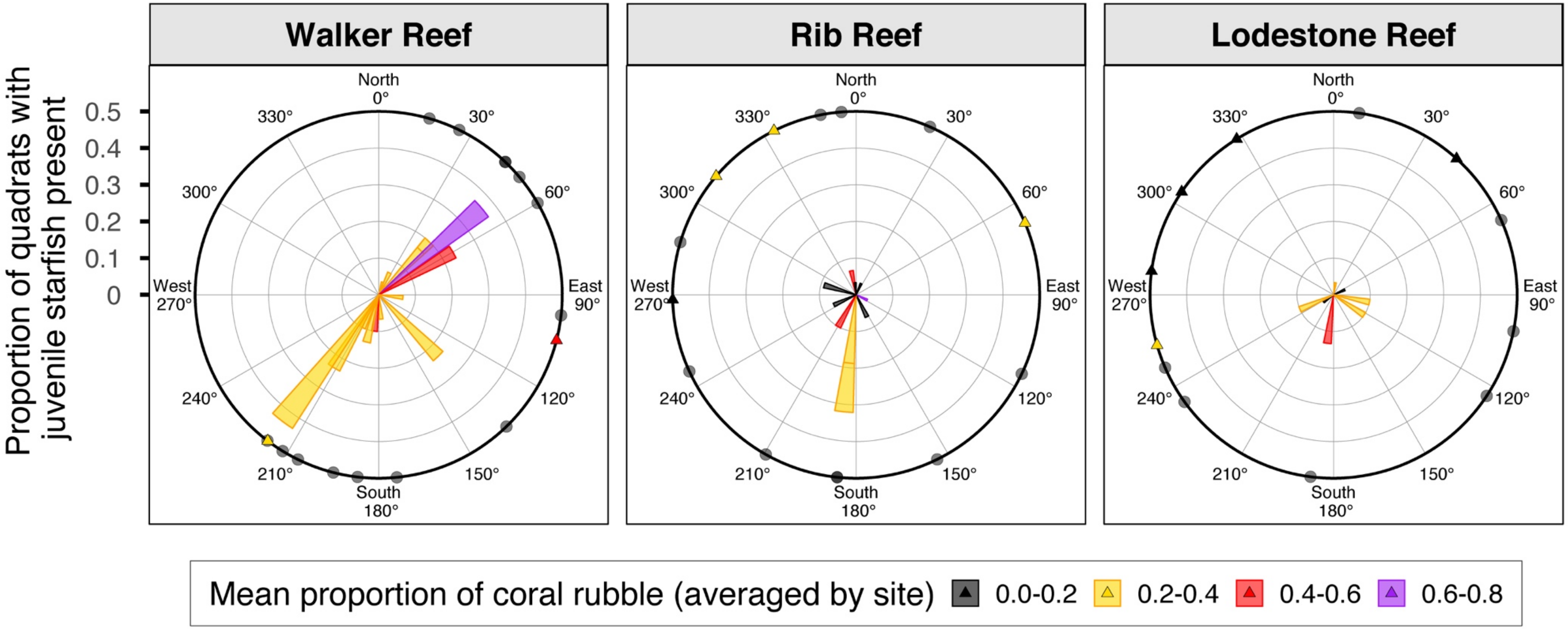


Figure 2. 6 Variation in the proportion of quadrats with early-stage juvenile starfish present by reef (from north to south) and survey site (n = 42), in relation to the mean proportion of coral rubble (averaged by site). For each rose diagram, the length of the wedge represents the proportion of quadrats with early-stage juvenile starfish present, whereas the wedge colour indicates the mean proportion of coral rubble at a given site. Black dots and triangles on the outermost concentric line represent individual observations where early-stage juvenile starfish were present (n = 31) and absent (n = 11, coloured by mean proportion of coral rubble) respectively.

2.5 Discussion

This study showed that early-stage juvenile *A.* cf. *solaris* were widely distributed (present in 74% of survey sites, **Figure 2.6**) around the circumference of three reefs (Walker Reef, Lodestone Reef and Rib Reef) in the central GBR, at the time of active outbreaks. The occurrence and density of early-stage juvenile starfish was, however, patchy within the scale of individual reefs, and best explained by a combination of aspect (or exposure), depth and benthic habitat (**Figure 2.3**). More specifically, occurrence and densities of early-stage juvenile crown-of-thorns starfish were greatest in northern and south-western locations, at intermediate depths (8–14 m, **Figure 2.4**), and positively related to cover of coral rubble at individual sites (**Figure 2.5**). These patterns may have been established at settlement, reflecting within-reef variation in larval supply and settlement success (*sensu* Black and Moran, 1991), or may have been augmented, if not completely modified, by spatial variation in post-settlement mortality (Keesing et al., 1996). Ultimately, patterns of abundance for early-stage juvenile starfish will reflect the combination of factors that influences larval supply, settlement success, and post-settlement survivorship, all operating at different spatial and temporal scales. For example, the increased occurrence and densities of early-stage juvenile starfish at obliquely exposed south-western and northern reef locations may reflect i) hydrodynamic features that concentrate and retain pelagic larvae, leading to corresponding increases in settlement rates at these locations (Black and Moran, 1991), and/or ii) the physical and biological structure of benthic habitats in these locations (e.g., Done, 1999) which may also influence settlement success, post-settlement survival and ultimately the abundance of early-stage juvenile starfish.

Mean densities of early-stage juvenile starfish recorded at each site in this study (range = 0.00–0.77 starfish m^{-2}) are broadly comparable to densities (0.82 starfish m^{-2}) that were recorded on the reef slope (depth = 6.0–9.3 m) in Japan (Habe et al., 1989), though much higher densities of early-stage juvenile *A*. cf. *solaris* were recorded (8.3 starfish m^{-2}) in shallow intertidal reef habitats in Fiji (Zann et al., 1987; 1990). There are, however, some important differences in the sampling methods (e.g., size of the sampling unit, and spatial extent of sampling) among these field studies that might influence resulting estimates of absolute abundance and hinder robust comparison. In addition, densities of early-stage juvenile starfish may also be influenced by the size and structure of reef systems, habitat availability and the population status of adult crown-of-thorns starfish. More information is therefore needed about the distribution and abundance of early-stage juvenile crown-of-thorns starfish in different geographic locations to inform ongoing debates about proximate causes of, and corresponding management responses to, outbreaks of *Acanthaster* spp. (Chapter 1).

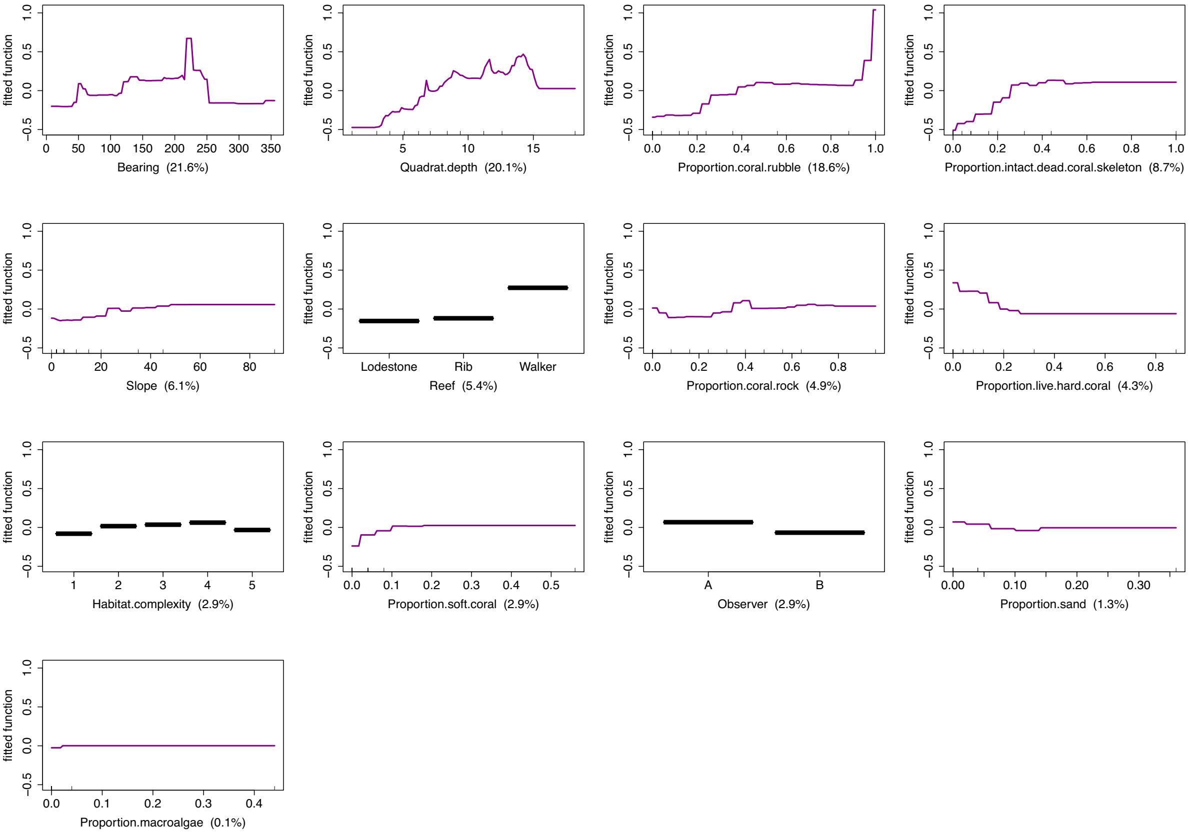
Early-stage juvenile crown-of-thorns starfish occurred over a wide range of habitat types, but were most frequently found in areas dominated by unconsolidated coral rubble. Accordingly, most juvenile starfish were found attached to the underside of coral rubble, feeding on various types of coralline algae (**Figure 2.2**). The predominance of early-stage juvenile crown-of-thorns starfish in rubble habitats has been reported previously (e.g., Zann et al., 1987; 1990; Yokochi and Ogura ,1987), and may be attributable to a higher abundance of specific coralline algae that induce settlement (Johnson et al., 1991) and/ or provide prey for algal-feeding starfish, as opposed to other reef habitats that also support extensive growth of coralline algae. Highest occurrence and densities of early-stage juvenile *A.* cf. *solaris* were at intermediate depths (8–14 m) and declined in both shallower and deeper habitats (**Figure 2.4**). This is much shallower than suggested by the deep-water recruitment hypothesis (i.e., 30–60 m, Johnson et al., 1991), although it should be acknowledged that we did not sample beyond 18 m depth and cannot discount that there might be even higher abundances of early-stage juvenile starfish in deeper reef habitats. Nonetheless, this study, together with previous more spatially extensive sampling (depth <15m; Chapter 3, 4, 5) demonstrates that early-stage juvenile *A.* cf. *solaris* can be found in relatively shallow reef habitats. Moreover, those crown-of-thorns starfish that settle in relatively shallow reef environments will not have to move far to recruit to coral-rich shallow reef habitats where sub-adults predominate (e.g., Pearson and Endean, 1969). In contrast, crown-of-thorns starfish that settle in deep-water habitats (>30 m) may have to travel quite large distances to access suitable coral prey, at a time when movement rates are highly constrained (Pratchett et al., 2017c) and risk of predation is very high (Keesing and Halford, 1992a; Keesing et al., 1996; 2018; Chapter 5). Crown-of-thorns starfish settling in relatively shallow, rubble-dominated, exposed reef habitats are therefore, likely to contribute more to population replenishment and outbreaks, than those settling in deep-water or isolated habitats. In this study, early-stage juvenile *A.* cf. *solaris* were recorded as shallow as 3 m, but were relatively scarce in these very shallow habitats. This pattern most likely relates to the structural complexity of habitats. Shallow reef environments were mostly comprised of consolidated reef matrix, whereas coral rubble occurred increasingly from 5–18 m, often associated with spur and groove systems that are common in fore reef environments of mid-shelf reefs in the central GBR (Duce et al., 2016). Depth-related differences in the availability of settlement inducing coralline algae and post-settlement food, as well as predation risk are likely to be important determinants of settlement success and post-settlement survival. However, there is not currently any information available to assess whether there are any meaningful differences in the availability of specific coralline algae (that induce settlement and/ or provide food for early-stage juvenile starfish), or changes in the density and composition of benthic predators over these depth ranges.

While crown-of-thorns starfish feed exclusively on coralline algae for at least several months post-settlement (Zann et al., 1987; Habe et al., 1989), their eventual dietary shifts and longer-term reliance on live hard corals would suggest that proximity to live coral might also be an important determinant of settlement preferences, if not post-settlement survival (Chapter 1, 4, 5). The occurrence and densities of early-stage juvenile crown-of-thorns starfish decreased with increasing cover of live coral in the present study. This result likely reflects the specific microhabitat preferences of early-stage juvenile starfish for coral rubble, and the generally low cover of live coral within rubble-dominated habitats. It is also possible that high cover of live corals directly constrains settlement success of *Acanthaster* spp., due to predation on settling larvae by corals and their commensals (Yamaguchi, 1973; Cowan et al., 2016a; 2016b; 2017a). High cover of live corals may therefore moderate settlement success even if it is beneficial for older juvenile and adult life stages. To maximise settlement success, it would be expected that crown-of-thorns starfish would preferentially settle in locations that are naturally depauperate of potential predators or select for microhabitats that provide effective refuges from predators (Cowan et al. 2017a). However, where there is a trade-off between availability of preferred food and increased predation risk, crown-of-thorns starfish may actually settle disproportionately in areas with highest predation risk. When comparing the incidence of injuries among early-stage juvenile starfish, Wilmes et al. (2019) showed in Chapter 5 that vulnerability to cryptofaunal predators (e.g., crustaceans and polychaetes) is likely to be higher in coral rubble than live coral. As such, increased availability of very specific or preferred food in rubble habitats may offset increased predation risk in rubble-dominated habitats.

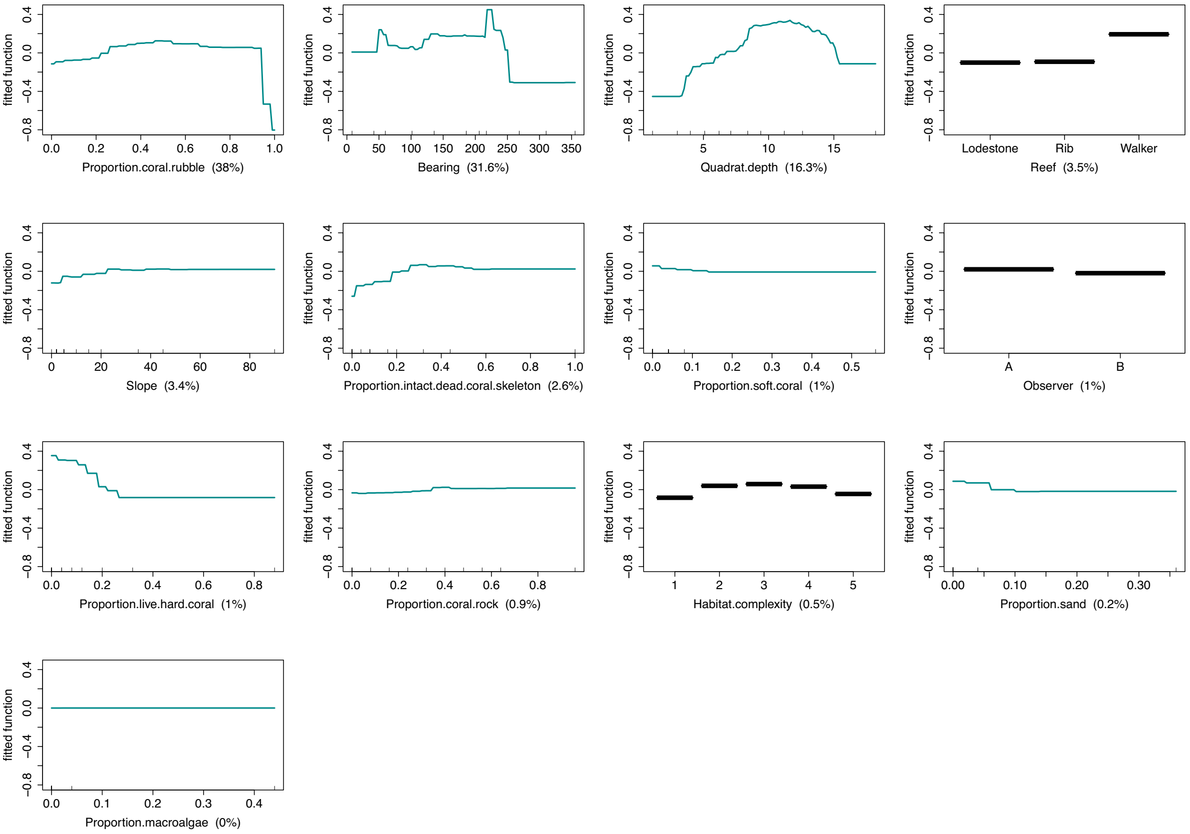
It is possible that the apparent prevalence of early-stage juvenile starfish in loose rubble habitats relates to detectability, as detectability of early-stage juvenile starfish in more complex and immovable habitats (e.g., contiguous carbonate matrix) is likely to be constrained (*sensu* Doherty and Davidson, 1988; Johnson et al., 1992). Although we carefully searched individual pieces of coral rubble and loose substrates in this study, we did not undertake any destructive sampling of reef matrix, thereby limiting detection of any starfish that were not visible from above, on and within immovable habitat types. However, even in studies that have excavated reef matrix (Doherty and Davidson, 1988; Yokochi and Ogura ,1987), detection of early-stage juvenile starfish has been extremely limited. At Iriomote Island, Japan, Yokochi and Ogura (1987) conducted meticulous searches for early-stage juvenile crown-of-thorns starfish across both loose and consolidated substrates, excavating (where necessary) to a depth of 10–20 cm and carefully searching for starfish on collected pieces of substrate under laboratory conditions. Despite this comparable sampling across different habitat types, no crown-of-thorns starfish were found in samples taken from contiguous reef matrix. Rather, all early-stage juvenile starfish recorded (n = 13, diameter = 5.5–14.9 mm) were found in samples from rubble habitats (Yokochi and Ogura, 1987). This suggests that it is not simply inter-habitat differences in detectability, but that early-stage juvenile *A.* cf. *solaris* are indeed predominantly associated with coral rubble.

In conclusion, this study showed that early-stage juvenile *A.* cf. *solaris* were relatively widespread around each of the three reefs studied (Walker Reef, Lodestone Reef and Rib Reef) in the central GBR. The occurrence and densities of early-stage juvenile starfish was, however, linked to reef aspect, habitat availability and water depth. Knowing where to find early-stage juvenile crown-of-thorns starfish is important to advance understanding and management of outbreaks. Most importantly, effective sampling of early-stage juvenile crown-of-thorns starfish will provide irrefutable evidence of changes in settlement success and recruitment, and could therefore forewarn of future outbreaks. While population irruptions of crown-of-thorns starfish are conditional upon elevated larval supply and high settlement rates, major population bottlenecks that can decouple larval supply and adult abundance occur throughout the early life history of crown-of-thorns starfish (Chapter 1). Monitoring the abundance of visually detectable early-stage juvenile crown-of-thorns starfish in rubble-dominated exposed fore reef habitats (e.g., spur and groove systems and rubble slips), in combination with the local availability of coral prey, provides a potential system for foretelling the occurrence of outbreaks. Increased information about early life history stages is also essential to advance understanding of the proximate causes of crown-of-thorns starfish outbreaks (Pratchett et al., 2014; Chapter 1), which may be critical in developing effective and long-lasting management responses. It is also important to extend this work to other geographical locations, testing for interspecific differences in settlement and recruitment dynamics, and demography of early life history stages of *Acanthaster* spp.

2.6 Supplementary material



Supplementary material Figure 2. 1 Partial dependence plots for all 13 predictor variables in the BT model for the occurrence (presence/absence) of early-stage juvenile starfish in quadrats. Y axis are on the logit scale. Rug plots show distribution of quadrats across respective predictor variables, in deciles.



Supplementary material Figure 2. 2 Partial dependence plots for thirteen predictor variables in the BT model for the density (individuals.m^{-2}) of early-stage juvenile starfish in quadrats. Y axis are on the log scale. Rug plots show distribution of quadrats across respective predictor variables, in deciles.

— Chapter 3 —

Modelling growth of early-stage juvenile crown-of-thorns starfish on the Northern Great Barrier Reef

Chapter 3: Modelling growth of early-stage juvenile crown-of-thorns starfish on the Northern Great Barrier Reef

Adapted from: Wilmes J, Matthews S, Schultz D, Messmer V, Hoey A, Pratchett M. 2016 Modelling growth of juvenile crown-of-thorns starfish on the Northern Great Barrier Reef. *Diversity* 9, 1 (doi:10.3390/d9010001)

3.1 Abstract

The corallivorous crown-of-thorns starfish (*Acanthaster* spp.) is a major cause of coral mortality on Indo-Pacific reefs. Despite considerable research into the biology of crown-of-thorns starfish, our understanding of the early post-settlement life stage has been hindered by the small size and cryptic nature of recently-settled individuals. Most growth rates are derived from either laboratory studies or field studies conducted in Fiji and Japan. The Great Barrier Reef (GBR) is currently experiencing its fourth recorded outbreak and population models to inform the progression of outbreaks lack critical growth rates of early life history stages. High numbers of early-stage juvenile starfish (n = 3,532) were measured during extensive surveys of 64 reefs on the northern GBR between May and December 2015. An exponential growth model was fitted to the size measurement data to estimate monthly ranges of growth rates for early-stage juvenile starfish. Estimated growth rates varied considerably and increased with age (e.g., 0.028–0.041 mm·day^{-1} for one-month-old juveniles versus 0.108–0.216 mm·day^{-1} for twelve-month-old juveniles). This pioneering study of early-stage juvenile starfish on the GBR will inform population models and form the basis for more rigorous ongoing research to understand the fate of early-stage juvenile *Acanthaster* spp.

3.2 Introduction

Crown-of-thorns starfish (*Acanthaster* spp.) are among the most intensively studied of all coral reef organisms (Moran 1986). This starfish species is renowned for its extreme temporal and spatial variation in abundance, which can result in extensive destruction of coral reef habitats if starfish occur at high densities (during outbreaks). Outbreaks of crown-of-thorns starfish are considered to be one of the foremost causes of significant and sustained declines in live hard coral cover on Indo-Pacific reefs (De'ath et al., 2012; Osborne et al., 2011; Baird et al., 2013; Chesher, 1969). On Australia's Great Barrier Reef (GBR), there have been four distinct episodes of outbreaks since the early 1960's, with the latest outbreak first apparent in 2010 (Pratchett et al., 2014; Vanhatalo et al., 2016). Over a period of 27 years (1985 to 2012), the GBR has lost approximately half of its initial coral cover, with 42% of this loss attributable to recurrent outbreaks of crown-of-thorns starfish (De'ath et al., 2012).

Outbreaks of crown-of-thorns starfish are fundamentally caused by changes in key demographic rates and population dynamics (Moore, 1990), resulting in either progressive accumulation of starfish over several successive cohorts (Pratchett, 2005) or the rapid onset of outbreaks following a single mass-recruitment event (Zann et al., 1987). However, the extent to which these demographic changes are caused by anthropogenic degradation of reef ecosystems (e.g., overfishing and/or eutrophication) versus inherent environmental changes and stochasticity (e.g., cycles of food availability for larvae, juveniles, and/or adult starfish) is largely unknown and widely debated (Pratchett et al., 2014; Caballes and Pratchett, 2014). Our understanding of the proximal and ultimate causes of outbreaks has been hampered at least in part by difficulties in studying the early life stages of crown-of-thorns starfish in natural environments (Pratchett et al., 2014; Caballes and Pratchett, 2014). Current models (Vanhatalo et al., 2016; Morello et al., 2014; MacNeil et al., 2016) that aim to understand and predict outbreak dynamics lack critical demographic rates, such as estimates of growth rates and survival for early life history stages in the field.

Field-based studies of early life stages of crown-of-thorns starfish have largely been constrained by the small size, cryptic nature, and largely nocturnal habits of early-stage juvenile starfish (Zann et al., 1987), making them difficult to detect and sample (Doherty and Davidson, 1988; Pearson and Endean, 1969; Johnson et al., 1992). Attempts to locate early-stage juveniles on the GBR have remained largely unsuccessful (Doherty and Davidson, 1988; Pearson and Endean, 1969; Johnson et al., 1992). However, studies conducted in Fiji and Japan that followed individual cohorts of crown-of-thorns starfish through time on single island reefs effectively sampled early-stage juvenile starfish (Zann et al., 1987; Habe et al., 1989). Resulting estimates of growth rates for coralline algae feeding juveniles (2–3 mm/month) (Zann et al., 1987; Habe et al., 1989) were consistent with early post-settlement growth estimates for laboratory reared juveniles (Yamaguchi, 1973; Lucas, 1974).

As the very early stages of juveniles (i.e., 1–3 months-old starfish after settlement, size = 0.3–5 mm) have rarely been detected in the field (Habe et al., 1989), demographic rates for these early stages are largely derived from aquarium-based studies (Yamaguchi, 1973; Lucas, 1974). Crown-of-thorns starfish have been reared in captivity since 1973, providing important insights into their early development and life history (Yamaguchi, 1973; 1974; Lucas, 1974; 1984). Once fully developed competent larvae (i.e., at the late brachiolaria stage) find a suitable settlement substrate (i.e., coralline algae), they metamorphose within two days into five-armed juvenile starfish that measure between 0.3 and 0.8 mm in diameter (Yamaguchi, 1973; Lucas, 1974; Henderson and Lucas, 1971; Fabricius et al., 2010). Yamaguchi (1973) found that laboratory-reared juveniles grew 0.076 mm·day^{-1} in the 20 weeks following settlement, while Lucas (1974) estimated that 3-month-old juveniles grew 0.048 mm·day^{-1} in the laboratory. Field-based estimates of juvenile growth rates averaged 0.10–0.15 mm·day^{-1} in the coralline algae feeding phase and 0.40–0.84 mm·day^{-1} in the coral feeding phase (Zann et al., 1987; Habe et al., 1989). So far, existing growth data has been fitted with logistic or Gompertz growth equations to describe the sigmoidal growth pattern of crown-of-thorns starfish (Zann et al., 1987; 1990; Habe et al., 1989; Yamaguchi, 1974; Lucas, 1984). However, these equations have been acknowledged to be limited in accurately describing growth during distinct life stages (Lucas, 1984), and so alternative equations have been suggested for distinct stages, such as for coralline algae-feeding and coral-feeding juveniles (Lucas, 1984; Kenchington, 1977; Okaji, 1996).

The purpose of this study was to reconstruct growth curves for early-stage juvenile crown-of-thorns starfish on the northern GBR, based on intensive (near monthly) field sampling of early-stage juvenile starfish. The exact ages of juvenile starfish cannot be verified, but may be inferred for early-stage juvenile starfish by assuming that settlement occurs within a relatively narrow period (Zann et al., 1987; Habe et al., 1989). Here we provide, for the first time, monthly ranges of growth rates for early-stage juveniles to inform crown-of-thorns starfish population models. In addition, we compare these results to previous field studies and present ranges of predicted mean sizes for different age classes that can be used to inform the planning of future juvenile monitoring studies on the GBR.

3.3 Materials and Methods

Field Collection

All field sampling was conducted in conjunction with the Association of Marine Park Tourism Operators' (AMPTO) crown-of-thorns starfish control vessels during the fourth recorded outbreak of *Acanthaster* cf. *solaris* (Haszprunar and Spies, 2014) on Australia's GBR. One hundred and eleven sites on 64 reefs within six geographic locations (or reef complexes) located between 14.72° S and 17.67° S were sampled between 7 May and 15 December 2015 (**Figure 3.1**). At each site, 1–2 SCUBA divers searched coralline algae encrusted pieces of dead coral and live coral colonies for juvenile crown-of-thorns starfish (target size ≤50 mm) and their feeding marks. Individual pieces of live and dead coral were thoroughly inspected for juvenile starfish if feeding marks were sighted on exposed surfaces. Each diver was able to cover up to 250 m^2 during a typical 40 min dive. However, if juvenile abundances were high (e.g., 40 individuals collected during a 40 min dive), search effort was restricted to a much smaller area (≈50 m^2). All starfish (target size ≤ 50 mm) were collected and placed in sampling jars underwater. This size threshold was selected, as previous growth models (Habe et al., 1989; Lucas, 1984; Zann et al., 1990) predict that the mean size of starfish from the previous year's cohort would be >50 mm at the time of our first sampling (May 2015). The size of individuals was not measured *in situ*, and as such, two of the 3,532 juveniles were slightly larger than 50 mm (52.5 mm and 64 mm). These larger individuals were collected in November/December 2015, and were retained in the analysis, as they were likely to have come from the same cohort. After each sampling dive, juvenile starfish were kept alive in containers filled with seawater, and their maximum diameter was measured to the nearest half millimetre with a stainless steel ruler. Once starfish were measured, all individuals were preserved in 95% ethanol for future analyses.

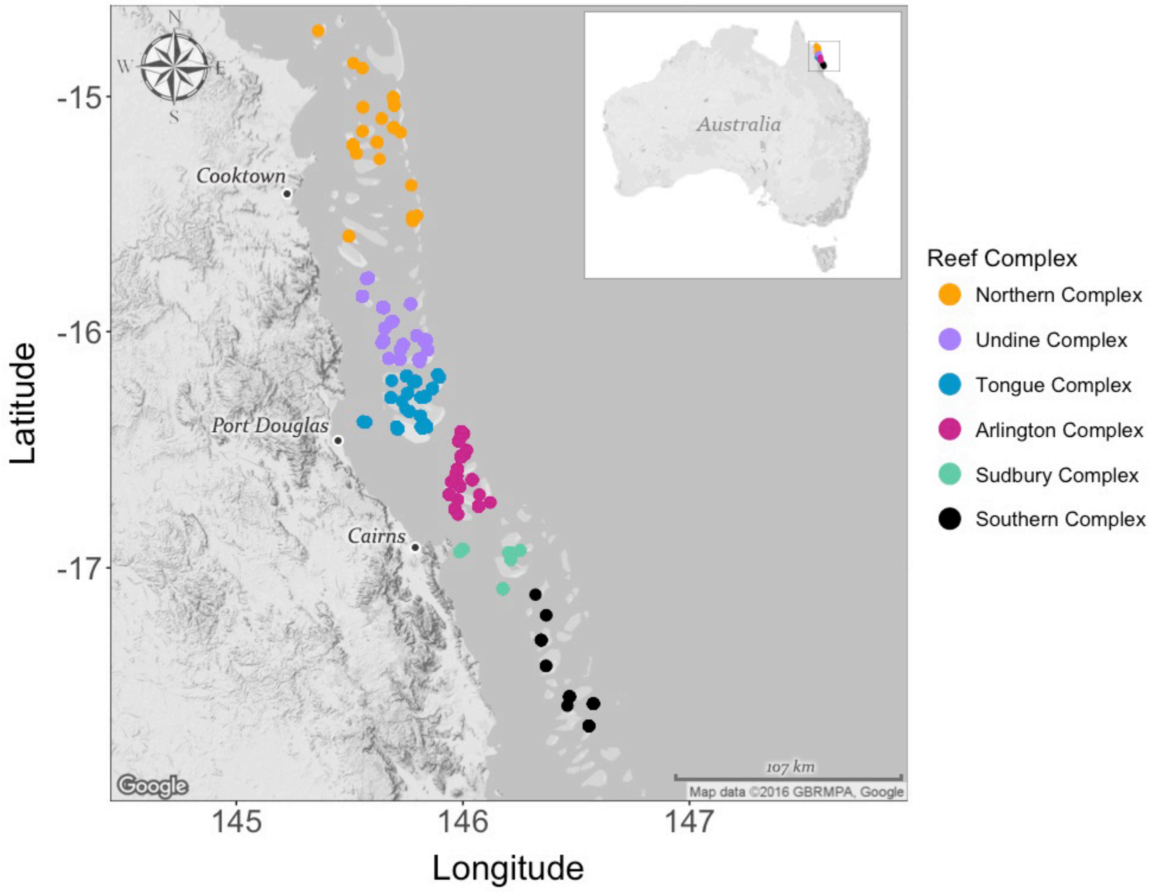


Figure 3. 1 Map of the north Queensland coast showing the sampling locations (*n* = 111) and designated reef complexes (*n* = 6) for the collection of early-stage juvenile crown-of-thorns starfish. (Map data©2016 Google, GBRMPA).

Growth Curve Analysis

On the GBR, spawning has been reported to occur throughout summer months, but is concentrated in December and January (Pratchett et al., 2014). In the year of sampling, Uthicke et al. (2015a) reported that spawning occurred between 10 and 21 of December 2014 in the area of the northern GBR relevant to our study (i.e., 1 to 7 days prior to sampling), and that there was no subsequent spawning throughout December or January. Assuming a planktonic larval duration of 10 to 40 days (Henderson and Lucas, 1971; Fabricius et al., 2010; Lucas, 1982; Uthicke et al., 2013; Uthicke et al., 2015b; Wolfe et al., 2015), settlement is likely to have occurred predominantly—if not exclusively—in early January 2015. As ages of sampled individuals cannot be verified, age of sampled juveniles for the model was based on the assumption that all juveniles settled on 1 January 2015 (i.e., 10–21 days after the reported spawning, which incorporates the 17–22 peak settlement window determined by Pratchett et al., 2017b). Ultimately, all growth estimates are presented as monthly growth rates, and so even if crown-of-thorns starfish settled over several days to weeks, it would have limited influence on our results.

All exploratory and growth curve analyses were conducted using R (R Core Team 2016). A series of preliminary models (e.g., logistic growth model and exponential growth model) were fitted to the 2015-juvenile size data to determine which type of model was most suitable to describe the relationship between size and age. Visual inspection and exploratory analysis of the fitted growth curves (based on least residual sum of squares) identified an exponential growth model (as suggested by Okaji, 1996) in the following form as the most accurate in describing the shape of the size measurement data:

$$Size_{Age} = \beta_0 \times e^{k\ x\ Age} + \beta_1 \qquad \text{(m1)}$$

where *Size* is the diameter of starfish in mm, *Age* is number of days since 1 January, and β_0, k, and β_1 are parameters to be estimated. As size measurements were missing for the initial four months of development (i.e., sampling period: January to April 2015), the y-intercept (i.e., $Size_{Age=0}$) was fixed to a biologically meaningful size (see below), representative of the range of predicted mean sizes for newly metamorphosed juvenile starfish in the laboratory (Fabricius et al., 2010; see **Supplementary material Table 3.1**). The growth model may therefore be represented as:

$$Size_{Age} = \beta_0 \times e^{k\ x\ Age} + (Size_{Age=0} - \beta_0) \qquad \text{(m2)}$$

Three estimates of size after metamorphosis (i.e., $Size_{Age=0}$ = 0.30 mm, 0.56 mm, and 0.82 mm) from Fabricius et al. (2010) were used to generate three different *m2* models ($m2_{Size\ at\ Age0=0.30}$, $m2_{Size\ at\ Age0=0.56}$, $m2_{Size\ at\ Age0=0.82}$). Best-fit parameter estimates for *m1* (β_0, k, and β_1) and *m2* (β_0, k) models were obtained with associated 95% confidence intervals using the *nlstools* package (Baty et al., 2015). Residuals from the preliminary models were found to display a distinct wedge pattern, indicating that variance was related to age of juveniles, and thus multiple variance functions (Age^2, Age^3, Age^4) were trialled to optimize best-fit parameter estimates for each model (*m1*, $m2_{Size\ at\ Age0=0.30}$, $m2_{Size\ at\ Age0=0.56}$, $m2_{Size\ at\ Age0=0.82}$). Best-fit parameter estimates for all 12 models were then used to perform linear mixed effect analysis of the relationship between *Size* and *Age* using the *nlme* package (Pinheiro et al., 2016). Reef complex and survey sites were included in the linear mixed effect models as nested random factors to account for variation at the site and reef complex scale, and variance structures (Age^2, Age^3, Age^4) were included to account for the variation in size with age. Best-fit models were selected based on lowest Akaike Information Criterion (AIC). No evidence of spatial autocorrelation was found after both visual (variograms and bubble plots) and statistical inspection (incorporating spatial correlation structures into mixed effects models).

A selection of best-fit models and corresponding 95% confidence intervals was then plotted using the *ggplot2* package (Wickham, 2009). The best-fit model of $m2_{Size\ at\ Age0=0.56}$ was plotted with the upper bound of the 95% confidence interval of $m2_{Size\ at\ Age0=0.82}$ and the lower bound of the 95% confidence interval of $m2_{Size\ at\ Age0=0.30}$, forming a so-called "combined 95% confidence interval". Growth rates (i.e., growth increment per unit time) were calculated for different time spans (i.e., 30-day intervals) for the upper bound of the 95% confidence interval of $m2_{Size\ at\ Age0=0.82}$, and the lower bound of the 95% confidence interval of $m2_{Size\ at\ Age0=0.30}$ to provide ranges of modelled growth rates.

3.3 Results

Size ranges of early-stage juvenile starfish increased as sampling progressed through the year (**Figure 3.2a**). Juveniles sampled in May measured between 3 and 15.5 mm in size (size range = 12.5 mm), while those sampled in December ranged from 8.5 to 52.5 mm (size range = 44 mm) (**Figure 3.2a**), representing a 3.5-fold increase in size range within this time period.

For *m1* models (variable intercept), growth was indeed exponentially related to age ($t_{3420} = 59.79$, $p<0.0001$), while including *site* ($\sigma \approx 0.0007$) and *reef complex* ($\sigma \approx 0.0003$) as random factors. Best model performance was achieved with a variance structure of Age^3 (AIC = 18,057), indicating that variance increased cubically with age. However, the best-fit *m1* model predicted mean size after metamorphosis ($Size_{Age=0}$) to be 5.42 mm. This appears to be erroneous, as it is in stark contrast with the range of expected mean sizes for newly metamorphosed individuals (i.e., 0.30–0.82 mm). Consequently, the *m2* models seemed to describe growth more accurately because their intercept was fixed to a biologically relevant size after metamorphosis. Again, for *m2* models (fixed intercept), growth was indeed exponentially related to age ($m2_{Size\ at\ Age0=0.82}$, $t_{3420} = 59.55$, $p<0.0001$), and a variance structure of Age^3 gave the best model performance ($m2_{Size\ at\ Age0=0.82}$, AIC = 18,071). Although overall model performance was slightly reduced using the fixed intercept models (based on a higher

AIC), fixing the intercept to a biologically meaningful size provides a better characterisation of the growth curves for early-stage juvenile crown-of-thorns starfish.

The growth curve analysis highlights increasing variation in size among older individuals. As shown by the distribution of size–frequency data for different sampling periods (**Figure 3.2a**) and the gradual widening of the combined 95% confidence interval (**Figure 3.2b**), variance increased considerably as juveniles grew older. The increased variation in size with age was further reflected by the increase of monthly ranges of modelled growth rates (**Table 3.1**). Ranges of modelled growth rates increased from 0.028–0.041 mm·day^{-1} for one-month-old juveniles to 0.108–0.216 mm·day^{-1} for twelve-month-old juveniles.

Table 3. 1 Range of modelled mean sizes and growth rates for estimated age (in months after metamorphosis) and different time spans (30-day intervals). See **Supplementary material Table 3.2** for parameter estimates.

Estimated Age after Metamorphosis (Months)	Time Span (30-Day Interval)	Range of Modelled Mean Sizes (mm)	Range of Modelled Growth Rates (mm·day^{-1})
1	0–30	0.30–2.04	0.028–0.041
2	30–60	1.15–3.46	0.032–0.047
3	60–90	2.11–5.12	0.036–0.055
4	90–120	3.19–7.04	0.041–0.064
5	120–150	4.41–9.28	0.046–0.075
6	150–180	5.79–11.89	0.052–0.087
7	180–210	7.35–14.93	0.059–0.101
8	210–240	9.11–18.47	0.066–0.118
9	240–270	11.09–22.58	0.075–0.137
10	270–300	13.33–27.37	0.084–0.160
11	300–330	15.87–32.94	0.095–0.186
12	330–360	18.73–39.43	0.108–0.216

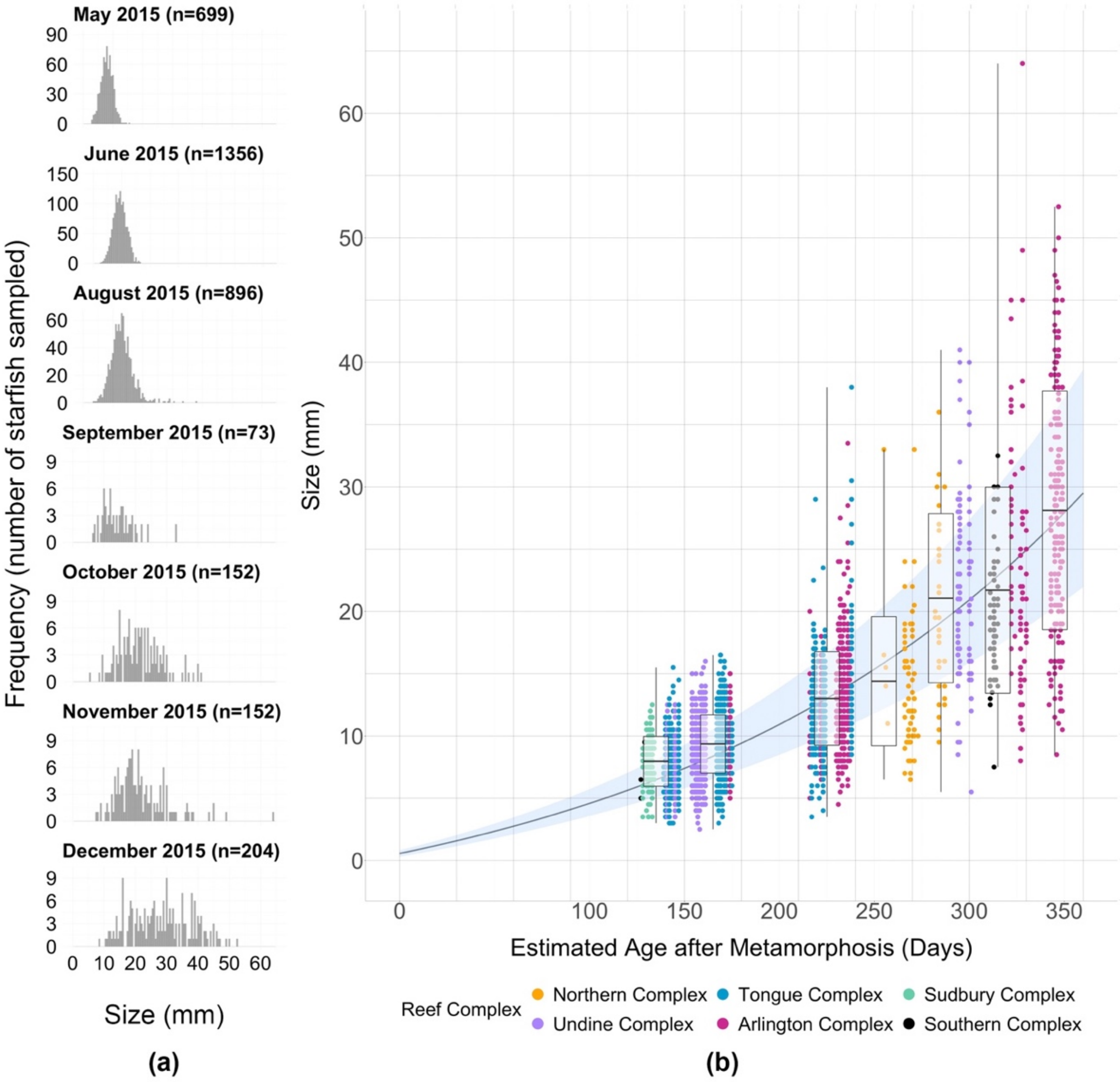


Figure 3. 2 a) Monthly size–frequency distributions of juvenile crown-of-thorns starfish sampled during May–December 2015; b) Fitted growth curve ($m2_{Size\ at\ Age0=0.56}$, black line) and combined 95% confidence interval (light blue) for the cohort of early-stage crown-of-thorns starfish sampled in the northern Great Barrier Reef (GBR). The combined 95% confidence interval is formed by the lower and upper bounds of the 95% confidence interval of *m2* growth models with size at age 0 set to 0.30 mm and 0.82 mm, respectively (**see Supplementary material Table 3.2** for parameter estimates). Individual starfish of the 2015 cohort are depicted as points, and the colours indicate the reef complex (see **Figure 3.1**). Each boxplot (by sampling month) is characterised by a mean size (horizontal middle line), ± one standard deviation (rectangle), and minimum and maximum size (vertical line). The vertical lines of the grid indicate 30-day intervals.

3.4 Discussion

This study provides the first estimates of monthly growth rates for early-stage juvenile crown-of-thorns starfish on the GBR based on intensive field sampling of early-stage juvenile starfish. Early-stage juvenile crown-of-thorns starfish exhibited exponential growth over the first year on the reef and reached a size of up to 52.5 mm by mid-December. Size ranges of early-stage juveniles increased by a factor of 3.5 from May to December. The marked increase in size range was also reflected in the results of the growth curve analysis, which showed that the variation in size increased cubically with age in the best-fit models. Similarly, ranges of modelled growth rates increase with age; while one-month old juveniles grow 0.028–0.041 $mm \cdot day^{-1}$, twelve-month-old juveniles grow 0.108–0.216 $mm \cdot day^{-1}$.

The increasing variation in size among older individuals may be attributed to variation in the availability of suitable coral prey within specific study sites and microhabitats. Although laboratory studies have shown that same-aged early-stage juvenile crown-of-thorns starfish vary in size from the beginning of their post-metamorphic life (Fabricius et al., 2010), marked variations in growth rates of juvenile starfish are generally attributed to the availability of suitable coral prey (Yamaguchi, 1974; Birkeland and Lucas, 1990). At settlement, crown-of-thorns starfish feed on coralline algae, and it is thought that they preferentially settle in locations (and microhabitats) where coralline algae are ubiquitous (Yamaguchi, 1973; Yokochi and Ogura, 1987). After an obligatory period of feeding on coralline algae (4.5—Yamaguchi, 1973), juvenile starfish may or may not transition to feeding on Scleractinian corals, depending upon the local availability of suitable coral prey (Zann et al., 1987). The fastest growth rates recorded in both field and laboratory settings are for individuals that make rapid transitions to coral feeding, resulting in accelerated growth and are reported to be significantly larger than siblings that continue to feed on algae (Lucas, 1984). Individual crown-of-thorns starfish that continue to feed on coralline algae after 4–5 months are thought to be more vulnerable to predation by epibenthic fauna (Yamaguchi, 1973), whereas fast-growing juveniles that make a rapid transition to feeding on coral—and thereby escape this predation pressure—are more likely to survive (Keesing and Halford, 1992). As sampling was conducted on 64 reefs across 111 sites, the availability of suitable coralline algae and coral prey would have differed considerably among microhabitats within and between sampling sites. Individual sampled starfish are likely to have been exposed to different environmental pressures (e.g., predation and food availability) in each of these microhabitats, which would have shaped their growth in the first year of development differently. Consequently, the gradual widening of the 95%

confidence interval likely reflects differential growth rates between individuals that have transitioned to feeding on live coral versus those continuing to feed on coralline algae. This appears to be driven by a varying availability of suitable coral prey within microhabitats.

Ranges of modelled growth rates were broadly comparable to both laboratory-reared individuals released into the field (Okaji, 1996) and the growth of early-stage juvenile cohorts in Japan and Fiji (Zann et al., 1987; Habe et al., 1989). Observed mean sizes, standard deviations, and size ranges of juveniles sampled in these studies (Zann et al., 1987; Habe et al., 1989; Okaji, 1996) were plotted to the fitted growth curve for comparison (Figure 3). Given the uncertainties related to the approach taken to estimate age in Zann et al. (1987) and Habe et al. (1989), and the discrepancies related to ages being estimated in months instead of days, estimated ages were not standardised across different studies. Care should therefore be taken when interpreting the results of this comparison. While Zann et al. (1987) and Habe et al. (1989) followed distinct cohorts of juvenile starfish in the field, Okaji (1996) deployed four groups of laboratory-reared juveniles of different ages (i.e., 2 × 0-, 2-, and 3-month old juveniles) for varying periods of time (i.e., 49, 37, 57, and 92 days, respectively). For each of these groups, he calculated an initial and final mean size before and after deployment in the field (Figure 3).

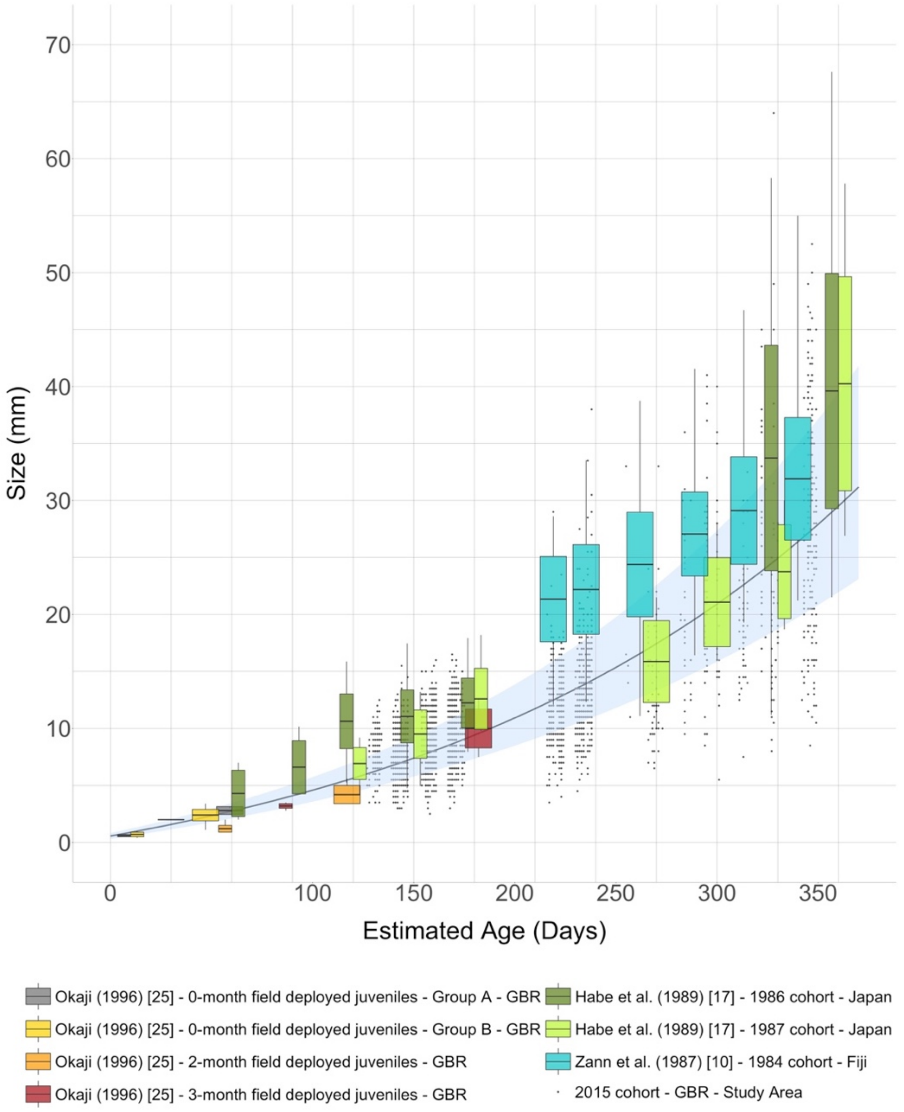


Figure 3. 3 Fitted growth curve (black line) and combined 95% confidence interval for the 2015 crown-of-thorns starfish cohort (GBR). Individual observations of the 2015 cohort are depicted as points, while boxplots represent the results of previous field studies (Zann et al., 1987 [10], n = 651; Habe et al., 1989 [17], n_{1986} = 683 and n_{1987} = 125; Okaji, 1996 [25], $n_{initial}$ = 1137 and n_{final} = 138). Each boxplot is characterised by a mean size (horizontal middle line), ± one standard deviation (rectangle), and minimum and maximum size (vertical line). Note that the estimated age in Zann et al. (1987) [10] and Habe et al. (1989) [17] likely represents the age after fertilisation without taking into account potentially long planktonic larval durations (PLDs); ages are therefore likely to be underestimated. In contrast, the estimated age in Okaji (1996) [25] and the present study represents the age after metamorphosis (i.e., after settlement).

Ten-day old juveniles set out in the field on the GBR for 37–49 days grew on average 0.045–0.046 mm·day^{-1}, mostly within the range of the modelled growth rates for the same time span (i.e., 0.030–0.045 mm·day^{-1}) (Okaji, 1996). Similarly, growth rates for 2-month-old starfish (deployment time = 57 days) averaged 0.053 mm·day^{-1} compared to 0.038–0.059 mm·day^{-1}; while 3-month-old starfish (deployment time = 92 days) grew at a rate of 0.074 mm·day^{-1} compared to 0.046–0.076 mm·day^{-1} (Okaji, 1996). Growth rates derived from the findings of field studies conducted in Fiji (Zann et al., 1987) and Japan (Habe et al., 1989) are also broadly comparable to the range of modelled growth rates of this study. In Fiji, growth rates averaged 0.087 mm·day^{-1} for juveniles between 7 and 12 months, largely falling within the modelled range of 0.073–0.135 mm·day^{-1}. Similarly, field studies conducted in Japan showed that juveniles (between 4 and 6 months old) from the 1986-cohort and 1987-cohort grew at 0.121 mm·day^{-1} and 0.139 mm·day^{-1} respectively, also within the modelled range of growth rates (i.e., 0.083–0.158 mm·day^{-1}) for the same time span. These results show that growth rates of early-stage juvenile *Acanthaster* spp. in the field appear to be remarkably consistent over large geographic scales. However, mean sizes of juveniles of the 1984-cohort (Fiji) and the 1986-cohort (Japan) deviate considerably from the modelled mean sizes (**Figure 3.3**). In both studies, age was estimated based on the date of spawning without considering potentially long planktonic larval durations (i.e., up to 43 days – Pratchett et al., 2017b). For instance, juveniles that were sampled in Fiji in July were estimated to be seven months old, based on the assumption of a January spawning (Zann et al., 1987). Similarly, in Japan, juvenile starfish sampled in July were assumed to be one month old, based on the assumption of a mid-June spawning (Habe et al., 1989). Assuming a mid-June spawning and a pelagic larval duration of two weeks, settlement would have occurred at the beginning of July at the earliest. However, juveniles that were collected in July and August were already 2 and 4.30 mm, respectively (Habe et al., 1989). These sizes seem considerably large, as we know from laboratory studies that juveniles measure between 0.3 and 0.82 mm after settlement and that it takes approximately 40–45 days to grow to 2 mm, and 80–90 days to grow to 4.3 mm (Yamaguchi, 1973). As a result, ages in Zann et al. (1987) and Habe et al. (1989) are likely to be underestimated by 0.5–1.5 months, resulting in overestimates of growth rates.

An implicit assumption of this study was that spawning occurred within a relatively limited period (in December 2014) across the entire study area. This assumption appears valid, given that the estimated growth rates for field-deployed juveniles of known age are broadly comparable to the range of modelled growth rates. The assumption of a single spawning event or narrow spawning window is also supported by the fact that smaller juveniles became rare as sampling progressed through the year (see **Figure 3.2**), indicating that settlement and so spawning did not occur throughout the entire year. Furthermore, spawning occurred in the study area between the 10 and 21 of December 2014 (temperature recorded at Lizard Island at 0.6 m between 12 and 30 December 2014: 28.58–29.29 °C – AIMS, 2016) according to Uthicke et al. (2015a). Assuming a planktonic larval phase of 10 to 40 days (Henderson and Lucas, 1971; Fabricius et al., 2010; Lucas, 1982; Uthicke et al., 2013; Uthicke et al., 2015b; Pratchett et al., 2017b), settlement would have occurred between the 20 of December 2014 and 30 of January 2015. However, new research is suggesting that peak settlement likely occurs within 22 days after spawning and fertilisation (Pratchett et al., 2017b), and few larvae persist beyond 30 days post-fertilisation. Accordingly, Uthicke et al. (2015a) failed to detect larvae in plankton samples from 13 of January onwards. If so, estimated ages (in days) of juveniles (measured from settlement) would have an accuracy of ±12 days.

Low ocean current velocities linked to El Niño-Southern Oscillation (ENSO) hydrodynamics that cause larval retention around reefs or within reef groups are thought to increase survival of crown-of-thorns starfish larvae when they co-occur with enhanced phytoplankton concentrations (Wooldridge and Brodie, 2015). According to Wooldridge and Brodie (2015), the 2009 spawning event—which led to the onset of the current outbreak in 2010/2011—coincided with nutrient-enriched stagnant shelf currents. Larvae of the studied cohort would have been present in the water column between 10 December 2014 and 13 January 2015 (temperature range recorded at Lizard Island weather station between 12 December 2014 and 15 January 2015: 27.9–29.5 °C – AIMS, 2016). Mean phytoplankton concentrations (i.e., chlorophyll a) during this period averaged in the Wet Tropics 0.55 $\mu g \cdot L^{-1}$ (range: 0–7.35 $\mu g \cdot L^{-1}$) for coastal areas, 0.31 $\mu g \cdot L^{-1}$ (range: 0.01–12.42 $\mu g \cdot L^{-1}$) for midshelf areas, and 0.16 $\mu g \cdot L^{-1}$ (range: 0–8.09 $\mu g \cdot L^{-1}$) for offshore areas (BOM, 2016). In comparison, mean chlorophyll *a* concentrations in December 2009 averaged in the Wet Tropics 0.67 $\mu g \cdot L^{-1}$ (range: 0–11.61 $\mu g \cdot L^{-1}$) for coastal areas, 0.31 $\mu g \cdot L^{-1}$ (range: 0.01–13.82 $\mu g \cdot L^{-1}$) for midshelf areas, and 0.19 $\mu g \cdot L^{-1}$ (range: 0–2.90 $\mu g \cdot L^{-1}$) for offshore areas (BOM, 2016). While the Southern Oscillation Index (SOI)—which provides an indication of ocean current velocity (neutral SOI = surrogate for low shelf currents)—was −5.5 in December 2014 (compared to −7 in December 2009) and −7.8 in January 2015 (compared to −10.1 in January 2010) (BOM, 2016). Subsequent SOI values continued to decrease in 2015 to a −20.2 low in October, indicating an El Niña event. Moderate increases in chlorophyll concentrations (up to 1.0–4.0

μg·L^{-1}) that significantly increase rates of larval development, survival, and settlement (Fabricius et al., 2010; Wolfe et al., 2015; Pratchett et al., 2017b) would have occurred on multiple occasions in the study area during the pelagic larval phase of the studied cohort. Consequently, larval development, survival, and settlement may have been enhanced in the study area during this time period, leading to high settlement rates and the development of this seemingly conspicuous cohort in 2015.

3.5 Conclusions

Demographic rates are fundamental to understanding population dynamics and creating meaningful population models. However, attempts to estimate these rates for early-stage juvenile crown-of-thorns starfish have been hindered by the ability to detect them in the field (Doherty and Davidson, 1988; Pearson and Endean, 1969; Johnson et al., 1991). The present study not only demonstrates that early-stage juveniles can be sampled in high numbers (n = 3,532), it also provides ranges of monthly growth rates to inform population models. Here, we also provide evidence that supports the assumption that spawning and subsequent settlement occurred in 2014–2015 during a relatively narrow period of time across a vast geographic area (i.e., 350 km) on the GBR. In addition, the predicted ranges of mean sizes for different sampling periods deliver valuable information to research and management bodies for the planning of juvenile monitoring studies. Rigorous ongoing monitoring should be conducted in the future on a number of selected sites to collect field-based data on demographic rates (e.g., growth, recruitment, mortality, and reproductive output rates) that can be related to variables such as food availability and adult population densities in order to inform population models and improve our understanding of population and outbreak dynamics.

3.6 Supplementary material

Supplementary material Table 3. 1 Mean sizes for newly metamorphosed starfish reared in the laboratory under naturally occurring chlorophyll *a* concentration (Fabricius et al., 2010).

Chlorophyll *a* (µg·L^{-1})	**Mean Size (mm)**	**Standard Error (SE)**	**95% Confidence Interval (mm)**
0.28	0.44	0.07	0.30–0.58
2.90	0.66	0.05	0.56–0.76
5.20	0.64	0.09	0.46–0.82

Supplementary material Table 3. 2 Parameter estimates for final growth model.

Final growth model		**Parameter**	
$Size_{Age} = \beta_0 \times e^{k\,x\,Age} + (Size_{Age=0} - \beta_0)$	**Size$_{Age=0}$**	**β$_0$**	**k**
Best fit model (black line)	0.56	6.982291	0.004550984
Lower bound of combined 95% confidence interval	0.30	6.562909	0.004051665
Upper bound of combined 95% confidence interval	0.82	7.450744	0.005059945

— Chapter 4 —

Contrasting size and fate of juvenile crown-of-thorns starfish linked to ontogenetic diet shifts

Chapter 4: Contrasting size and fate of juvenile crown-of-thorns starfish linked to ontogenetic diet shifts

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4.1 Abstract

Population dynamics of organisms are shaped by the variation in phenotypic traits, often expressed even among individuals from the same cohort. For example, individual variation in the timing of ontogenetic shifts in diet and/or habitat greatly influences subsequent growth and survival of some organisms, with critical effects on population dynamics. Few studies of natural systems have, however, demonstrated that marked phenotypic variation in growth rates or body size among individuals within a modelled cohort is linked to dietary shifts and food availability. Outbreaks of the crown-of-thorns starfish are one of the foremost contributors to the global degradation of coral reefs, but causes of outbreaks have been debated for decades. Here we demonstrate, based on extensive field sampling of early-stage juvenile starfish (n = 3,532), that marked variation in body size among juvenile starfish is linked to an ontogenetic diet shift from coralline algae to coral. This transition in diet leads to exponential growth in juveniles and is essential for individuals to reach maturity. Because smaller individuals experience higher mortality and growth is stunted on an algal diet, the ontogenetic shift to corallivory enhances individual fitness and replenishment success. Our findings suggest that the availability of coral prey facilitates early ontogenetic diet shifts and may be fundamental in initiating outbreaks.

4.2 Introduction

Growth (changes to the size or quantity of existing features) and ontogeny (appearance of new features or the reorganisation and loss of existing ones) are key components of an organism's development (Fuiman and Higgs, 1997), and are often constrained by access to specific resources. Theory posits that when survival and fecundity are positively related to body size, lifetime fitness is largely dictated by how fast individuals grow (Werner and Gilliam, 1984). Traits that maximise growth rates, especially during distinct life history stages when vulnerability to predation is greatest, should therefore be favoured (Werner and Gilliam, 1984). The fitness of individuals both within and among cohorts, in turn, dictates the trajectory of population dynamics. A key question in developmental and evolutionary biology is therefore "What determines the variation in growth rates or body size among individuals from the same cohort?". Ontogenetic shifts in diet and/or habitat (or niche shifts) greatly influence growth, survival and maturation of many terrestrial and aquatic organisms, with critical effects on population replenishment and dynamics (Werner and Gilliam, 1984). For example, growth of small juvenile green sea urchins (*Strongylocentrotus droebachiensis*) is limited on a diet of coralline algae (Himmelman, 1986; Raymond and Scheibling, 1987; Meidel and Scheibling, 1999), but larger juveniles that graze on fleshy macroalgae exhibit faster growth, earlier maturation and enhanced survival (Raymond and Scheibling, 1987; Meidel and Scheibling, 1999) and consequently contribute disproportionately to population replenishment and growth.

Each ontogenetic stage is characterised by its own phenotypic variation, which typically has both genetic and environmental bases. Phenotypic variation in growth rates or body size may be carried over from one ontogenetic stage to the next (McCormick and Hoey, 2004). Which environmental factors, and at which specific ontogenetic stage these factors are most influential in shaping growth trajectories is therefore often obscured. Variability in growth generally scales with age, suggesting that factors that affect development during early ontogenetic stages will be particularly influential (Kirkpatrick, 1984; Houde, 1987). Few field studies have, however, demonstrated that variation in growth rates or body size is indeed largely dictated by environmental conditions experienced during the early life history phase. One of the most cited aquatic field studies that provides empirical support to this hypothesis relates to populations of largemouth sea bass (*Micropterus salmoides*) (Olson, 1996; Post, 2003). These field studies demonstrated that marked variations in growth rates and body size were linked to size-related ontogenetic shifts in the diet of juveniles (from invertebrates to fish), which occurred in their first year of life once their primary fish prey became available. Juveniles that shifted their diet to piscivory early, grew faster for longer than those that transitioned later and were therefore, suggested to have increased lifetime fitness.

Ontogenetic shifts in diet also occur during the juvenile phase of several starfish species (Birkeland et al., 1971; Anger et al., 1977; Barker, 1979; Sloan, 1980; Manzur et al., 2010), which have been linked to marked changes in demography. Crown-of-thorns starfish (*Acanthaster* spp.) exhibit marked ontogenetic shifts in diet and habitat, settling and feeding on coralline algae before moving to feed on scleractinian corals (Yamaguchi, 1974; Lucas, 1984; Zann et al., 1987; Deaker et al., 2020a). Because high densities of coral-feeding crown-of-thorns starfish can substantially reduce coral cover (Chesher, 1969; Mellin et al., 2019), this species has attracted considerable research and management attention since the 1960s. Causes of outbreaks have been debated for decades and a lack of key demographic rates has undermined consensus (Pratchett et al., 2014; Chapter 1). The importance of early ontogenetic diet shifts in determining the occurrence of outbreaks has, however, been largely overlooked. This is due, at least in part, to difficulties in detecting and studying early algal-feeding juvenile stages of crown-of-thorns starfish in the field (Doherty and Davidson, 1988; Johnson et al., 1992), which were up until recently considered to be elusive in shallow waters of Australia's Great Barrier Reef (Chapter 2, 3, 5). In this study, a total of 3,532 juvenile *Acanthaste*r cf. *solaris* (ranging in size from 2–64 mm diameter) were sampled over eight months during extensive surveys across 64 reefs of the GBR. Comparisons of growth trajectories for algal-feeding (herbivorous) versus coral-feeding (corallivorous) juvenile crown-of-thorns starfish highlight important demographic consequences of ontogenetic diet shifts.

4.3 Materials and methods

Field sampling

All field sampling was conducted between 7 May and 15 December 2015. Juvenile starfish (n = 3,532) were sampled from 64 reefs (as defined by unique marine park reef ID) across 111 sampling sites (Wilmes and Schultz, 2019). At each sampling location, one to two divers searched the reef substratum for feeding marks of juvenile starfish to depths of 15 m. Searches were conducted on dead coral substratum (predominantly coral rubble), as well as adjacent live corals (Scleractinia). Starfish that were found associated with pieces of dead coral (encrusted with coralline algae), were presumed to be feeding on coralline algae and those that were associated with hard coral were presumed to be feeding on coral, based on the presence of conspicuous feeding scars on coralline algae versus coral respectively. All starfish located were sampled ensuring that those collected from dead coral and coral rubble were kept separate from those collected from live corals. Target size was set to a maximum of 50 mm, at the time of our first sampling, as starfish from the previous cohort were expected to be larger than 50 mm in diameter. Two of the 3,532 sampled juveniles were slightly larger than 50 mm (52.5 mm and 64 mm). Following collection, the diameter of all starfish was measured to the nearest 0.5 mm, before preservation in 95% ethanol.

Statistical analyses

All analyses were conducted in R (R Core Team, 2018). Ages of all starfish were estimated based on the explicit assumption that all individuals sampled were from a single cohort, arising from documented spawning in December 2014 (Uthicke et al., 2015a) (where fertilisation assumed to occur on 10th December 2014). The relationship between body size (diameter in mm) of algal-feeding starfish (n = 3,042) and age was modelled with a quadratic polynomial regression (orthogonal polynomial, where covariance between the two terms is assumed to be 0) using a Gaussian error distribution. Model fitting was conducted using the *lme*() function of the *nlme* package (Pinheiro et al., 2018). By contrast, the relationship between body size of coral-feeding starfish (n = 490) and age was modelled with a generalised linear mixed effects model, using a Gamma error distribution to account for heterogeneity of variance, and with a log link function to satisfy underlying model assumptions. Model fitting was carried out using the *glmmPQL*() function of the *MASS* package (Venables and Ripley, 2002).

The proportion of algal-feeding starfish within a given sample (n = 131) was modelled against age with a generalised linear mixed effects model, and a binomial error distribution with logit link function. Similarly, the proportion of starfish ≤8 mm within a given sample (n = 131) was modelled against day of the year, with a generalised linear mixed effects model, and a binomial error distribution with logit link function. Model fitting was again carried out using the *glmmPQL*() function.

For all four models, reef and site were included as nested random effects to account for variation that may occur at the reef and site level. Underlying model assumptions (homogeneity of variance and normality of residuals) were evaluated based on inspection of diagnostic plots and goodness of fit was in addition assessed statistically using a lack of fit test. Spatial autocorrelation was explored through visual inspection of residuals (bubbleplot and variograms). The significance of trends was established based on p-values (significant if $p<0.05$).

To explicitly compare body size between individuals that were recorded feeding on coralline algae versus scleractinian corals, all individuals were assigned to one of three size classes (≤8 mm, >8–20 mm, >20 mm) reflecting reported size thresholds for dietary shifts from aquarium studies (Yamaguchi 1973; 1974; Lucas 1984; Keesing and Halford, 1992b; Deaker et al., 2020a). Given the opportunity, most crown-of-thorns starfish shift their diet from coralline algae to hard coral at approximately 8 mm in diameter (Yamaguchi, 1973; 1974; Lucas, 1984), and reach a maximum size of 20 mm in diameter if kept on an algal diet for years (Lucas, 1984; Keesing and Halford, 1992b; Deaker et al., 2020a). Variation in the frequency of algal- versus coral-feeding starfish recorded within each size class from field collections was analysed using Pearson's Chi-squared test of independence.

4.4 Results and discussion

Most juvenile starfish (86.1%) sampled during this study were found on, and presumed to be feeding on, coralline algae, whereas 13.9% of starfish were found on scleractinian corals. The size of starfish differed greatly with feeding substrate ($X^2 = 2{,}102$, df = 2, $p<0.001$), where all starfish ≤8 mm in diameter were found on coralline algae, and virtually all individuals >20 mm (322 out of 338), were found on coral. Most juvenile starfish were ≤8 mm in diameter until the end of May (**Table 4.1**, $p<0.05$). Assuming all individuals sampled were from a single annual cohort, our results suggest that ontogenetic dietary shifts for crown-of-thorns starfish may occur as early as 6 months post-spawning (**Figure 4.1b**, that is early June on the GBR). This is much earlier than previously reported from field studies, which suggested that ontogenetic diet shifts occur between 9–15 months of age (Zann et al., 1987; Habe et al., 1989; Sweatman, 2008). However, spawning may occur throughout summer months (November–February, with peaks in December–January on the GBR – Babcock and Mundy, 1992b, Uthicke et al., 2019) such that the ages of starfish are imprecise. Our findings are consistent with aquarium studies, showing that captive reared juvenile crown-of-thorns starfish may begin feeding on corals once they reach a size threshold of 8–10 mm in diameter at 4–6 months post-settlement (Yamaguchi, 1974; Lucas, 1984). At this size and age the starfish have typically developed their full number of arms (Yamaguchi, 1974), but their spines are not yet fully formed and their body colour ranges from dark pink to purple (**Figure 4.2d**). The appearance of juvenile starfish changes rapidly once they begin to feed on corals, with the development of spines, papulae and madreporites (**Figure 4.2c**). Importantly, coral-feeding crown-of-thorns starfish exhibit accelerated growth, while individuals that continue to feed on coralline algae cease to grow beyond 17 mm (**Figure 4.2a**, see also Lucas, 1984; Deaker et al., 2020a). Consequently, individuals that transition early to coral feeding may reach reproductive size (100–120 mm diameter – Zann et al., 1987; Westcott et al., 2016) in less than 2 years (**Figure 4.2a**).

Our model (**Figure 4.2a**, **Table 4.1**, $p<0.05$) predicts that coral-feeding starfish reached 55–73 mm in diameter (as per 95% CI, **Figure 4.2a**) 18 months after spawning, when seasonal gametogenesis would be expected to begin (Yamaguchi, 1974). However, the onset of first gametogenesis is also size related (size threshold of 100–120 mm – Zann et al., 1887; Lucas, 1984), and so not all starfish may have reached reproductive size in time to spawn during summer months at two years of age, or may have done so at a relatively small size, with a resulting reduced fecundity (Babcock et al., 2016a; Rogers et al., 2017). Reduced fecundity among individuals of the same cohort would, in turn, limit the reproductive output (production of fertilised eggs) of the entire cohort and of the population itself (Rogers et al., 2017), ultimately constraining larval supply to settlement habitats and population replenishment. Whereas, if juvenile starfish remained on a diet of coralline algae, our model (**Figure 2a**, **Table 1**, $p<0.05$) predicts that size at first opportunity of reproduction would not be reached with near certain negative effects on population replenishment.

Despite the unprecedented early onset of ontogenetic dietary shifts, most juvenile crown-of-thorns starfish continued to feed on coralline algae until 11 months of age (**Figure 4.3, Table 4.1**). The proportion of juvenile starfish feeding on coralline algae decreased from 100% in May 2015 (presumed to be 5 months old after spawning) to 10.3% in December 2015, 13 months post-spawning (**Figure 4.1b**) and varied with location (**Figure 4.3**). Such variability in the timing of ontogenetic diet shifts may be linked to the local availability of coral prey, thereby contributing to coupled oscillations in the abundance of crown-of-thorns starfish and live coral cover. These coupled oscillations may result in “stable limit cycles” at the scale of individual reefs. Stable limit cycles (sensu May, 1972) are used to account for well-documented oscillations in the abundance of predators and their prey and may account for cyclical outbreaks of crown-of-thorns starfish observed on the GBR (Antonelli and Kazarinoff, 1984; Bradbury et al., 1985). However, the lack of empirical evidence for inherent feedback mechanisms in the crown-of-thorns starfish-coral system has fostered the development and presentation of alternative tangential explanations for outbreaks.

Table 4. 1 Parameter estimates and significance of fitted models. Results of linear mixed effects models testing for i) the effect of age (where 0 days old since spawning = 10th December 2014) on body size (diameter in mm), and on the proportion of juvenile starfish within individual samples that were feeding on coralline algae (as opposed to feeding on scleractinian coral) and ii) the effect of date (as in day of year 2015) on the proportion of juvenile starfish within individual samples that were ≤8mm in diameter. Reef and sampling site are included as nested random effects in all models.

Response variable	**Diet**	**Fixed effect structure**	**Random effect structure**	**Link function**	**Parameter**	**Parameter estimate**	**Standard error**	**p-value**
Size in diameter (mm)	Coralline algae	Poly(age,2)	Reef/site	Identity	Intercept	-3.1019038	1.5277476	-
					1st term	0.0825099	0.0134958	0.000
					2nd term	-0.0000833	0.0000280	0.003
Size in diameter (mm)	Scleractinian coral	Age	Reef/site	Log	Intercept	1.7074510	0.10749234	-
					Slope	0.0045186	0.00032311	0.000
Relative proportion of herbivorous starfish (0–1)	Coralline algae	Age	Reef/site	Logit	Intercept	13.570168	0.7257470	-
					Slope	-0.041472	0.0024095	0.000
Relative proportion of starfish (≤8mm in diameter)	Coralline algae	Day of year	Reef/site	Logit	Intercept	4.366940	0.3812083	-
					Slope	-0.030201	0.0022365	0.000

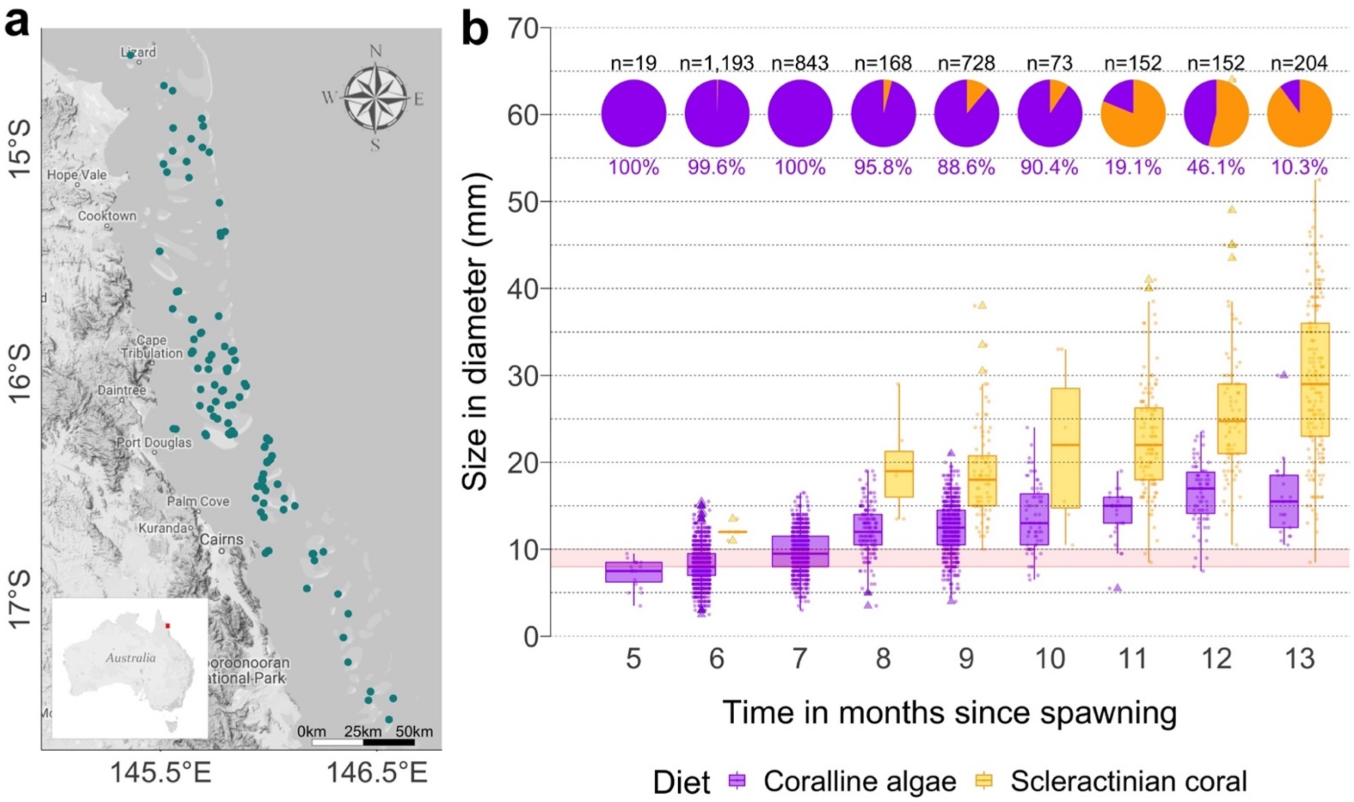


Figure 4. 1 Increased variation in size of juvenile starfish with time. a, Map of sampling locations (turquoise circles) on the Great Barrier Reef (Map data©2018 Google, GBRMPA). b, Monthly size distribution of coralline algal- (in purple) and coral-feeding (in orange) juvenile *Acanthaster* cf. *solaris*. Data points represent individual observations of juvenile starfish (n = 3,532, by sampling month and diet). Each boxplot is characterised by a median size (horizontal middle line), an interquartile range of size (rectangle), a minimum and maximum non-outlier (vertical line), and outliers (triangles). Individual pie charts indicate the proportion of coralline algal-feeding starfish in relation to coral-feeding starfish, by month since spawning. The red shaded horizontal rectangle indicates the threshold size for the ontogenetic shift in diet (8–10 mm).

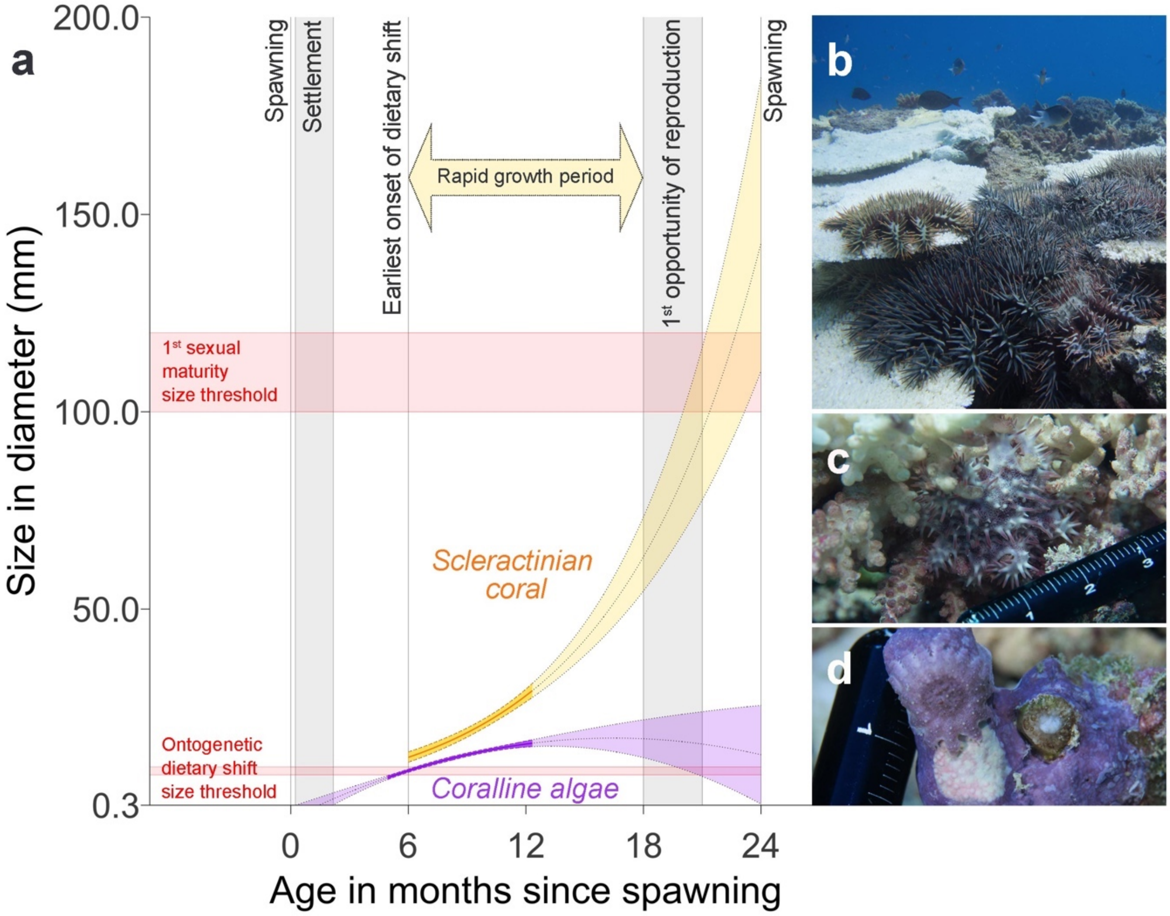


Figure 4. 2 Contrasting early growth trajectories by diet of juvenile crown-of-thorns starfish. a, Fitted growth models for *A.* cf. *solaris* by diet (i.e., coralline algae in purple and scleractinian coral in orange) with major life history traits and events. The dark shaded purple and yellow areas represent the 95% confidence intervals of individual models; within the bounds of our data (i.e., 148–370 days since spawning, n = 3,432). The lightly shaded purple and yellow areas indicate the model predictions, beyond the bounds of our data (148 –370), from 0–720 days since spawning. b, Example of a typical aggregation of mature *A.* cf. *solari*s from the Great Barrier Reef, of varying sizes, on recently eaten tabulate *Acropora* coral. c, Cryptic coral-feeding juvenile starfish hiding at the base of a bottlebrush *Acropora* coral, adjacent to its recent feeding scar. d, Cryptic algal-feeding juvenile starfish, camouflaged against crustose coralline algae, adjacent to a recent feeding scar. Imagery by Daniel J. Schultz.

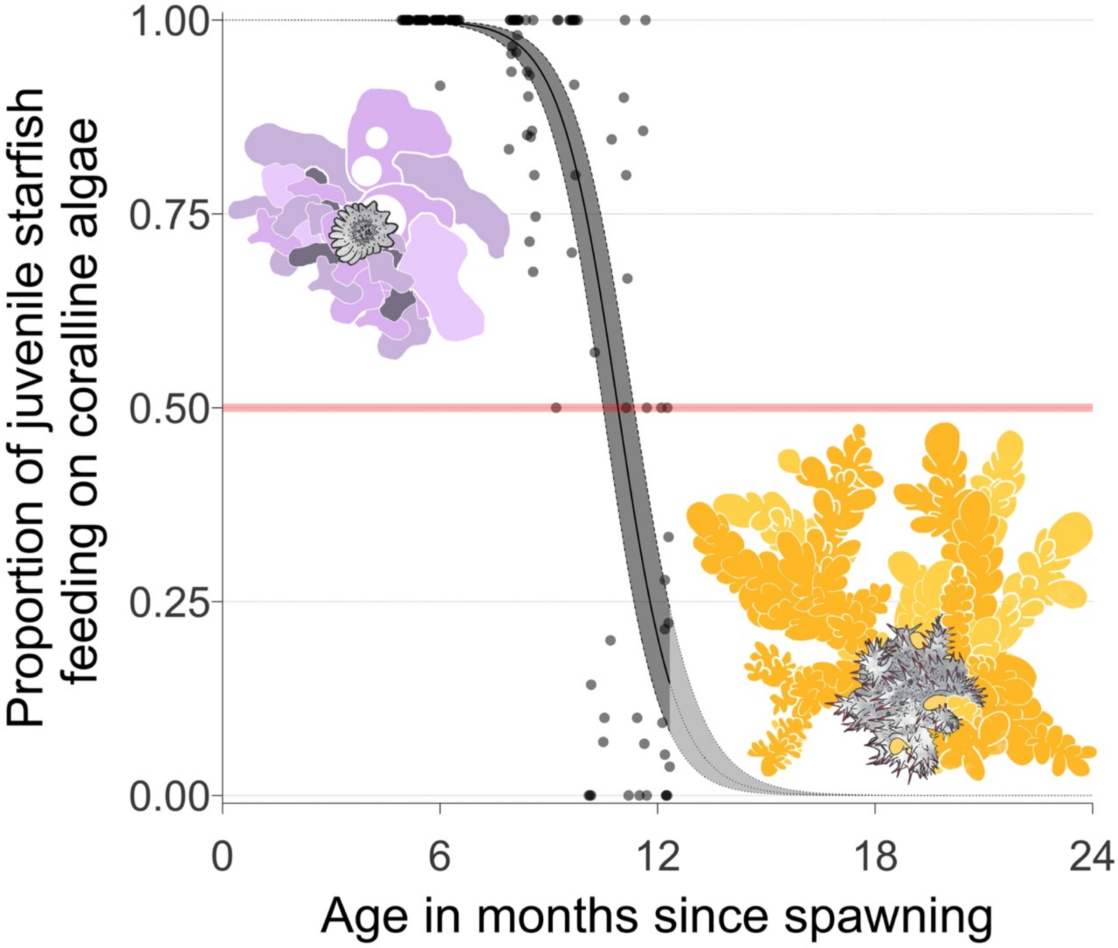


Figure 4. 3 Variation in the ontogenetic shift in diet. Points indicate individual observations (n = 131). A relative proportion of 1 indicates that all juvenile starfish within a sample were feeding on coralline algae, while a proportion of 0 indicates that all juvenile starfish within a sample were feeding on scleractinian coral. The trend was modelled using a frequentist linear mixed effects model with a binomial distribution. The dark black line illustrates the best fit model with its 95% confidence band (dark shaded grey area); extending from 148–370 days since spawning. The lightly shaded area indicates the model prediction, beyond the bounds of our data (148–370), from 0–720 days after spawning. The red line indicates the timing at which half of our sample population is predicted to have shifted their diet from coralline algae to scleractinian coral (i.e., 327 days after spawning).

Our study provides evidence of an inherent link between the individual fitness of crown-of-thorns starfish and the availability or accessibility to coral prey. We show that the ontogenetic shift in diet from coralline algae to hard coral accelerates growth of crown-of-thorns starfish and is essential for individual starfish to reach reproductive size. Because survivorship of early-stage juvenile starfish is size-related (Keesing and Halford, 1992a; Keesing et al., 2018; Chapter 5) and growth is stunted on a coralline algal diet for years (Lucas, 1984; Keesing and Halford, 1992b; Deaker et al., 2020a), ontogenetic shifts in diet and habitat will have a fundamental impact on individual fitness and population replenishment. Enhanced population replenishment may initiate positive feedbacks that drive the onset of outbreaks. Accordingly, abundant coral prey near settlement areas promotes early ontogenetic shifts in diet, enhances individual growth and resulting fitness, and accelerates the rate of development of outbreaks. In contrast, a paucity of coral prey (such as might be caused by sustained feeding activities of high densities of adult starfish) would delay ontogenetic shifts in diet and result in reduced individual fitness and replenishment success, thereby contributing to the demise of outbreaks. Annual cohorts of juvenile starfish may then build-up over multiple years and gradually join and replace the remnant adult starfish population. As coral prey recovers on individual reefs, this negative feedback mechanism (DeAngelis et al., 1986) may then give rise to “stable limit cycles”.

Both pre- and post-settlement processes (Chapter 1) are likely to influence the specific timing of size-related ontogenetic shifts in diet by constraining development and behaviour, as well as accessibility to coral prey. For example, food availability during the planktonic larval phase, maternal provisioning (related to coral prey availability) and other abiotic factors (temperature and pH) are considered key constraints to larval development, and size and age at settlement (Johnson and Babcock, 1994; Caballes et al., 2016; Pratchett et al., 2017b; Uthicke et al., 2013; 2018), with likely effects on size- and stage duration-related mortality rates (via “stage duration” – Miller et al., 1988, and “bigger is better” mechanisms – Houde et al., 1987) and early post-settlement growth. In turn, biotic (predation risk – Chapter 5) and abiotic factors (temperature and pH – Kamya et al., 2018) may further influence behaviour, growth and survival following settlement. Various pre- and early post-settlement processes are therefore likely to influence the time at which starfish reach the ontogenetic stage for the dietary shift, and could effectively account for differences in size among algal-feeding starfish from our field study (e.g., mean ± 1 SD = 7.49 ± 1.74 mm, ~ presumed to be 160 days after spawning) and tank-based studies (e.g., mean ± 1 SD = 11.07 ± 0.85 mm, ~ 160 days after spawning – Yamaguchi, 1973). While most juvenile starfish had reached the size threshold for the ontogenetic shift in diet by the end of May (**Table 4.1**), starfish can survive on an algal diet for years (Lucas, 1984; Keesing and Halford, 1992b; Deaker et al., 2020a) and may therefore shift their diet much later in the year or in life when coral prey is not accessible or available near where they initially settled. Under this scenario, post-settlement processes such as sub-lethal predation (Chapter 5) would be expected to continue to influence the age at which starfish ultimately reach the size threshold for the ontogenetic shift in diet.

Early-stage juvenile crown-of-thorns starfish are reported to predominate in coral reef habitats with limited coral cover and high fine-scale structural complexity (Zann et al., 1987; Yokochi and Ogura, 1987), presumably due to a combination of spatial patterns in larval distribution, settlement preferences and/or predation risk (Black and Moran, 1991; Johnson et al., 1991; Cowan et al., 2016a,b; Chapter 2). Herbivorous juvenile starfish have been observed to move actively out of such coral poor habitats towards areas where coral prey is more abundant (Zann et al., 1987). Accessibility to live coral, and in particular preferred coral prey, is therefore likely to greatly constrain the ontogenetic shift to corallivory. While we recorded juvenile starfish feeding on 13 coral genera, largest numbers of corallivorous starfish were typically observed within thickets of branching bottlebrush *Acropora* spp. Not all coral prey may therefore be equally nutritious (Keesing and Halford, 1992b) suitable for consumption (Yamaguchi, 1974; Johansson et al., 2016) or as a microhabitat that provides protection from predators, and may result in trade-offs between rapid growth and survival.

Variability in ontogenetic dietary shifts among cohorts of crown-of-thorns starfish, which has largely been overlooked until now (Yamaguchi, 1974; Lucas, 1984; Zann et al., 1987; Habe et al., 1989; Zann et al., 1990), will have major ramifications for individual survival and replenishment success. Growth rates of *A.* cf. *solaris* during the rapid growth period (i.e., after shifting to feeding on coral and before the onset of first sexual maturity; see **Figure 4.2a**) are strikingly similar among studies conducted in different locations (Yamaguchi, 1974; Lucas, 1984; Zann et al., 1987; Habe et al., 1989; Deaker et al., 2020a). Moreover, laboratory reared crown-of-thorns starfish that were constrained from feeding on coral for 6.5 years after settlement, subsequently grew at the same rate as individuals from a different cohort that were allowed to feed on coral after 10 months (Deaker et al., 2020a). While growth rates following ontogenetic diet shifts may be insensitive to specific timing of such shifts (Deaker et al., 2020a), disparity in the timing of these shifts is likely to result in substantial variation of body size within and between cohorts, with important consequences for subsequent fitness and population dynamics.

Although we did not explicitly consider mortality of juvenile starfish, it is well established that body size is a major determinant of individual survival, especially under natural conditions where there is high predation risk (Werner and Gilliam, 1984; Keesing and Halford, 1992a; Fuiman and Higgs, 1997; Gosselin and Qian, 1997; Keesing et al., 2018). Herbivorous starfish can survive in aquaria for at least 6.5 years (Deaker et al., 2020a), and growth to sexual maturity resumes once suitable coral prey is available, even if the shift in diet was delayed for years (Lucas, 1984; Deaker et al., 2020a). However, survivorship of crown-of-thorns starfish is (as for many other marine organisms), considered lowest for smallest life history stages (Keesing and Halford, 1992a; Fuiman and Higgs, 1997; Gosselin and Qian, 1997; Hunt and Scheibling, 1997; Almany and Webster, 2006), and remaining in the smallest potentially most vulnerable herbivorous life stage for years is therefore likely to substantially reduce survival (Chapter 5). Crypsis is also a well-known anti-predator strategy (Stevens and Ruxton, 2019; Stevens and Merilaita, 2009), and it would seem likely that the observed prominent cryptic coloration (**Figure 3d**) and behaviour of herbivorous starfish, results from strong selective pressure on this life stage by visual predators.

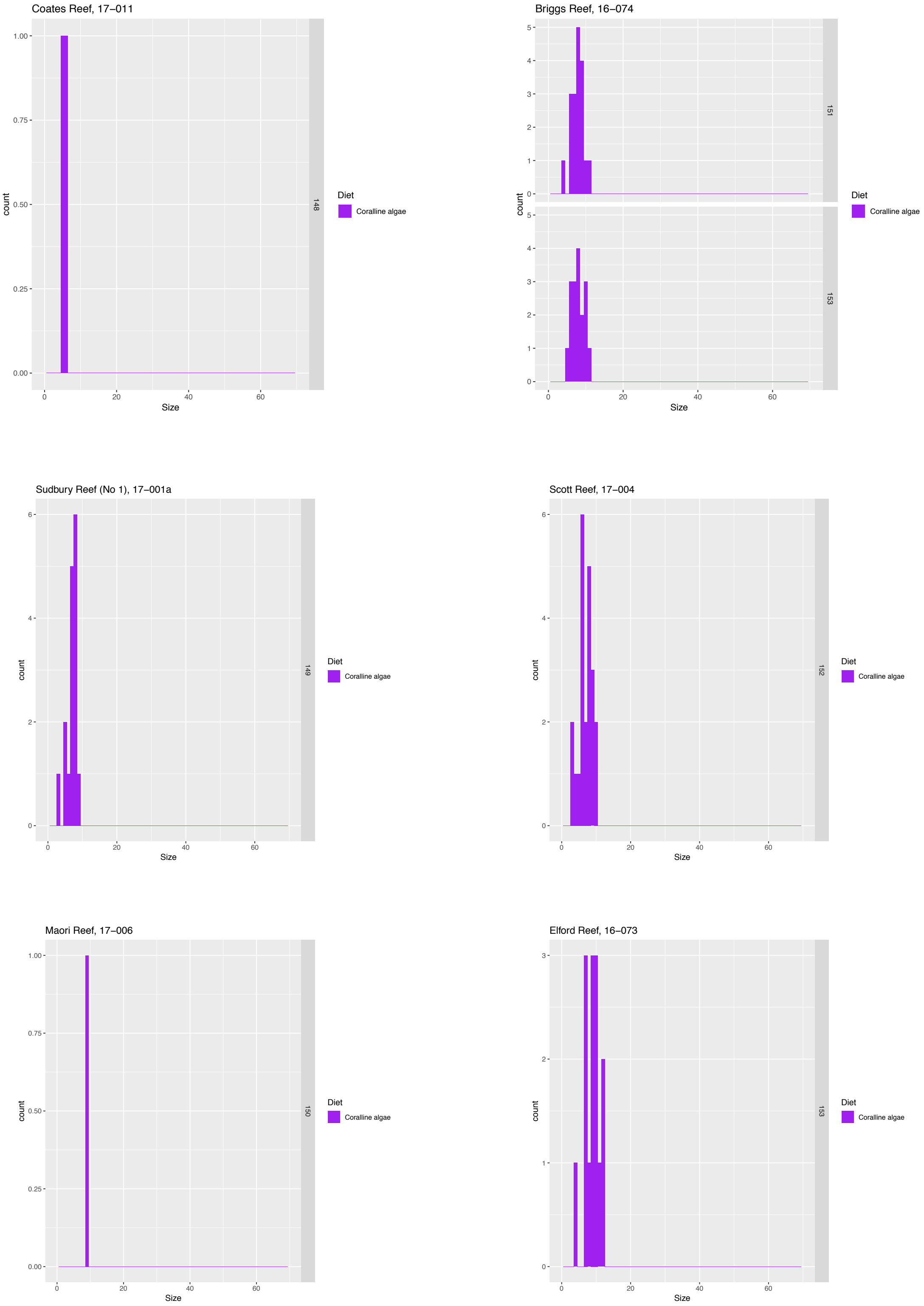
While mortality rates of small juvenile starfish may be inherently high, our results suggest that herbivorous starfish can still survive in the field for >1 year (**Figure 1b**). Though it would seem likely that most starfish >8 mm in diameter would shift their diet as soon as coral prey is available and accessible (Yamaguchi, 1974), as deferral of the shift in diet ultimately leads to maximised growth rates at the herbivorous life stage (Lucas, 1984; Deaker et al., 2020a) and constrains individual fitness (Chapter 5). Moreover, we have very rarely observed herbivorous starfish on GBR reefs from January to March, the months immediately following their annual spawning, when early-stage juvenile starfish are too small to be visually detected and effectively sampled *in situ*. This would suggest that most herbivorous starfish from previous year class cohorts either shift their diet, do not survive and/or move out of our range of detectability by January–March. Although we cannot discount the possibility that at least some individuals from our sample population belong to previous year class cohorts, the diet-related bimodal size frequency distributions (**Supplementary material Figure 4.1**) suggest that most (if not all) starfish are from the same cohort.

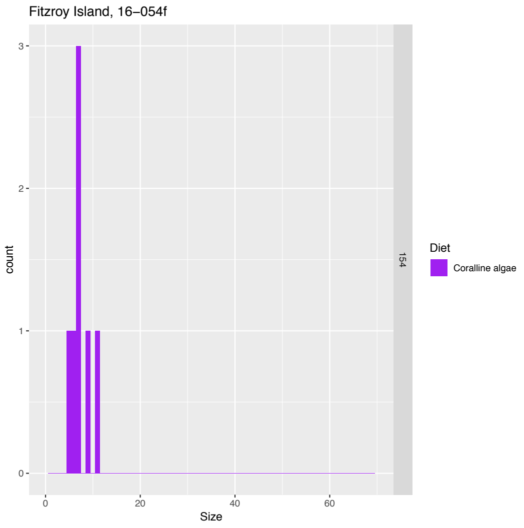
Dormant stages are believed to have evolved to tolerate harsh environments outside the temporal window of favourable conditions (Ellis et al., 1965; Danks, 1987; Vrtílek et al., 2018), and this evolutionary adaptation may allow juvenile starfish to persist in coral poor habitats or reefs until coral prey becomes accessible (Chapter 2). High density aggregations of crown-of-thorns starfish, may therefore evolve naturally over time during the early stages of coral recovery via population build-up of successive year class cohorts (Parslow, 1990; Pratchett, 2005), as opposed to via anthropogenically caused nutrient-induced mass settlement events (Birkeland, 1982; Brodie et al., 2005; 2017; Fabricius et al., 2010) or release from predation pressure (Endean, 1969; Ormond et al., 1990).

Our capacity to predict the incidence and spread of outbreaks (in light of anthropogenic changes) relies heavily on our ability to understand and measure spatial and temporal variability in replenishment success. Understanding the mechanisms that determine population replenishment is essential to develop effective early management intervention strategies. Failing to develop well-informed decision tools risks to produce counterproductive management outcomes and could in the worst case contribute to the collapse of the system itself (Holling, 1978; Bradbury et al., 1985; Bradbury, 1988; Reichelt et al., 1990b), with potentially devastating and irreversible impacts on reef ecosystems.

4.5 Supplementary material

Supplementary material Figure 4.1 Size frequency distributions by reef (as per GBRMPA's unique reef ID) and diet, over time (as in days since spawning).

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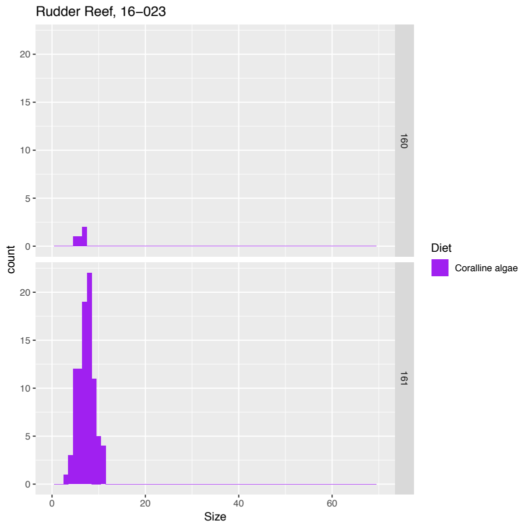
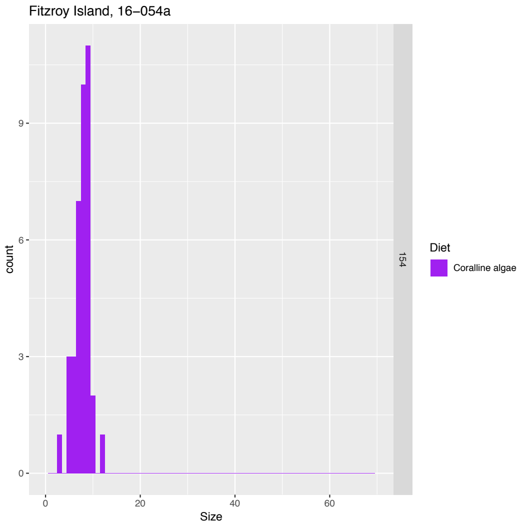
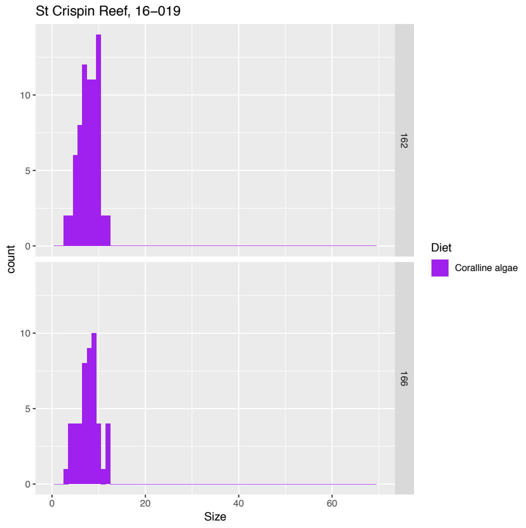
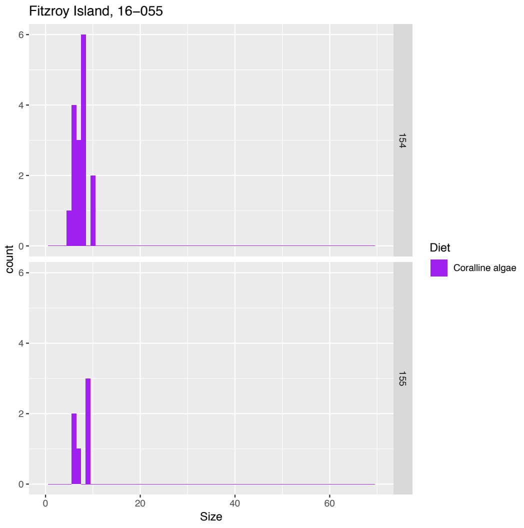
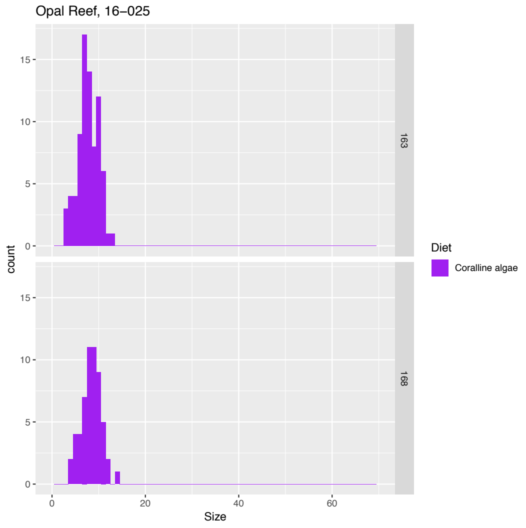
Size
Diet
Coralline algae

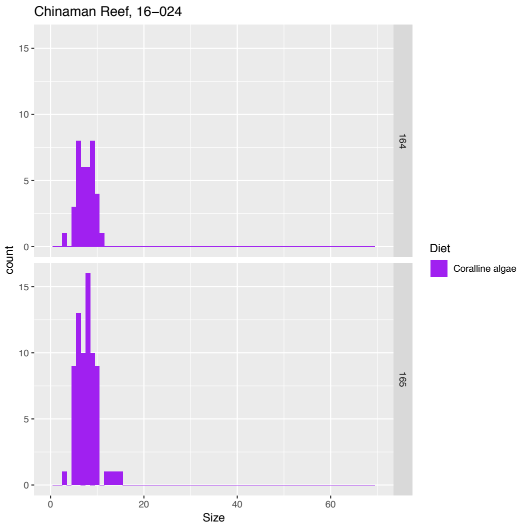

Rudder Reef, 16–023
count
20
15
10
5
0
160
20
15
10
5
0
161
0
20
40
60
Size
Diet
Coralline algae

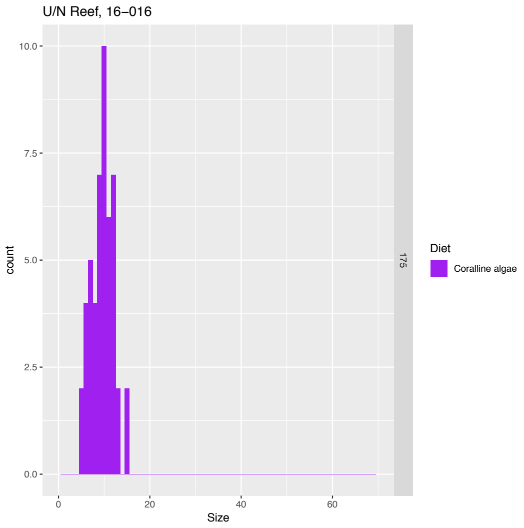

Fitzroy Island, 16–054a
count
9
6
3
0
154
0
20
40
60
Size
Diet
Coralline algae

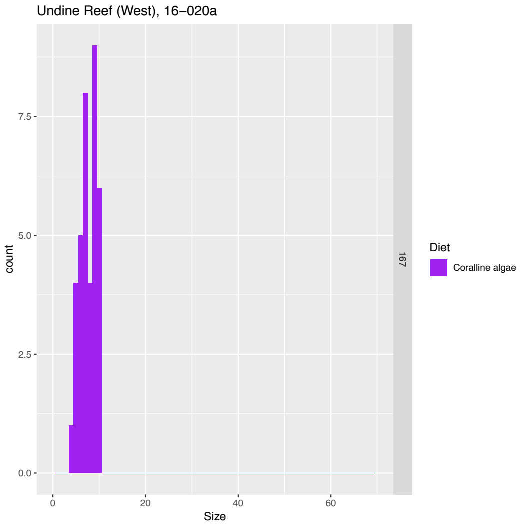

St Crispin Reef, 16–019
count
10
5
0
162
10
5
0
166
0
20
40
60
Size
Diet
Coralline algae

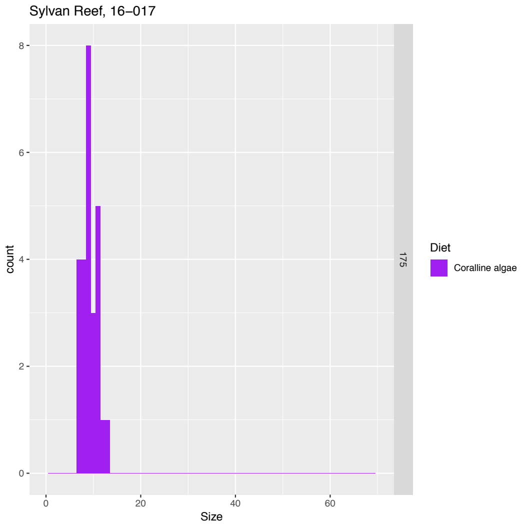

Fitzroy Island, 16–055
count
6
4
2
0
154
6
4
2
0
155
0
20
40
60
Size
Diet
Coralline algae

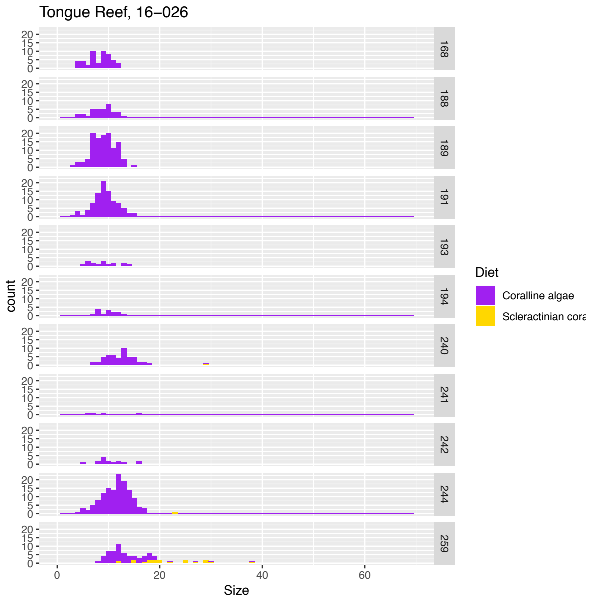

Opal Reef, 16–025
count
15
10
5
0
163
15
10
5
0
168
0
20
40
60
Size
Diet
Coralline algae

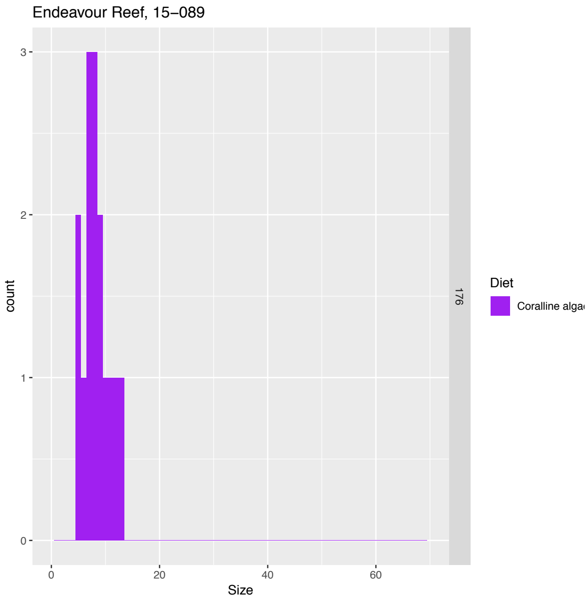

Chinaman Reef, 16–024
count
0
5
10
15
164
165
0
20
40
60
Size
Diet
Coralline algae

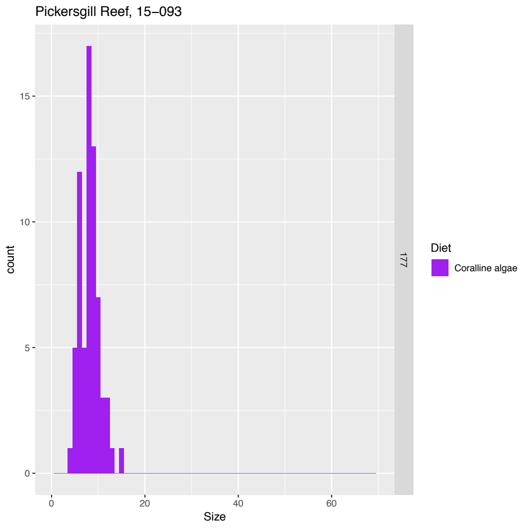

U/N Reef, 16–016
count
0.0
2.5
5.0
7.5
10.0
175
0
20
40
60
Size
Diet
Coralline algae

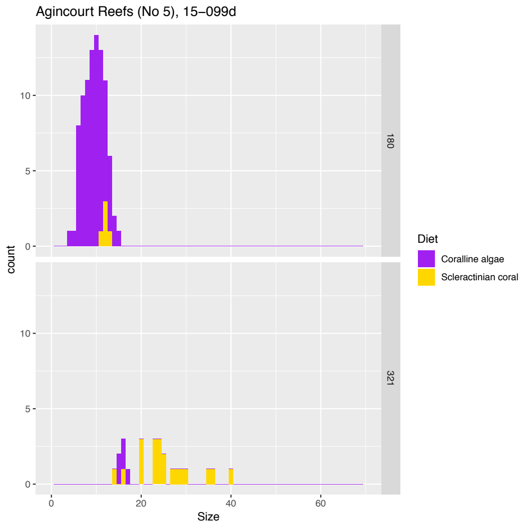

Undine Reef (West), 16–020a
count
0.0
2.5
5.0
7.5
167
0
20
40
60
Size
Diet
Coralline algae

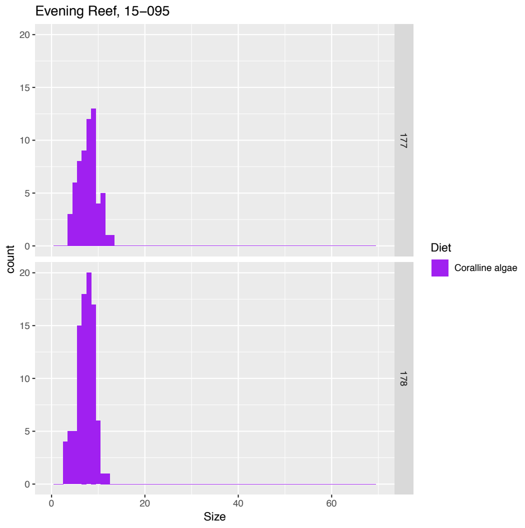

Sylvan Reef, 16–017
count
0
2
4
6
8
175
0
20
40
60
Size
Diet
Coralline algae

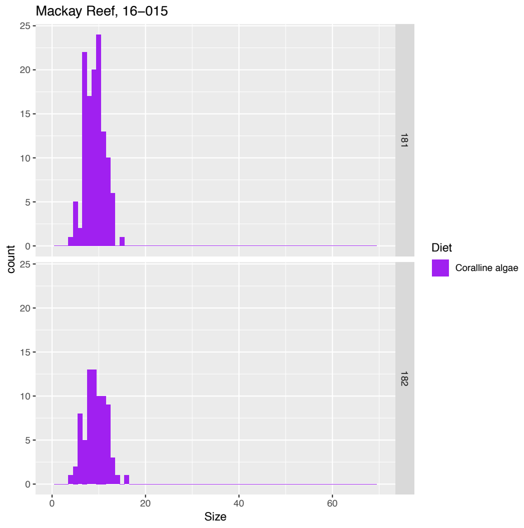

Tongue Reef, 16–026
count
0
5
10
15
20
168
188
189
191
193
194
240
241
242
244
259
0
20
40
60
Size
Diet
Coralline algae
Scleractinian cora

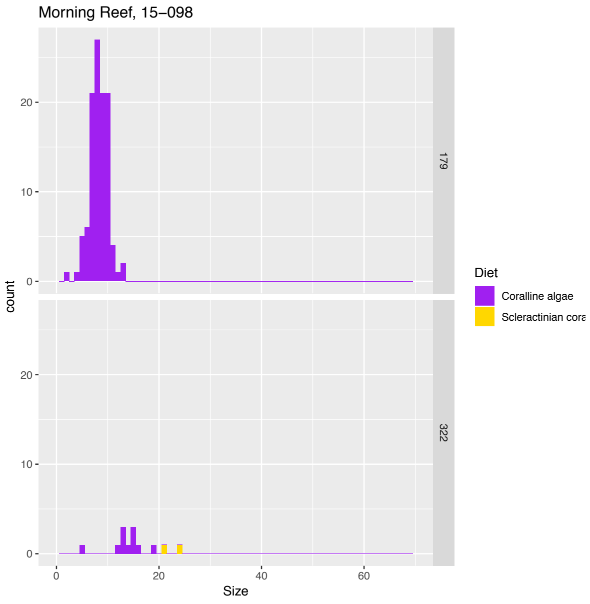

Endeavour Reef, 15–089
count
0
1
2
3
176
0
20
40
60
Size
Diet
Coralline alga

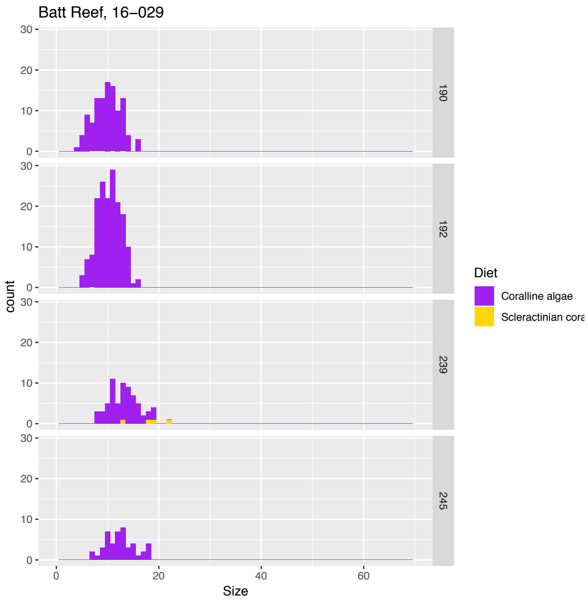

Pickersgill Reef, 15–093

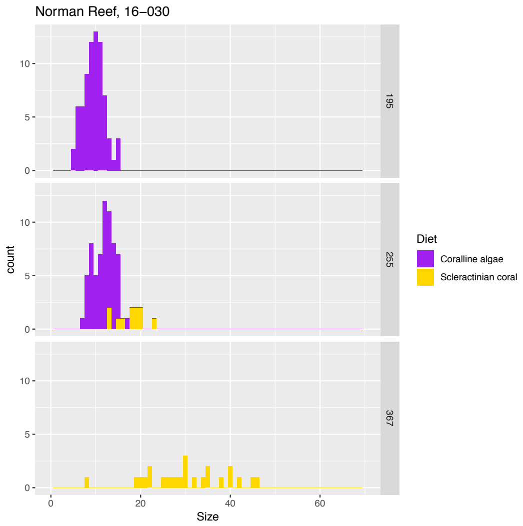

Agincourt Reefs (No 5), 15–099d

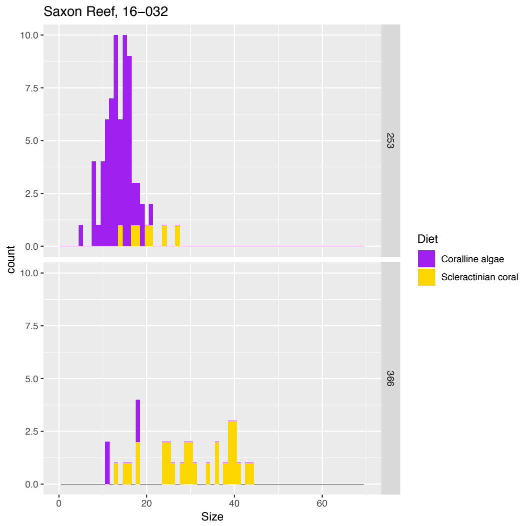

Evening Reef, 15–095

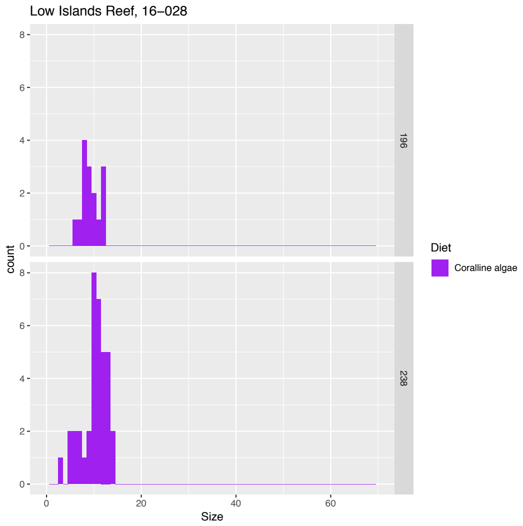

Mackay Reef, 16–015

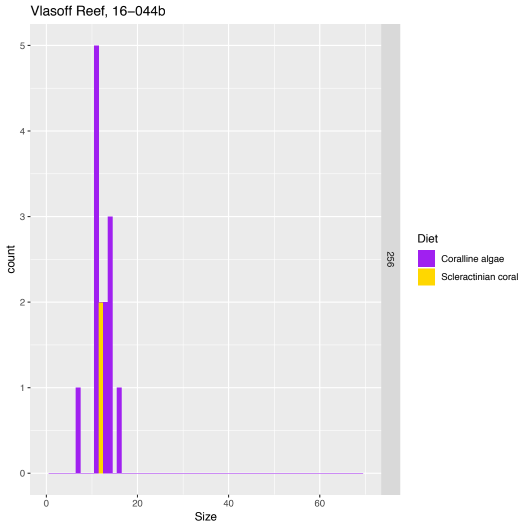

Morning Reef, 15–098

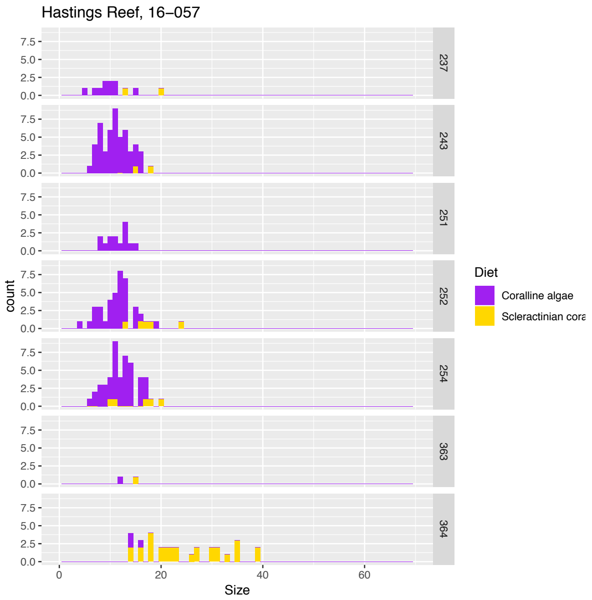

Batt Reef, 16–029

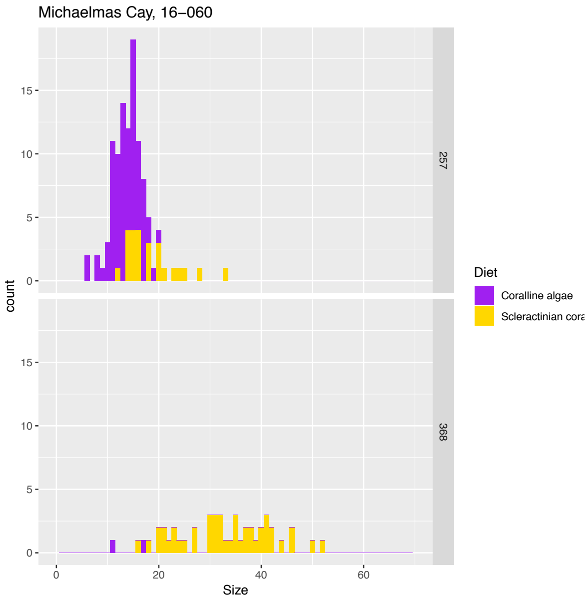

Norman Reef, 16–030
count
10
5
0
195
255
367
0
20
40
60
Size
Diet
Coralline algae
Scleractinian coral

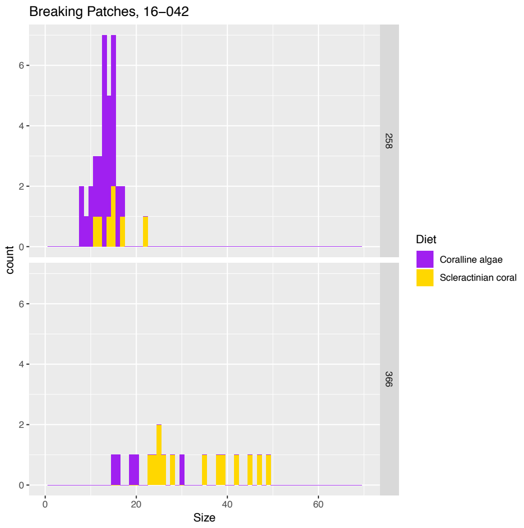

Saxon Reef, 16–032
count
10.0
7.5
5.0
2.5
0.0
253
366
0
20
40
60
Size
Diet
Coralline algae
Scleractinian coral

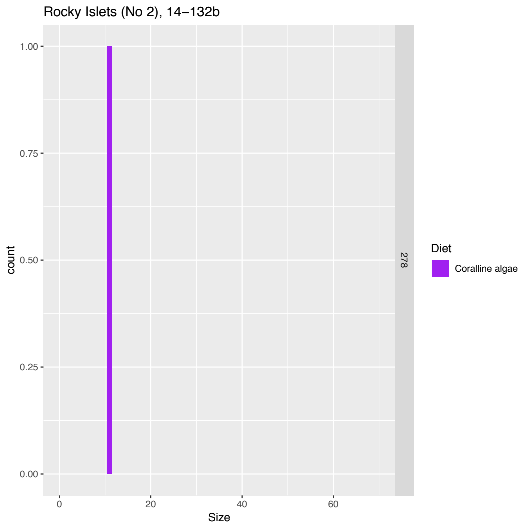

Low Islands Reef, 16–028
count
8
6
4
2
0
196
238
0
20
40
60
Size
Diet
Coralline algae

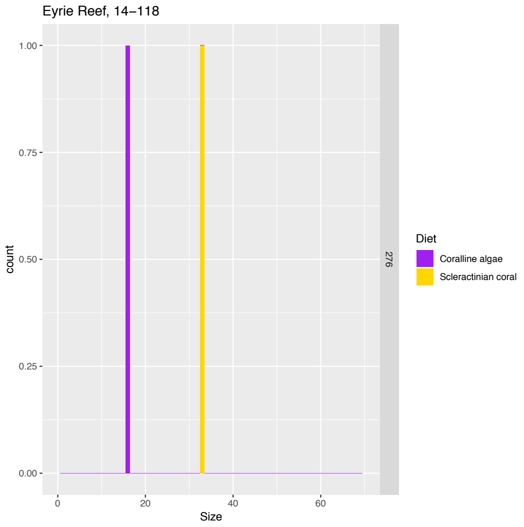

Vlasoff Reef, 16–044b
count
5
4
3
2
1
0
256
0
20
40
60
Size
Diet
Coralline algae
Scleractinian coral

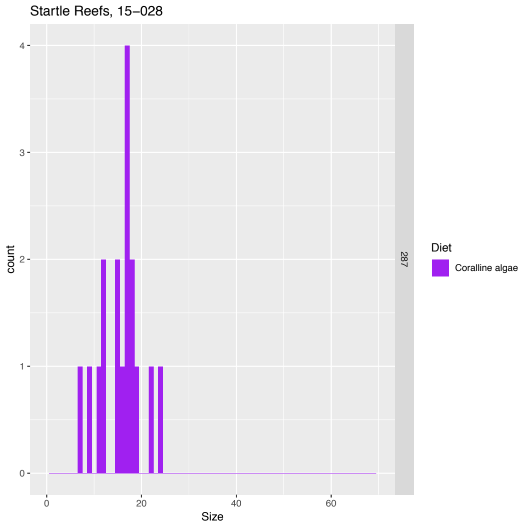

Hastings Reef, 16–057
count
7.5
5.0
2.5
0.0
237
243
251
252
254
363
364
0
20
40
60
Size
Diet
Coralline algae
Scleractinian cora

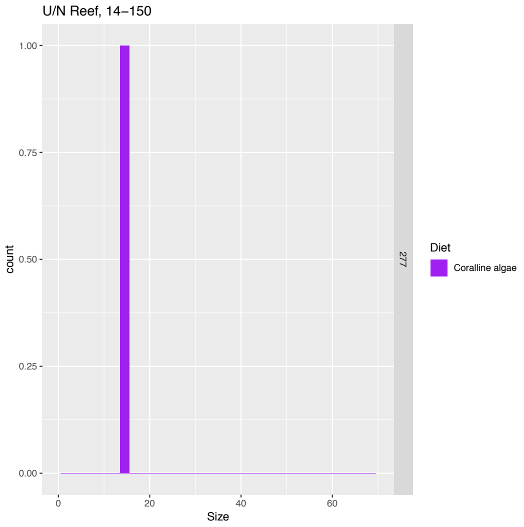

Michaelmas Cay, 16–060
count
15
10
5
0
257
368
0
20
40
60
Size
Diet
Coralline algae
Scleractinian cora

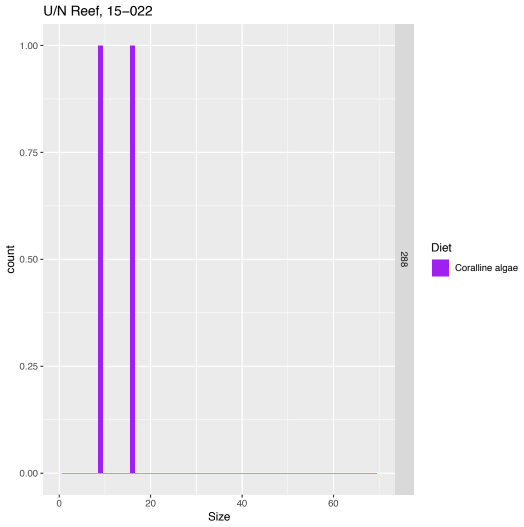

Breaking Patches, 16–042

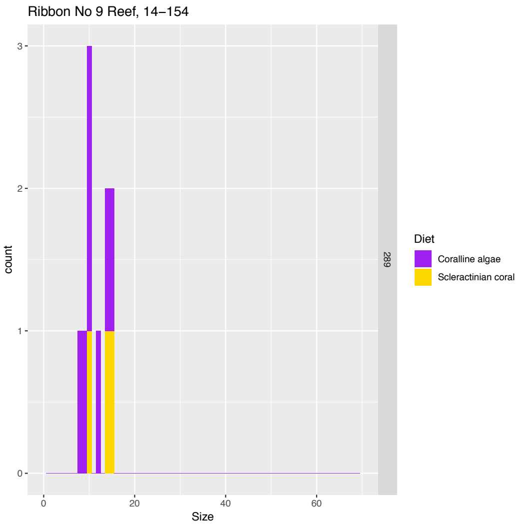

Rocky Islets (No 2), 14–132b

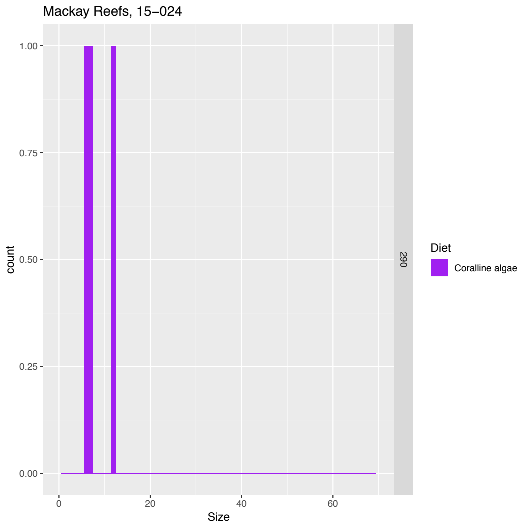

Eyrie Reef, 14–118

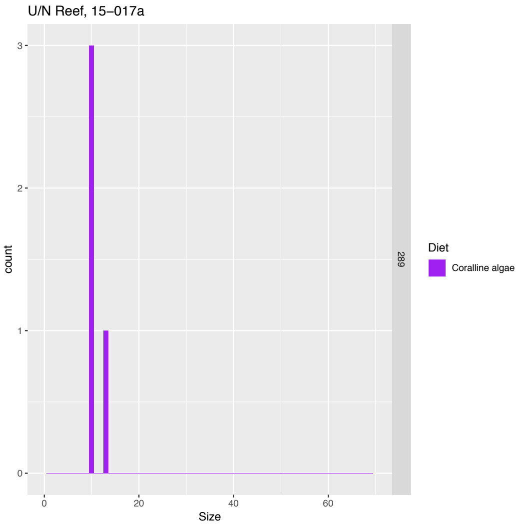

Startle Reefs, 15–028

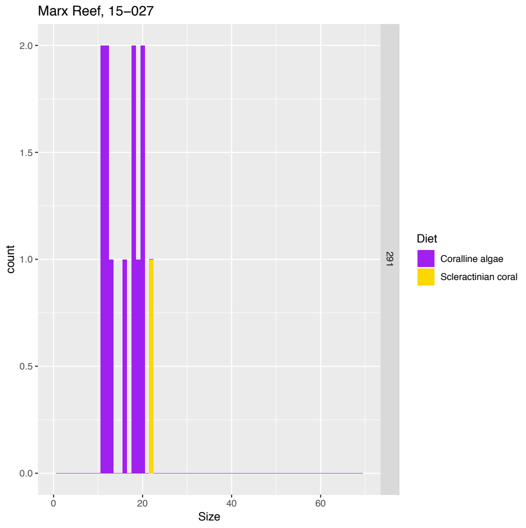

U/N Reef, 14–150

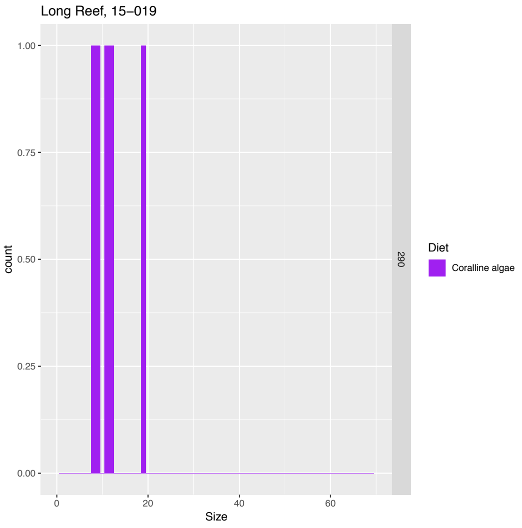

U/N Reef, 15–022

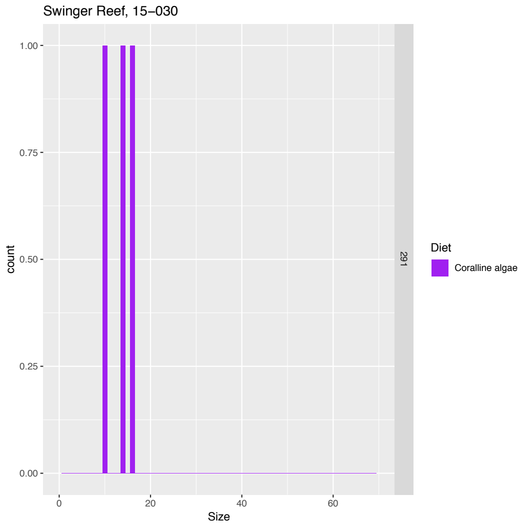

Ribbon No 9 Reef, 14–154
count
3
2
1
0
0
20
40
60
Size
289
Diet
Coralline algae
Scleractinian coral

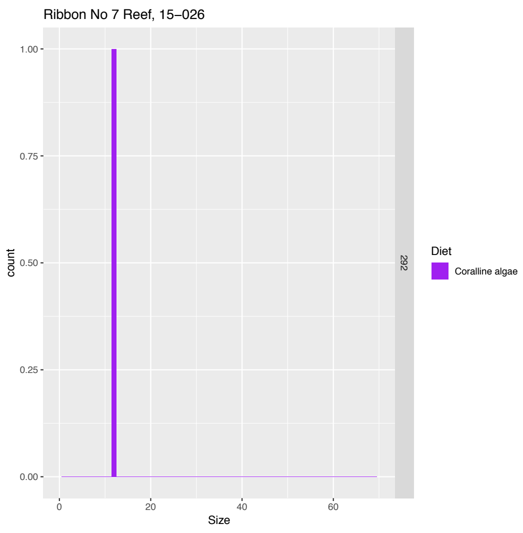

Mackay Reefs, 15–024
count
1.00
0.75
0.50
0.25
0.00
0
20
40
60
Size
290
Diet
Coralline algae

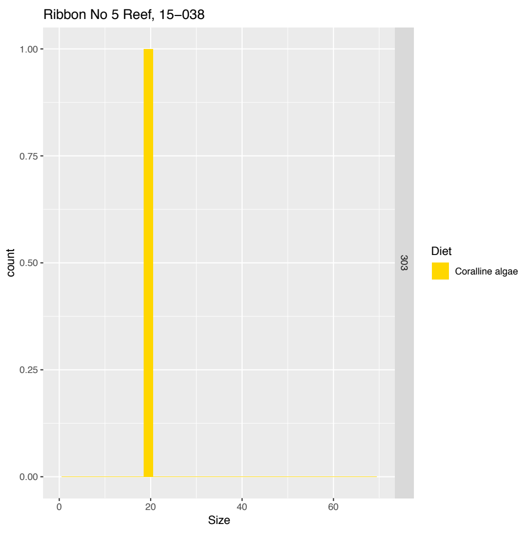

U/N Reef, 15–017a
count
3
2
1
0
0
20
40
60
Size
289
Diet
Coralline algae

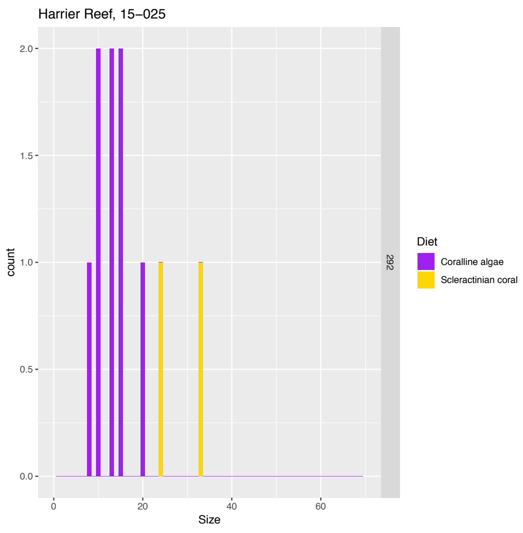

Marx Reef, 15–027
count
2.0
1.5
1.0
0.5
0.0
0
20
40
60
Size
291
Diet
Coralline algae
Scleractinian coral

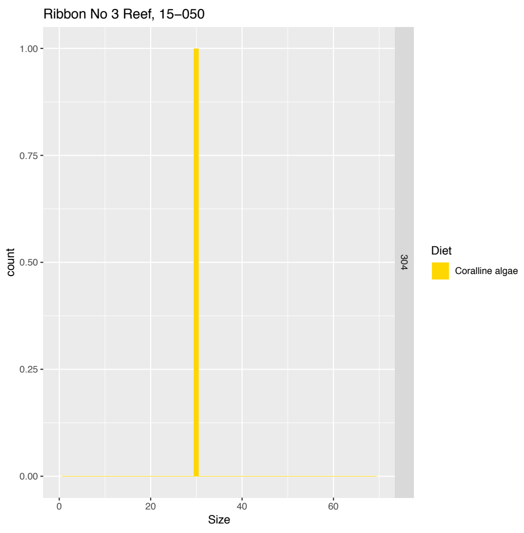

Long Reef, 15–019
count
1.00
0.75
0.50
0.25
0.00
0
20
40
60
Size
290
Diet
Coralline algae

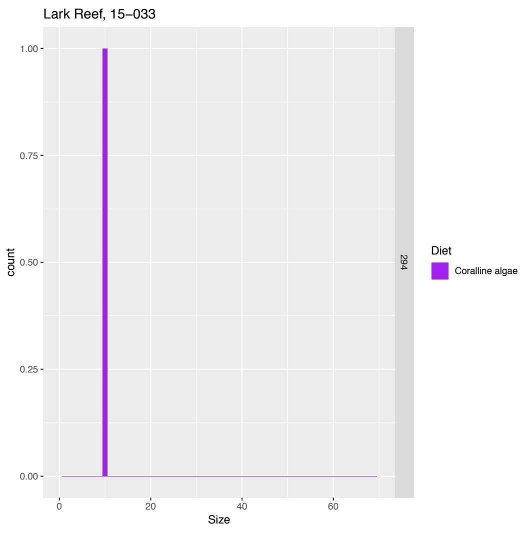

Swinger Reef, 15–030
count
1.00
0.75
0.50
0.25
0.00
0
20
40
60
Size
291
Diet
Coralline algae

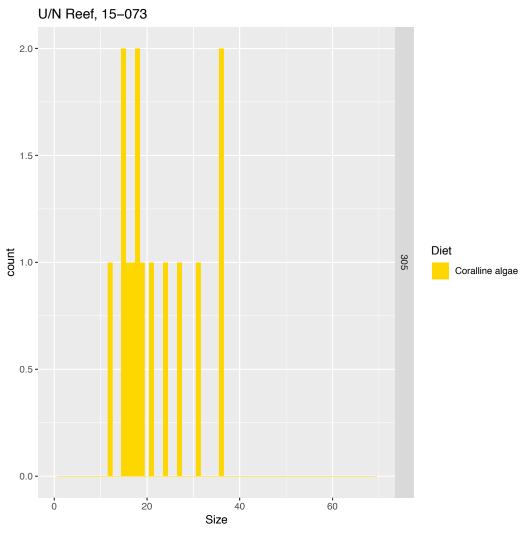

Ribbon No 7 Reef, 15–026

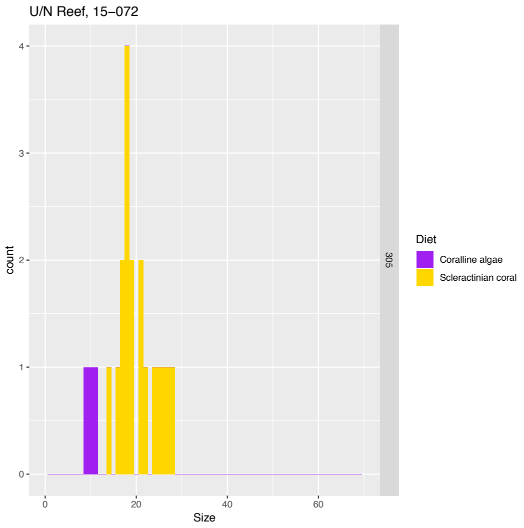

Ribbon No 5 Reef, 15–038

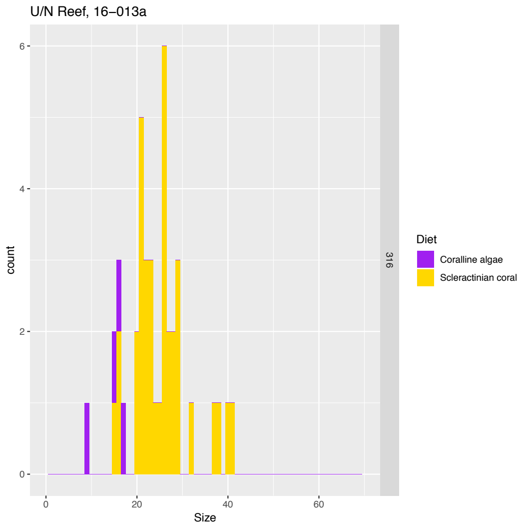

Harrier Reef, 15–025

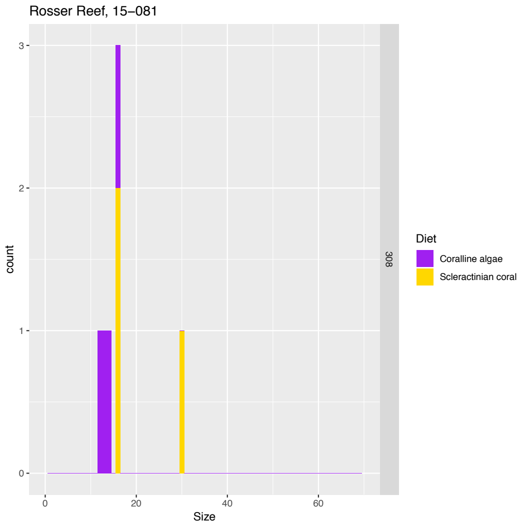

Ribbon No 3 Reef, 15–050

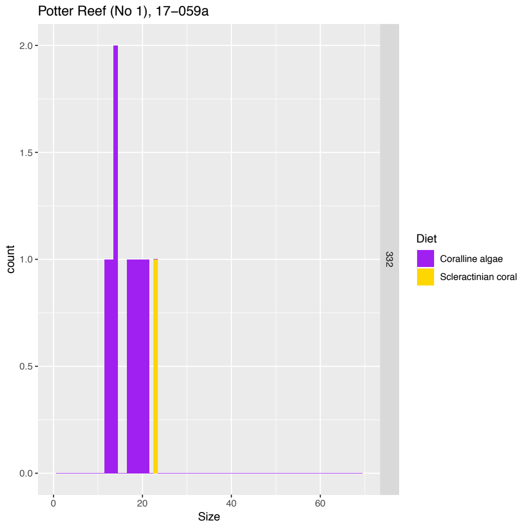

Lark Reef, 15–033

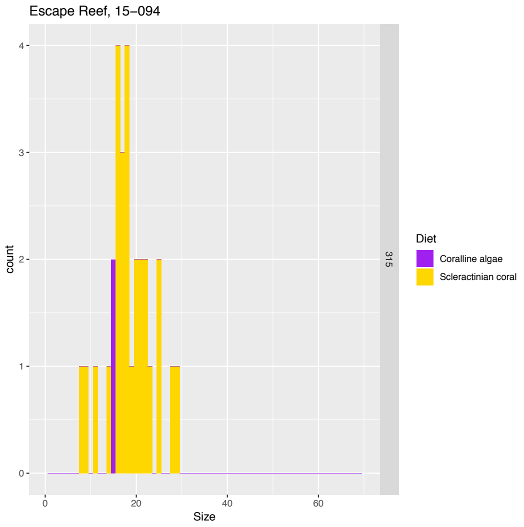

U/N Reef, 15–073

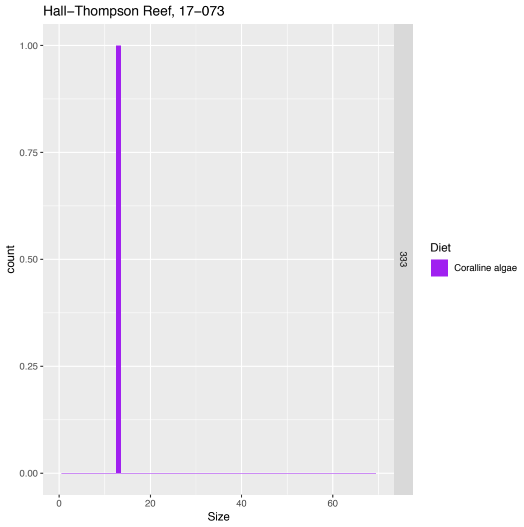

U/N Reef, 15–072
count
4
3
2
1
0
0
20
40
60
Size
305
Diet
Coralline algae
Scleractinian coral

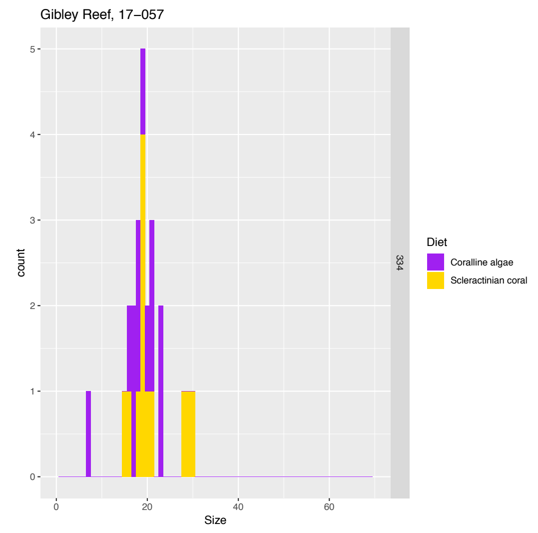

U/N Reef, 16–013a
count
6
4
2
0
0
20
40
60
Size
316
Diet
Coralline algae
Scleractinian coral

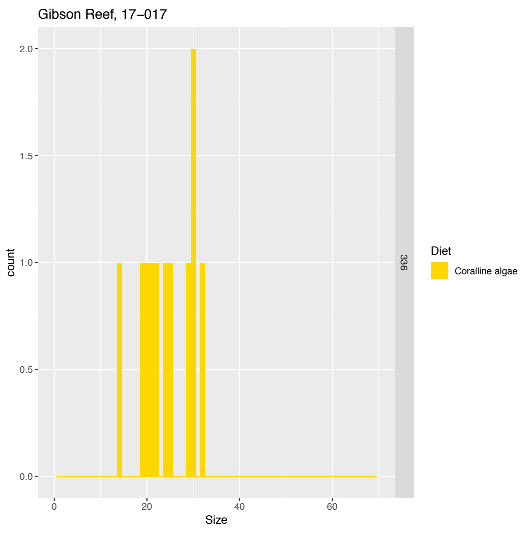

Rosser Reef, 15–081
count
3
2
1
0
0
20
40
60
Size
308
Diet
Coralline algae
Scleractinian coral

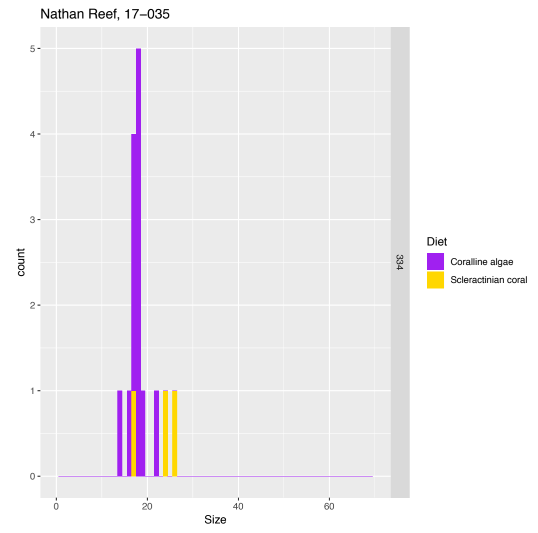

Potter Reef (No 1), 17–059a
count
2.0
1.5
1.0
0.5
0.0
0
20
40
60
Size
332
Diet
Coralline algae
Scleractinian coral

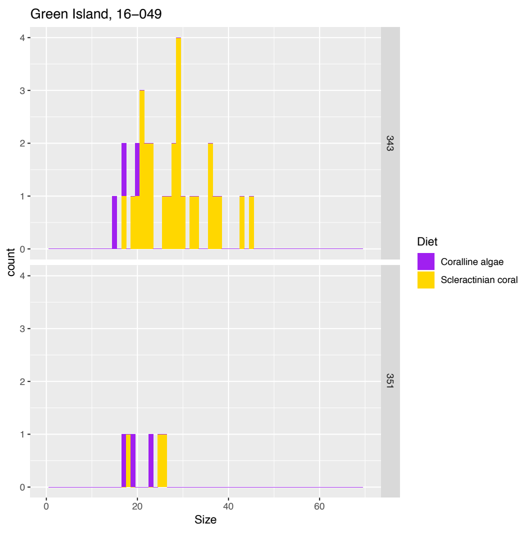

Escape Reef, 15–094
count
4
3
2
1
0
0
20
40
60
Size
315
Diet
Coralline algae
Scleractinian coral

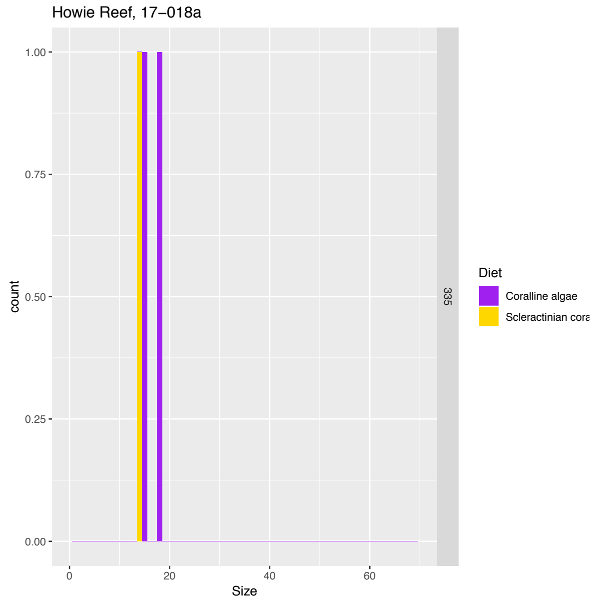

Hall–Thompson Reef, 17–073
count
1.00
0.75
0.50
0.25
0.00
0
20
40
60
Size
333
Diet
Coralline algae

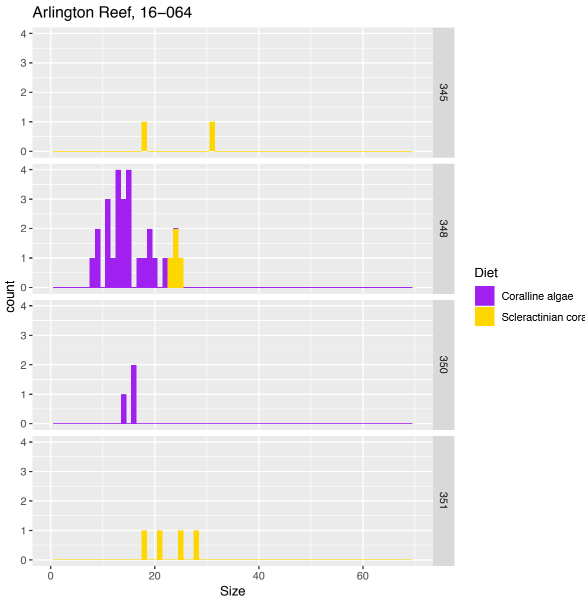

Gibley Reef, 17−057

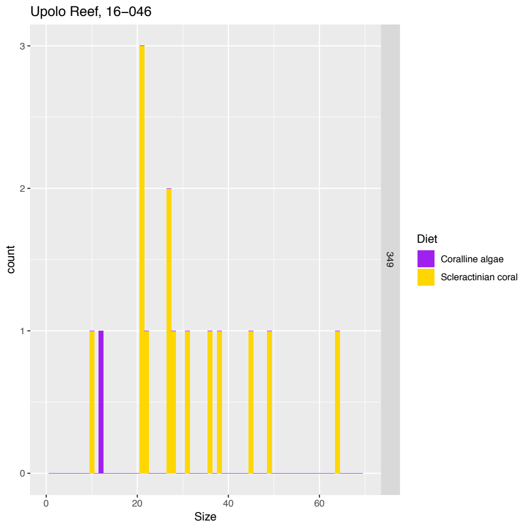

Gibson Reef, 17−017

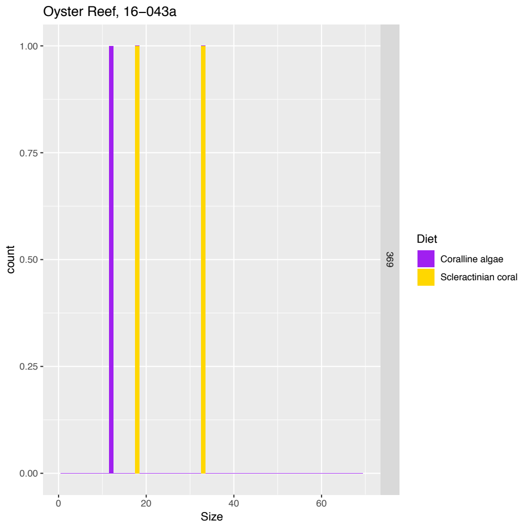

Nathan Reef, 17−035

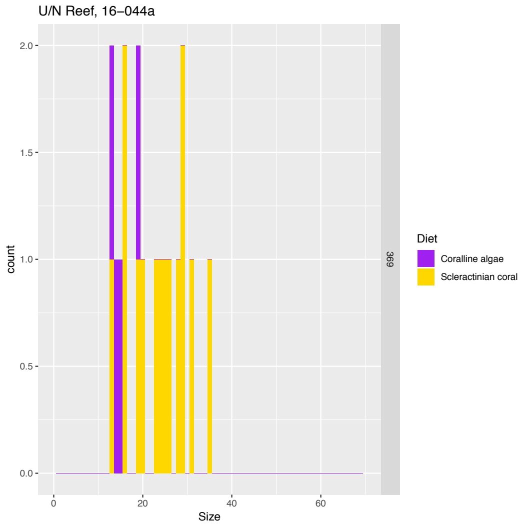

Green Island, 16−049

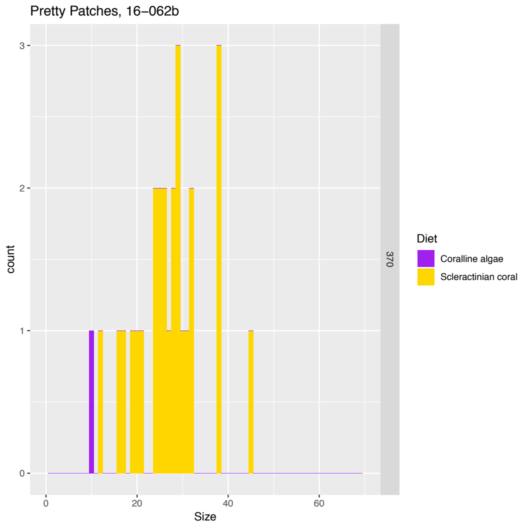

Howie Reef, 17−018a


Arlington Reef, 16−064


Upolo Reef, 16–046
count
3
2
1
0
0
20
40
60
Size
349
Diet
Coralline algae
Scleractinian coral


Oyster Reef, 16–043a
count
1.00
0.75
0.50
0.25
0.00
0
20
40
60
Size
369
Diet
Coralline algae
Scleractinian coral


U/N Reef, 16–044a
count
2.0
1.5
1.0
0.5
0.0
0
20
40
60
Size
369
Diet
Coralline algae
Scleractinian coral


Pretty Patches, 16–062b
count
3
2
1
0
0
20
40
60
Size
370
Diet
Coralline algae
Scleractinian coral

— Chapter 5 —

Incidence and severity of injuries among early-stage juvenile crown-of-thorns starfish on Australia’s Great Barrier Reef

Chapter 5: Incidence and severity of injuries among early-stage juvenile crown-of-thorns starfish on Australia's Great Barrier Reef

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5.1 Abstract

Outbreaks of crown-of-thorns starfish (*Acanthaster* spp.) represent a major threat to coral reef ecosystems throughout the Indo-Pacific, and there is significant interest in whether no-take marine reserves could moderate the frequency or severity of outbreaks. Herein, we investigate whether the incidence and severity of sublethal injuries among early-stage juvenile Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*, 5–45 mm diameter) differs between areas that are open versus closed to fishing, between microhabitats (i.e., dead coral substratum versus live coral) and with body size. The majority (180 out of 200) of juvenile starfish had conspicuous injuries, presumably caused by predation. The incidence of injuries in juvenile starfish was negatively related to body size, but links between body size and severity of injuries was only evident in individuals collected from dead coral microhabitats. Small (3 mm radius) starfish from dead coral microhabitats had injuries to 68.06% of arms, compared to 12.00% of arms in larger (12 mm radius) starfish from the same microhabitat. Juvenile starfish associated with dead coral habitats had a higher incidence (95% versus 87% respectively) and severity (i.e., the percentage of injured arms; 21% versus 6%) of injuries, compared to those associated with live corals. Interestingly, there was no difference in the incidence or severity of injuries between areas that are open versus closed to fishing. Our results show that small juvenile *A.* cf. *solaris* are extremely vulnerable to sublethal, if not lethal, predation, and predation risk declines as they grow and change their microhabitat. Predation during and immediately following settlement is, therefore, likely to have a major influence on population dynamics and ontogenetic changes in microhabitat use for *A.* cf. *solaris*.

5.2 Introduction

Crown-of-thorns starfishes (CoTS, *Acanthaster* spp.) exhibit boom and bust population dynamics (e.g., Antonelli and Kazarinoff, 1984; Bradbury et al., 1985; Pratchett et al., 2014;

Condie et al., 2018). Given their diet of reef-building or scleractinian corals (Chesher, 1969; Branham et al., 1971), CoTS have a major influence on coral reef ecosystems during population booms or outbreaks (e.g., Chesher, 1969; De'ath et al., 2012; Baird et al., 2013). While CoTS outbreaks are increasingly considered to be a natural phenomenon (Pratchett et al., 2018), debate continues about the extent to which human activities, such as fishing (e.g., Endean, 1969; Sweatman, 2008; Vanhatalo et al., 2017) or runoff from catchments with intensive agriculture (Brodie et al., 2005; 2017; Fabricius et al., 2010), contribute to increased frequency or severity of outbreaks (Pratchett et al., 2014). One of the earliest and foremost hypotheses to explain population outbreaks of CoTS is the *predator removal hypothesis* (Endean, 1969), suggesting that declines in the abundance of predators, and concomitant increases in survivorship of CoTS, may cause or exacerbate population outbreaks (e.g., Endean, 1969; Dulvy et al., 2004; Sweatman, 2008; Cowan et al., 2017b; Vanhatalo et al., 2017). Declines in the abundance of predatory organisms is generally ascribed to direct exploitation (Endean, 1969), but might also occur due to trophic cascades (Dulvy et al., 2004) or general degradation of reef ecosystems (Mendonça et al., 2010; Cowan et al., 2017b). For example, Dulvy et al. (2004) showed that when densities of predatory fishes declined along a fishing intensity gradient by 61% at the most heavily fished sites in Fiji, CoTS densities increased by three orders of magnitude. Similarly, CoTS outbreaks were shown to have occurred 3.75 times more often on midshelf reefs of Australia's Great Barrier Reef (GBR) that were open to fishing (albeit restricted) compared to those that were closed to fishing (no-take reefs) (Sweatman, 2008).

The initial formulation of the *predator removal hypothesis* (*sensu* Endean, 1969) was focussed on predators that were capable of killing adult CoTS. Endean (1969) suggested that giant triton (*Charonia tritonis*) were one of the few predators that attack and completely consume healthy adult starfishes, albeit smaller individuals. Excessive harvesting of giant triton therefore, may have allowed for increased densities and larger sizes of CoTS (Endean, 1969), which together would have greatly increased reproductive output (Babcock et al., 2016a). Subsequent studies have revealed many more reef organisms (including fishes and invertebrates) that will feed on healthy adult CoTS (reviewed by Cowan et al. 2017b), though it is still unclear to what extent they actually kill adult starfish. Nonetheless, predation may contribute to reductions in population size (and may moderate outbreaks) in several ways, including i) direct reductions in local densities of larvae, juveniles or adults; ii) reducing individual size and fecundity through partial predation, or iii) disrupting normal feeding or spawning behaviour. Moreover, predation rates on CoTS may be particularly pronounced during early life history stages (including settlement, and early post-settlement stages) and have an important influence on population dynamics (Chapter 1).

Estimates of natural rates of predation on early life history stages of CoTS (and variation therein) are scarce, largely due to difficulties in detecting and following the fate of juvenile starfish *in situ* (Chapter 1). To date, estimates of predation on early-stage juvenile CoTS (i.e., starfish in their first year post-settlement) have been derived from aquarium studies or experimental studies in which captive naïve starfish were deployed in the field (e.g., Sweatman, 1995). Aquarium studies indicate that both gametes and larvae of CoTS may be heavily preyed upon by planktivorous reef fishes, such as damselfishes (Cowan et al., 2016a; 2017a). In turn, settling larvae and newly metamorphosed juvenile CoTS are likely to experience strong predation pressure from benthic invertebrates (Yamaguchi, 1973), and this is supported by the results of an aquarium study which investigated predation on settling CoTS larvae by polychaetes and trapeziid crabs (Cowan et al., 2016b). Field estimates of predation rates on captive-bred naïve early-stage juvenile starfish indicate that predation rates generally decrease with body size but are highly variable (Keesing and Halford, 1992a; Keesing et al., 1996; 2018). For instance, predation rates by epibenthic fauna were highest for small 1-month old starfish (mean diameter = 1.1 mm) at 5.05% d^{-1}, and decreased to 0.85% d^{-1} for larger 4-month old starfish (mean diameter = 2.7 mm) (Keesing and Halford, 1992a). Notably, predation rates on 1-month old starfish varied markedly among small habitat units, indicating that the composition and/or abundance of cryptofaunal predators (e.g., polychaetes and crustaceans) varied substantially within these units (Keesing et al., 1996).

Although the vulnerability of juvenile CoTS to different types of predators is expected to change as they grow (Keesing, 1995), very little is known about how body size and ontogenetic shifts in microhabitat (i.e., from coralline algae encrusted pieces of dead coral to live scleractinian coral) affect predation on wild early-stage juvenile CoTS. Despite apparent evolutionary adaptations in behaviour (i.e., cryptic and nocturnal) and coloration to evade diurnal visual predators such as fishes (Yamaguchi, 1973; Zann et al., 1987; Stump, 1996), observations of predation on small juvenile CoTS, especially on early-stage juvenile starfish, have been limited (Endean, 1969; Pearson and Endean, 1969; Zann et al., 1987; Sweatman, 1995). Aquarium studies indicate, however, that small juvenile CoTS (i.e., diameter <70 mm) are vulnerable to predation, mostly by crustaceans (e.g., hermit crabs and spiny lobster – Zann et al., 1987; *Hymenocera* shrimp – Keesing et al., 2018).

The objective of this study was to quantify the incidence and severity of injuries in early-stage juvenile CoTS, and assess whether rates of injury (and thereby predation rates) vary with zoning status (i.e., no-take marine reserves versus restricted fishing zones), microhabitat (i.e., dead coral substratum versus live scleractinian coral) and/or body size. Although sublethal predation was not witnessed *per se*, it is generally assumed that sublethal injuries in starfish result from predatory attacks or defensive interactions (Lawrence and Vasquez, 1996). High incidence of sublethal injuries is therefore thought to reflect intense predation on starfish (McCallum et al., 1989; Bos et al., 2011; Rivera-Posada et al., 2014), such that high rates of partial injury may be a proxy for high levels of overall mortality from predation. While the frequency and extent of injuries has been used previously as proxy for predation pressure among subadult and adult CoTS (Rivera-Posada et al., 2014; Messmer et al., 2017), no such investigation has been conducted for early-stage juvenile CoTS.

5.3 Materials and methods

Sampling and identification of injured arms

A total of 200 juvenile starfish (5–45 mm diameter) were sampled from an extensive collection of early-stage juvenile CoTS from reefs in the northern GBR during outbreaking conditions in 2015 (see Chapter 3, 4). All starfish were collected on SCUBA (max depth = 15 m), with searches focussing in reef slope areas where there was unconsolidated coral rubble, interspersed with patches of consolidated carbonate and live corals. All starfish were measured (diameter to the nearest mm) and preserved in 95% ethanol. During collection, we explicitly distinguished between individuals recovered from dead coral substratum (mostly coral rubble) encrusted with coralline algae, which were presumed to be feeding on coralline algae, versus those living within live (mostly branching) scleractinian coral, presumed to be feeding on coral (Chapter 3, 4).

To test for variation in the incidence and severity of injuries, we sampled 100 early-stage juvenile starfish from each of the two microhabitats (i.e., pieces of dead coral substratum versus live coral colonies). All starfish were collected between 11 October and 15 December 2015 from 19 reefs located between 15.51 and 17.67° S (**Table 5.1**). Of the 200 early-stage juvenile starfish, 76 originated from marine national park zones and 124 from restricted fishing zones (habitat protection and conservation park zones). Starfish were photographed (Olympus OM-D E-M5) for image analysis in ImageJ1. Sampling was intentionally biased towards the largest individuals to avoid confusion between newly forming versus regenerating arms. Because several starfish were severely injured and regeneration of lost body arms is prioritised over somatic growth in starfish (Lawrence and Lane, 1982; Diaz-Guisado et al., 2006), maximum radius was chosen, over diameter, as a more robust indicator for body size at the time of injury. For each starfish, the number of arms was counted and its maximum radius was measured from the centre of the aboral disc area to the tip of the longest arm (**Figure 5.1b**). Injured arms were defined as those that were >10% shorter than the maximum radius (**Figure 5.1b**), following Bos et al.'s (2011) criterion for the identification of injured arms, which conformed most with our visual identification of injuries.

Table 5. 1 List of reefs (from north to south) from which juvenile *Acanthaster* cf. *solaris* originated, together with descriptive statistics. Key: MNPZ = Marine National Park Zone, HPZ = Habitat Protection Zone, CPZ = Conservation Park Zone.

Reef Name, Reef ID	**GBR Marine Park Zoning**	**Sample Size**	**Percentage of Injured Starfish**	**Proportion of Injured Arms**		
				Lower Quartile	**Median**	**Upper Quartile**
U/N Reef, 15-072	MNPZ	3	100.00	0.27	0.31	0.39
Rosser Reef, 15-081	HPZ	3	100.00	0.29	0.31	0.49
Escape Reef, 15-094	HPZ	2	100.00	0.13	0.13	0.13
Morning Reef, 15-098	HPZ	11	90.91	0.19	0.38	0.63
U/N Reef, 16-013a	MNPZ	4	100.00	0.18	0.19	0.22
Agincourt Reefs (No 5), 15-099d	MNPZ	5	100.00	0.18	0.31	0.38
Hastings Reef, 16-057	MNPZ	14	78.57	0.06	0.23	0.36
Pretty Patches, 16-062b	HPZ	22	90.91	0.07	0.13	0.18
Oyster Reef, 16-043a	CPZ	3	100.00	0.26	0.26	0.43
U/N Reef, 16-044a	CPZ	14	92.86	0.23	0.29	0.47
Upolo Reef, 16-046	MNPZ	12	91.67	0.12	0.17	0.28
Arlington Reef, 16-064	HPZ	36	91.67	0.13	0.27	0.43
Green Island, 16-049	MNPZ	30	90.00	0.13	0.24	0.31
Gibson Reef, 17-017	HPZ	11	90.91	0.13	0.29	0.45
Howie Reef, 17-018a	HPZ	2	100.00	0.15	0.16	0.17
Nathan Reef, 17-035	MNPZ	8	87.50	0.12	0.19	0.44
Gilbey Reef, 17-057	HPZ	12	91.67	0.13	0.23	0.31
Hall-Thompson Reef, 17-037	HPZ	1	100.00	0.86	0.86	0.86
Potter Reef (No 1), 17-059a	HPZ	7	85.71	0.10	0.31	0.35

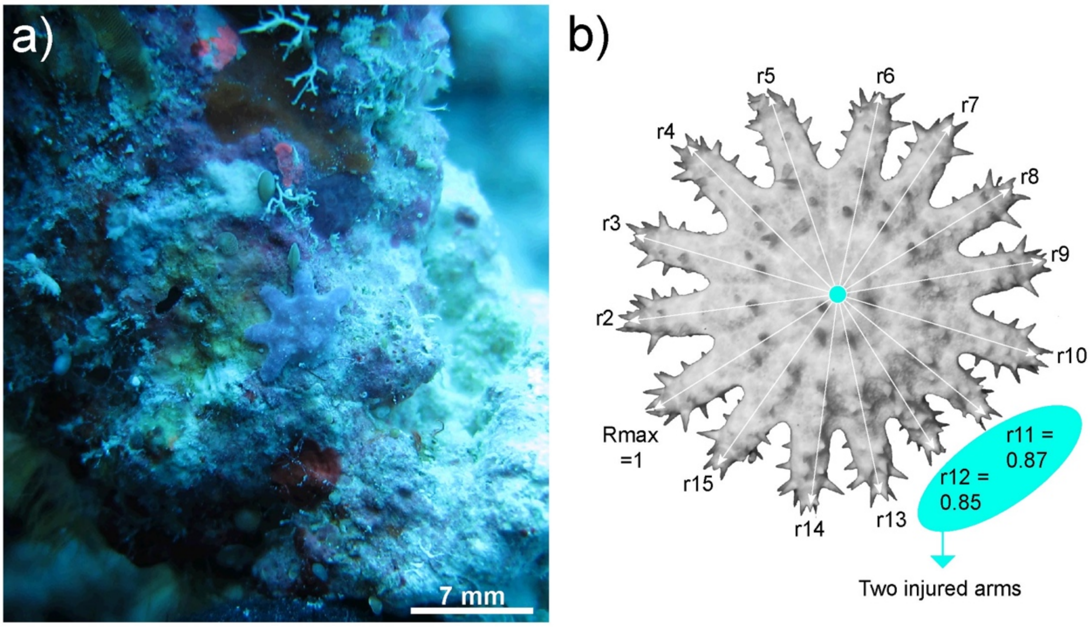

Figure 5. 1 a) Example of juvenile *Acanthaster* cf. *solaris* found *in situ* associated with dead coral, b) definition of injured arms; an arm was defined as injured if the arm's length was > 10% shorter than the maximum arm radius.

Statistical analysis

Incidence of sublethal injuries

The incidence of sublethal injuries was modelled as the presence/absence of injuries against the maximum radius of individuals to test whether body size affected the probability of injury incidence in juvenile starfish. Modelling was conducted using a generalised linear mixed effects model (glmmPQL function from the MASS package – Venables & Ripley, 2002) with a binomial error distribution and a logit link function, conducted in R (R Core Team, 2018). Reef was included as random effect to account for variations in the incidence ~ size relationship among reefs, while explicitly testing for differences between no-take marine reserves and restricted fishing zones (habitat protection and conservation park zones). Goodness of fit was evaluated by comparing the sum of the squared Pearson's residuals to chi squared (lack of fit if $p<0.05$). The significance of fixed effects was based on p values (significant if $p<0.05$), as provided by the summary function.

To test for variation in the incidence of different levels of sublethal injuries among juvenile starfish from different microhabitats and marine park zones, injuries were divided into five categories of severity depending on the percentage of injured arms: 0% (no arms injured), >0–

25%, >25–50%, >50–75% and >75–100%. Frequencies of juvenile starfish in different injury severity categories were then compared between different microhabitats and marine park zones separately, using Pearson's Chi-squared test of independence. As sample sizes between no-take (n = 76) and restricted fishing zones (n = 124) differed, frequency data is displayed as percentages for ease of interpretation.

Severity of sublethal injuries

The proportion of injured arms (as proxy for injury severity) was modelled against the maximum radius to test whether injury severity was related to body size in juvenile starfish. Modelling was again conducted in R, using generalised linear mixed effects models (glmmPQL function) with binomial error distribution and logit link function. In addition, zoning (i.e., no-take zone versus restricted fishing zone) was added in the model as an additive fixed effect, to test for an effect of zoning on the injury severity ~ size relationship. Because the dietary shift of juvenile starfish from coralline algae to scleractinian coral is size related (size threshold ~ 8–10 mm – Yamaguchi, 1974) and is accompanied by a shift in microhabitat (i.e., dead coral substratum versus live scleractinian coral), microhabitat and size are inevitably correlated. As a result, injury severity was modelled separately for juvenile starfish from different microhabitats. All models included reef (n = 19) as random effect and goodness of fit was again evaluated by comparing the sum of the squared Pearson's residuals to chi squared (lack of fit if p value <0.05), and by inspecting diagnostic plots of residuals (see Logan, 2011). The significance of fixed effects was based on p values (significant if p<0.05), as provided by the summary function.

5.4 Results

Incidence of sublethal injuries

The proportion of juvenile CoTS with injuries in samples from the 19 reefs varied between 78.57% and 100% (median = 91.67%, IQR = 90.91–100%) (Table 1). The incidence of injury was negatively related to body size (p<0.05) and most juvenile starfish showed signs of sublethal injuries (i.e., 91%); overall, only 9% were intact (**Figure 5.2**). The incidence of injuries was slightly higher in starfish that were found among pieces of dead coral (95%), than in those associated with live coral (87%). The frequency of starfish in different injury severity categories differed significantly between microhabitats; X^2 (df = 4, n = 200) = 15.358, p = 0.004. Notably, 21% of starfish found in dead coral showed signs of severe sublethal injuries (i.e., >50% arms injured), compared to 6% of starfish found in live coral (**Figure 5.2**). By contrast, a higher proportion of starfish associated with live coral (63%) showed no or minor signs of injury (i.e., 0–25% of arms injured), compared to 44% of individuals that were found associated with dead coral. We found no indication that the frequency of juvenile starfish in different injury severity categories differed between no-take and restricted fishing zones (**Figure 5.3**); X^2 (df = 4, n = 200) = 2.366, p = 0.669.

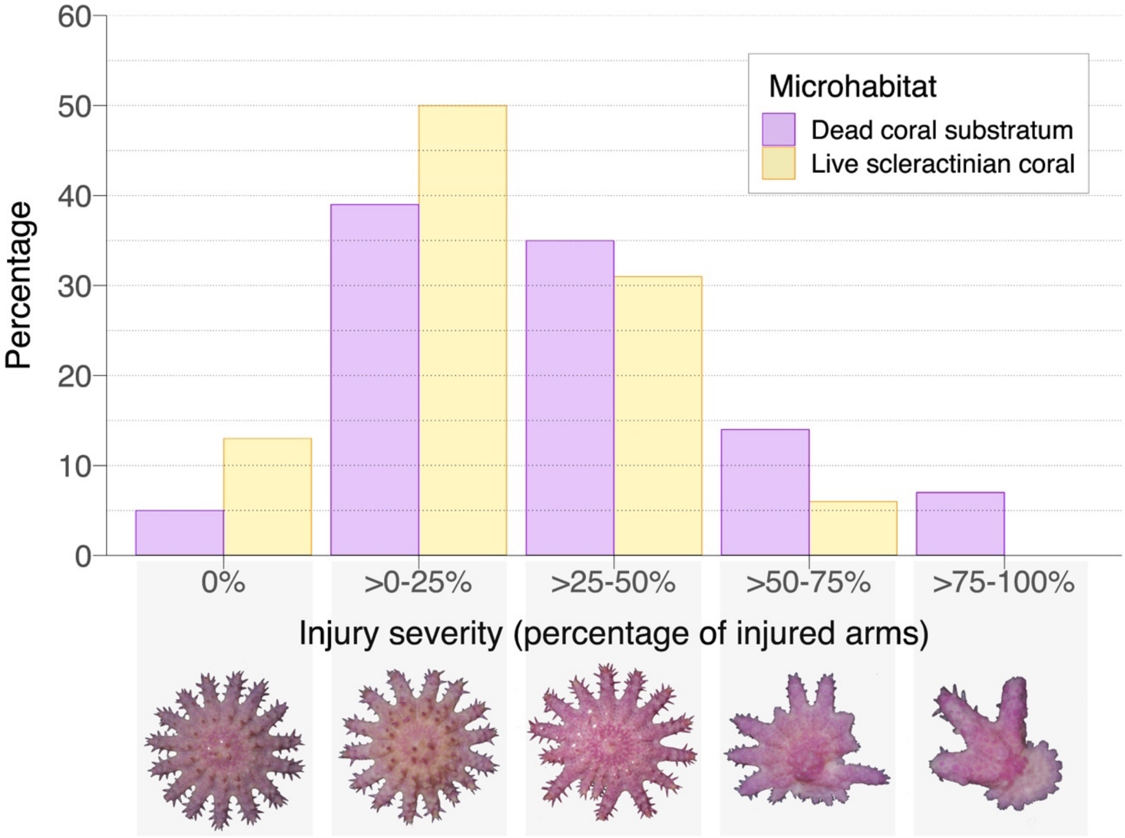

Figure 5. 2 Percentage of juvenile *A*. cf. *solaris*, in different injury severity categories, by microhabitat (dead coral substratum, n = 100; live scleractinian coral, n = 100).

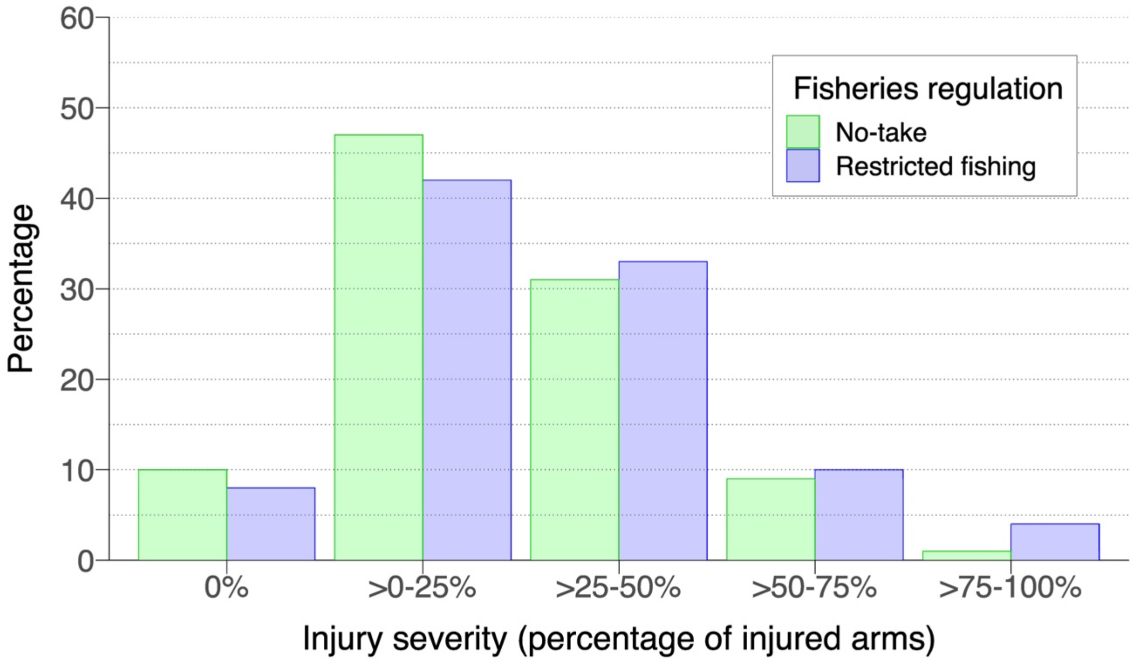

Figure 5. 3 Percentage of juvenile *A.* cf. *solaris*, in different injury severity categories, by marine park zone (no-take zone, n = 76; restricted fishing zone, n = 124).

Severity of sublethal injuries

The median percentage of injured arms in juvenile starfish varied among reefs, ranging from 12.5% and 85.71% (median = 26.32%, IQR = 19.06–30.77%, Table 1). Injury severity was significantly related to size in juvenile starfish, especially for starfish found in dead coral (**Table 5.2**, **Figure 5.4**). For starfish from dead coral microhabitats, the model estimates that 68.06% (CI [54.01–79.45%]) of arms were injured in small starfish (3 mm radius), compared to just 12.00% (CI [7.14–19.47%]) in larger starfish (12 mm radius). While the proportion of injured arms in starfish found in live coral tended to decline with increasing body size, this trend was not significant (**Table 5.2**, **Figure 5.4**). Marine park zoning did not significantly affect the proportion of injured arms in juvenile starfish.

Table 5. 2 Results of generalised linear mixed effects models (with logit link function) testing for the effect of size and zoning on injury severity in juvenile *A*. cf. *solaris* from different microhabitats (i.e., pieces of dead coral versus live coral colonies). Reef is included as random effect in all models.

Sample Population	Response Variable	Parameter	Estimate	SE	p-value
Juvenile starfish associated with dead coral substratum (n = 100)	Proportion of injured arms (proxy for injury severity)	Intercept	1.6729	0.4829	
		Maximum radius	-0.3055	0.0622	**0.0000**
		Intercept	1.5868	0.5135	
		Maximum radius	-0.3043	0.0625	**0.0000**
		Zoning (restricted fishing)	0.1091	0.2169	0.6217
Juvenile starfish associated with live scleractinian coral (n = 100)	Proportion of injured arms (proxy for injury severity)	Intercept	-0.6887	0.4234	
		Maximum radius	-0.0489	0.0335	0.1474
		Intercept	-0.7641	0.4619	
		Maximum radius	-0.0486	0.0337	0.1531
		Zoning (restricted fishing)	0.1245	0.2834	0.6758

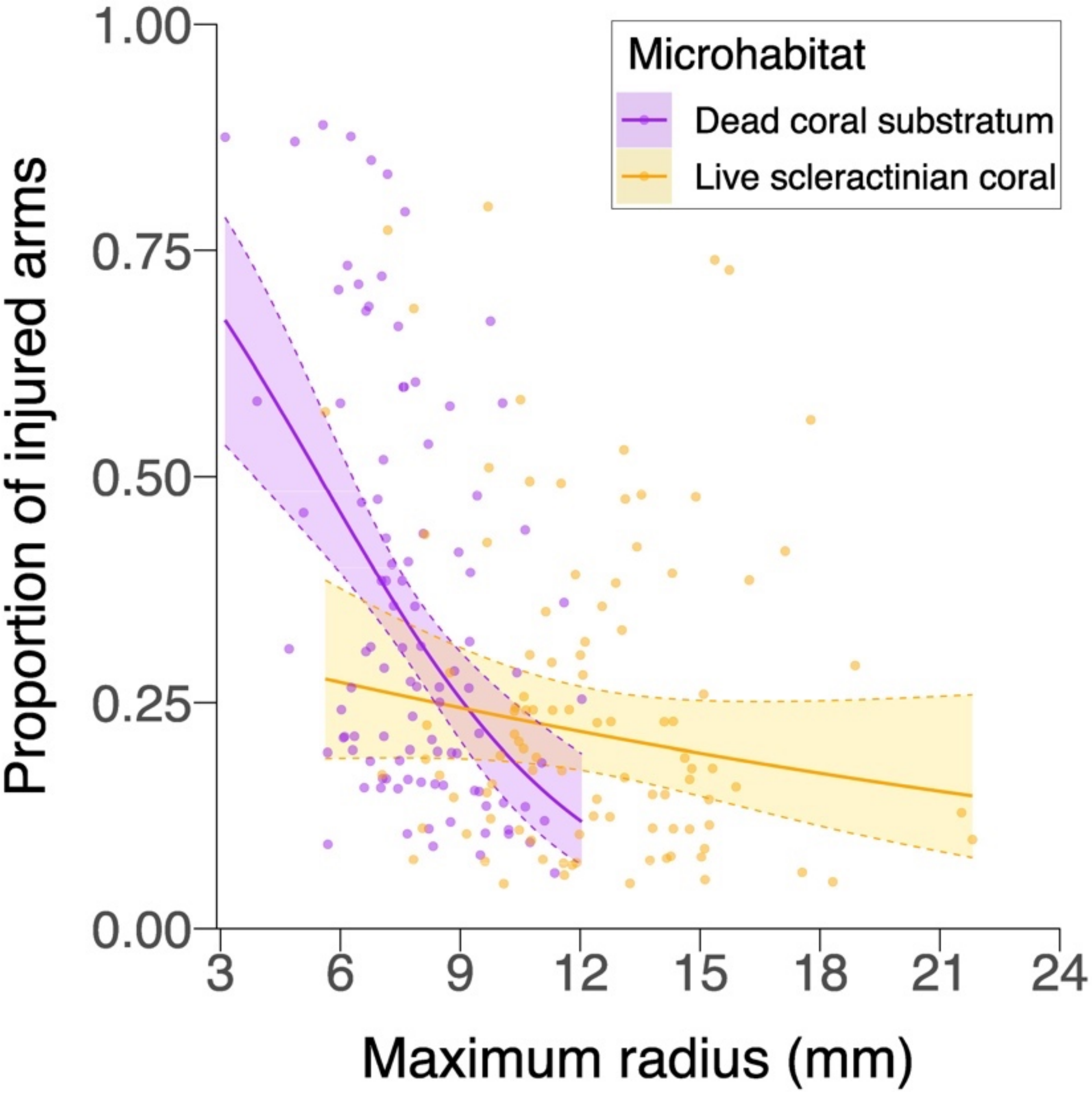

Figure 5. 4 The relationship between modelled proportion of injured arms (as proxy for injury severity) and maximum radius (mm) of juvenile *A*. cf. *solaris* from live coral and dead coral microhabitats. Dots represent partial residuals modelled at the reef level derived from the models.

5.5 Discussion

This study shows that the incidence and severity of sublethal injuries in early-stage juvenile starfish (3–22 mm radius) decreases with increasing body size, and was largely driven by changes in the extent of injuries in starfish (3–12 mm radius) from dead coral microhabitats. The incidence and severity of injuries was higher for starfish associated with dead coral than for larger starfish that had transitioned to feeding on, and living among, live corals. Although predatory attacks were not witnessed *per se*, differences in the incidence and severity of injuries among starfish from the two microhabitats may be explained by differences in the composition and abundance of potential predators, including cryptofaunal invertebrates (Enochs and Manzello, 2012; Takada et al. ,2012) and fish assemblages (e.g., Messmer et al., 2011; Komyakova et al., 2018). However, as body size and microhabitat are inevitably confounded, the reduced incidence and severity of injuries among juveniles from the live coral habitat may also, at least in part, be explained by their inherently larger size and faster growth rates (Yamaguchi, 1974). Interpretation of our results is further obfuscated by the fact that sublethal injuries in starfish associated with live coral may have been carried across from the dead coral microhabitat or could have resulted from defensive interactions with coral polyps (Yamaguchi, 1974) or symbionts (e.g., trapeziid crabs – Pratchett et al., 2001; Rouzé et al., 2014) during the transition to live coral. Nonetheless, coral rubble dominated dead coral habitats are extremely diverse environments that support high numbers of predatory cryptofaunal invertebrates and fishes (Takada et al., 2012; Enochs and Manzello, 2012). Species richness of motile cryptofauna is indeed estimated to be greater in dead coral habitats than in live coral habitats (Enochs and Manzello, 2012). Our results show that early-stage juvenile CoTS living on live corals have lower incidence of injuries compared to those on dead corals, suggesting that there may be increased densities of predators and higher rates of predation in rubble habitats.

These results suggest that as for other marine invertebrates and fishes, population bottlenecks (i.e., major reductions in population size) are likely to occur during settlement and the early post-settlement phase of the CoTS life cycle, when individuals are smallest and most vulnerable (e.g., Gosselin and Qian, 1997; Almany and Webster, 2006). Indeed, the incidence of injuries in early-stage juvenile starfish (i.e., 91%) from this study was much higher than the incidence of injuries previously reported from subadult and adult CoTS populations from the GBR (i.e., 33–51% – Pearson and Endean, 1969; McCallum et al., 1989; Stump, 1996; Messmer et al., 2017). This suggests that the predation pressure during and immediately after settlement has a marked influence on population dynamics of crown-of-thorns starfish (see also Keesing and Halford 1992a; Cowan et al. 2017b; Chapter 1; Keesing et al., 2018).

While individuals that experience sublethal injuries may survive and ultimately reproduce, the regeneration of lost and/or damaged body components incurs an energetic cost. Depending on the life history stage and severity of the injuries, sublethal injuries can constrain the capacity to forage (Ramsay et al., 2001) and limit energy available for growth and reproduction

(Lawrence and Lane, 1982; Lawrence and Vasquez ,1996; Bingham et al., 2000; Diaz-Guisado et al., 2006; Barrios et al., 2008). For instance, feeding and growth rates were demonstrated to be substantially reduced in severely injured (i.e., 6 arms lost, ~ 33% of total arms) juveniles (~ 20 mm radius, 17–27 arms) of the South American sun-star, *Heliaster helianthus,* while moderately injured (i.e., 3 arms lost, ~ 17%) starfish showed similar feeding and growth rates to intact ones (Barrios et al., 2008). Recovery was slow in severely injured starfish and even after five months, feeding rates were ~ 30% lower than those of intact starfish, resulting in comparatively low growth rates (Barrios et al., 2008). By comparison, recovery rates of injured arms in juvenile CoTS are essentially unknown and limited to a sole record of a 90 mm juvenile/subadult CoTS from the GBR, which was able to regenerate an injured arm (i.e., 4 times shorter than its average arm length) within 3 months, while increasing its overall diameter by 36 mm (Pearson and Endean, 1969).

Most early-stage juvenile starfish sampled from the dead coral microhabitat (i.e., 74%) showed minor to moderate signs of sublethal injuries (i.e., >0–50% of arms damaged), and a substantial proportion of starfish (i.e., 21%) were severely injured, with some even missing parts of their central disc (**Figure 5.2**). Such severely injured starfish are not just extremely likely to have a reduced capacity to escape predators, but also to have a reduced capacity to forage that would likely negatively affect growth and ultimately size related reproductive output and chances of survival. Severe sublethal injuries could even substantially delay the timing of the ontogenetic dietary shift from coralline algae to live coral, especially if injuries result in body size being reduced below the size threshold of the ontogenetic dietary shift (i.e.; 8–10 mm in diameter – Yamaguchi 1974). In turn, this may have important flow-on effects on population dynamics, considering that marked delays in the ontogenetic dietary shift are likely to negatively affect individuals' lifetime fitness and ultimately constrain population growth (Chapter 4).

We found no evidence that the incidence and/or severity of sublethal injuries in early-stage juvenile starfish differed significantly between areas that were open versus closed to fishing (**Table 5.2**). This finding is consistent with the results of a previous study on sublethal injuries in subadult and adult starfish populations from the GBR (n = 3,846), which detected no significant difference in the incidence or severity of sublethal injures among starfish from different marine park zones (Messmer et al., 2017). While coral trout (*Plectropomus* spp.), the primary target species on fished reefs of the GBR, has consistently been reported to be more abundant in no-take marine reserves (Williamson et al., 2004; Russ et al., 2008; Emslie et al., 2015), this piscivorous fish is unlikely to prey on early-stage juvenile CoTS. Rather, it has been suggested that declines in densities of coral trout result in increased densities of benthic carnivorous fishes, such as wrasses, and subsequent flow-on reductions in densities of coral rubble inhabiting invertebrates that prey on early-stage juvenile CoTS, thereby effectively releasing predation pressure on early-stage juveniles (Sweatman, 2008). Effect sizes of no-take marine reserves on densities of benthic foragers are, however, small and inconsistent between inshore and offshore reefs of the GBR (Emslie et al., 2015), and evidence in support of mesopredator release or prey release is weak (Rizzari et al., 2015; Casey et al., 2017), suggesting limited top-down control on reef fish and benthic assemblages on the GBR (Emslie et al., 2015; Rizzari et al., 2015; Casey et al., 2017). Nonetheless, sublethal injuries may not be directly correlated with mortality and potential differences in survivorship of early-stage juvenile and older starfish among marine park zones may therefore simply not be detectable with this approach.

Our study results have been difficult to interpret, mostly owing to the fact that predatory attacks were not actually observed within respective microhabitats. Both body size at the time of injury and the severity of injuries in early-stage juvenile starfish may be underestimated, as regeneration and regrowth could have occurred since the predatory attack. Further, some injuries in larger coral-feeding juvenile starfish could be a legacy of those received as smaller algal-feeding juvenile starfish from the dead coral microhabitat, thereby over-estimating the incidence and severity of injuries in larger coral-feeding juvenile starfish. This would then further reinforce that predation pressure on the smallest stages of algal-feeding juvenile CoTS is very high. Determining whether or not the observed higher frequency of CoTS outbreaks on fished midshelf reefs of the GBR is indeed related to increased survivorship of early-stage juvenile starfish that live among pieces of dead coral (Sweatman, 2008), will therefore necessitate ongoing *in situ* measuring of settlement and post-settlement survivorship of early-stage juvenile starfish cohorts among reefs that are open and closed to fishing, across different types of habitats and starfish densities, and during different stages of the outbreak cycle. Supporting information on the identity and relative abundance of predators among habitats and between differently zoned reefs is also required. Difficulties associated with detecting early-stage juvenile starfish have greatly hindered previous attempts to monitor CoTS field populations on the GBR (Doherty and Davidson, 1988; Johnson et al., 1992). However, the proven ability to detect herbivorous early-stage starfish (Zann et al., 1987, 1990; Habe et al., 1989; Chapter 2, 3, 4) provides an opportunity to fill critical knowledge gaps and improve understanding and management of crown-of-thorns starfish outbreaks.

— Chapter 6 —

General discussion

Chapter 6: General discussion

The research presented in this thesis provides new and largely unprecedented field-based estimates of demographic rates (and variation therein) for early-stage juvenile crown-of-thorns starfish (CoTS; *Acanthaster* cf. *solaris*). More specifically, I quantified — for the first time on Australia's Great Barrier Reef (GBR) — rates of recruitment (Chapter 2) and growth (Chapter 3, 4) for early-stage juvenile CoTS. The majority of this research was conducted *in situ*, demonstrating the capacity to not only detect, but effectively sample recently-settled and early-stage juvenile CoTS in shallow (<20 m) water habitats on the GBR. Previous attempts to detect and study early-stage herbivorous juvenile CoTS on the GBR (Johnson et al., 1992; Doherty and Davidson, 1988), had very limited success, which greatly constrained understanding of the early life history and population dynamics of CoTS in this reef system. The apparent paucity of recently-settled and early-stage juvenile CoTS in shallow reef environments led to the suggestion that *A*. cf. *solaris* settle mainly in deep water environments (at 30–60 m depth), after which individual starfish move up exposed reef fronts to recruit to adult populations in shallow coral-rich habitats; *sensu* the deep-water recruitment hypothesis (Johnson et al., 1991; Johnson, 1992). The deep-water recruitment hypothesis was further supported by studies of settlement that were conducted in field-deployed flow-through containers, whereby the coralline algae (*Lithothamnium pseudosorum*) that was most effective in inducing settlement of *A.* cf. *solaris*, was believed to be mainly restricted to deeper habitats (Johnson et al., 1991).

Contrary to the suggestions of the deep-water recruitment hypothesis, research presented in this thesis clearly shows that recently-settled and early-stage juvenile *A.* cf. *solaris* (2–70 mm diameter) regularly occur in shallow reef environments of the GBR, where there is a high availability of coral rubble (e.g., spur and groove systems, Chapter 2), and are therefore likely to settle in these shallow habitats. However, as field surveys did not extend beyond 18 m water depth, I cannot discount the possibility that substantial settlement also occurs in deeper waters. In all, 3,160 small (≤20 mm diameter) herbivorous juvenile CoTS were sampled through the course of this research, of which virtually all (99.8%) were found in <15 m water depth. Aside from detecting these very small early-stage juvenile starfish, I measured the size (diameter) of 3,672 individuals (3,176 algal-, and 496 coral-feeding juveniles) and recorded the substrate on which they were found and likely feeding. In Chapter 2, I recorded the water depth at which 134 early-stage herbivorous juvenile starfish (2–14 mm diameter) were detected: 11.9%

occurred at ≤5 m, 46.3% at 5–10 m, 37.3% at 10–15 m and 4.5% at 15–18 m. The few coral-feeding juvenile starfish (n = 6) that were detected during this study, were at least twice the diameter (28–65 mm diameter) of algal-feeding individuals and all occurred in <10 m (Chapter 2), suggesting differences in depth-related habitat associations of small algal- and coral-feeding juvenile stages. Such data on population structure and depth-related habitat associations of juvenile CoTS are extremely limited, but critical for modelling studies that aim to i) better understand/predict CoTS population dynamics and the incidence and severity of outbreaks, and/or ii) test which type of management action would be most effective in reducing the severity and/or incidence of outbreaks.

Although a starfish's size is considered to be a poor indicator for its age (e.g., Mead, 1990), field research suggests that cohorts of young, early-stage juvenile starfish can be distinguished from older ones (i.e., >1 year old) based on size–frequency distributions — if sampling is conducted early following spawning (see for *Asterias rubens* – Barker and Nichols, 1983; Nichols and Barker, 1984; Guillou et al., 2012). The results from Chapter 2, 3 and 4 also suggest that annual cohorts of CoTS can be identified based on narrow unimodal size–frequency distributions of early-stage herbivorous juvenile CoTS; even if estimated ages of individuals may be imprecise (Chapter 2, 3, 4). However, algal-feeding juvenile CoTS can remain for years in a "waiting stage" (*sensu* Nauen, 1978), during which growth plateaus on an algal diet (Lucas, 1984; Keesing and Halford, 1992b; Deaker et al., 2020a). Such stunted algal-feeding juvenile CoTS have indeed survived for >6 years in aquaria (Deaker et al., 2020a). Size–frequency distributions of herbivorous juvenile starfish could therefore, at least theoretically, comprise multiple year-class cohorts, particularly if these settled to reefs during conditions of low coral prey availability (Deaker et al., 2020 a; b; Chapter 4).

The existence of the algal-feeding juvenile "waiting stage" further led to the suggestion that successive cohorts of juveniles may accumulate within the reef infrastructure for 4–5 years (following eutrophication events), after which they would then emerge in outbreak numbers (Deaker et al. 2020a). However, such a year-long accumulation of herbivorous juvenile CoTS seems unlikely, given the inherently short generation time of CoTS (1.5–2 years), the high incidence of injury and mortality of small juvenile CoTS (Chapters 4, 5), and the fitness advantages associated with early shifts to corallivory (Chapter 4, 5). Rather, algal-feeding juvenile CoTS are likely to search their environment for suitable coral prey, as soon as they reach the ontogenetic stage at which they are presumed to be capable of consuming live coral

— instead of retreating into the consolidated reef matrix for extended periods. As such, there would be a continuous flow of early-stage herbivorous CoTS into the population of coral-feeding juvenile CoTS (Chapter 4), whereby early post-settlement survivorship of algal-feeding individuals would be expected to markedly decline with increasing exposure to predators and limited availability of suitable coral prey (e.g., Keesing et al., 1996; Keesing et al., 2018) — contrary to survivorship in aquaria, in the absence of predators. Indeed, proportionally few algal-feeding juvenile starfish were detected 11–13 months following spawning during extensive field sampling in 2015, and most (95 out of 100) of these starfish showed signs of injury, whereby 21% were severely injured (>50% arms injured) (Chapter 4, 5). This suggests that most early-stage herbivorous juvenile CoTS do not survive, shift their diet or move out of our range of detectability within the first year following their detection (Chapter 4). Unimodal size–frequency distributions of visually-detectable herbivorous juveniles (see Figure 2.2, Supplementary material Figure 4.1) are therefore, likely to represent mostly — if not completely — a single year-class cohort. To test whether these size–frequency distributions can be used to quantify annual recruitment strength, future research needs to locate high-density aggregations of early-stage herbivorous juvenile CoTS and follow their movement, growth and survivorship *in situ* across different reef habitats.

The precise age of visually-detectable herbivorous juvenile CoTS may be largely irrelevant to demographic modelling studies and management actions, as major life history traits such as the timing of the shift in diet, and resulting fecundity and survival, are all fundamentally size-related (e.g., Babcock et al., 2016a; Keesing et al., 2018; Chapter 4). Essentially, to predict where and when outbreaks are likely to develop within a reef (to allow for early detection and timely management actions), we need to know how many algal-feeding juvenile CoTS recruited to different parts of the reef, irrespective of their age, and what proportion of these individuals will shift their diet from coralline algae to coral, and thereafter, survive until maturity. It would make sense therefore, that demographic models that underpin management actions would be size-structured (Ebenman and Persson, 1988), or ontogenetic stage-structured (e.g., herbivorous/corallivorous early-stage juveniles, and adult stages) to account for age and size effects on growth and survival, rather than being age-structured (e.g., Morello et al., 2014).

The results from Chapter 2 showed that visually-detectable early-stage juvenile CoTS occurred over a wide range of shallow (<20 m) habitats, but were most abundant in semi-exposed south-western and/or north-eastern marginal areas of mid-shelf reefs, at intermediate depths (8–14

m) where there is high abundance of dead coral substratum (i.e., coral rubble and intact dead coral) and corresponding low cover of live corals. While Chapter 2 brings novel insights into the microhabitat and habitat of these early-stage juvenile CoTS, it does not identify the mechanisms that are most influential in dictating the spatial variability in their relative abundance. It is also possible that variability in their detectability obscures spatial patterns in their abundance. Destructive sampling (see Doherty and Davidson, 1988; Yokochi and Ogura, 1984) to sample cryptic habitats (e.g., within the consolidated reef matrix or structurally complex habitats) may therefore, ultimately be required to establish whether the observed spatial patterns reported in Chapter 2 are reflective of overall patterns of recruitment or relate to differences in the detectability of early-stage juveniles.

Importantly, the long-standing question how reproductive output/larval supply, settlement preferences/success and/or post-settlement mortality shape the abundance of coral-feeding juvenile and adult starfish populations *in situ* (Chapter 1) remains unresolved. To address this question will require a holistic sampling across all life stages to explicitly relate local patterns of larval supply to rates of settlement, recruitment and ultimately adult abundance across a range of different reef habitats (Pratchett et al., 2017a), along with field and laboratory experimental studies to better establish causes of mortality at different life stages. For example, established technologies could be used to relate vertical and horizontal spatial patterns in the relative abundance of early-stage juvenile starfish (Chapter 2) to patterns in larval supply (plankton tows – Uthicke et al., 2015; Doyle et al., 2017), settlement (settlement collectors – Keesing et al., 1993; Uthicke et al., 2019) and the availability of post-settlement prey (e.g., coral recruits – Nakamura et al., 2014). These studies would, however, also need to be supported with field and laboratory experimental studies to quantify rates of settlement and early post-settlement survivorship across different natural habitats (or mesocosms), as well as environmental and density gradients. This could greatly clarify which mechanisms (e.g., settlement cues and preferences – Johnson et al., 1991; predation – Sweatman, 1995; Keesing and Halford, 1992a; availability of post-settlement prey and microhabitat) are most influential in dictating spatial patterns in the abundance of early-stage juvenile starfish from dead and live coral microhabitats.

Although growth of *A*. cf. *solaris* had previously been identified as indeterminate (Lucas, 1984), the importance of the variability in the timing of ontogenetic shifts in diet to populations dynamics had been largely overlooked (Yamaguchi, 1973; 1974; Lucas, 1984; Zann et al., 1987; 1990; Habe et al., 1989). In Chapter 4, I provided field-based empirical evidence for a strong link between coral prey availability and individual fitness of juvenile CoTS. I suggested that juvenile starfish that shift their diet from coralline algae to coral early, reach a larger body size — because early ontogenetic shifts in diet lead to an extended rapid growth period — with important consequences on lifetime fitness and population dynamics. Variability in the timing of ontogenetic shifts in diet could therefore contribute to, if not drive, the hypothesised de-phased coupled oscillations between CoTS and its coral prey (Antonelli and Kazarinoff, 1984; Bradbury et al., 1985). My results also support the existence of a size threshold (8 mm – Yamaguchi, 1974), below which juvenile CoTS do not seem to shift their diet from coralline algae to live coral. I then discussed pre- and post-settlement processes that could affect the time at which this critical size threshold may be reached, as well as the emerging controversy in relation to their *in situ* survivorship (Deaker et al., 2020 a; b). What proportion of early-stage juvenile CoTS survives to the next settlement event is a key question for future research, not only to inform demographic models, but also to establish whether measuring annual changes in their abundance can be used as a measure for annual recruitment strength.

The research in this thesis adds greatly to increasing evidence that human-induced environmental changes are not a prerequisite for the initiation of CoTS outbreaks (see Pratchett et al., 2014). Though it is important to acknowledge that anthropogenic activities may, nonetheless, enhance the severity and incidence of outbreaks. For example, as discussed in Chapter 5, it has been suggested that changes to trophic cascades on fished reefs could enhance survivorship of algal-feeding juvenile CoTS within dead coral habitats, resulting in an increased probability of outbreaks on these reefs (Sweatman, 2008). However, there is not currently any empirical evidence in support of a link between survivorship of algal-feeding juvenile CoTS and GBR fisheries regulation, nor strong support for substantial top-down (i.e., fishing) effects on reef fish (other than those directly targeted) and benthic assemblages from GBR reefs (Emslie et al., 2015; Rizzari et al., 2015; Casey et al., 2017). As shown in Chapter 5, differences in the incidence and severity of sublethal injuries among early-stage juvenile starfish from different marine park zones did not suggest that their vulnerability to predation differed between protected (i.e., no-take) and fished reefs of the GBR. However, differences in survivorship of early-stage juvenile starfish may not be detectable with this approach, and changes in their survivorship could also be influenced by fishing-induced changes in bottom-up processes. Accordingly, changes in human-induced bottom-up and/or top-down processes (e.g., due to fishing or increased loads of fine sediments in terrestrial runoff) may still influence settlement, post-settlement growth, and resulting survivorship of early-stage herbivorous or corallivorous juvenile CoTS.

Despite the inherently low detectability of early life history stages of CoTS (MacNeil et al., 2016), early-stage juvenile starfish were detected in 31 out of 42 sites (73.8%) across three mid-shelf reefs in the central GBR (Chapter 2). This suggests that when using my developed method (see Chapter 2), the rate of false negatives is relatively low at the site level. The surveys were, however, conducted during active outbreaks, when the relative abundance of early-stage juvenile starfish is likely to be comparatively high due to enhanced larval supply. A potentially major drawback of my method, or any method that quantifies abundances of early life history stages, is its performance at low densities. If south-ward progressing outbreak waves of CoTS (*sensu* Kenchington et al., 1977) initiate near Lizard Island as a result of gradual population build-up (Pratchett, 2005; Pratchett et al., 2014), then it could be difficult to detect differences in the relative abundance of early-stage juvenile CoTS among sites and reefs within the initiation area. However, if low to moderate densities of adult starfish result in localised high rates of recruitment of early-stage juvenile CoTS, which is possible given their immense reproductive capacity, then the proposed method (Chapter 2) may be viable as an early warning system. A long-term time series of the relative abundance of herbivorous juvenile starfish (linked to the availability of suitable coral prey), measured annually during austral winter months (May–August) at selected locations and reefs near Lizard Island, could establish whether primary outbreaks arise from infrequent mass-recruitment events of algal-feeding early-stage juveniles (e.g., Zann et al., 1987; Deaker et al., 2020 a) and/or from the progressive accumulation of adult starfish over multiple successive recruitment events (e.g., Chapter 4). This data would still need to be related to the relative abundance of coral-feeding juvenile (and adult) CoTS populations, to establish whether high rates in recruitment of algal-feeding juvenile starfish ultimately lead to high (or low) densities of adult starfish populations.

Measuring annual changes in the relative abundance of visually-detectable herbivorous juvenile starfish has the potential to provide a measure for annual recruitment strength. This does not only provide an opportunity to greatly enhance our understanding of the relative importance of anthropogenic activities in the incidence and severity of outbreaks, but also provides a potentially viable option for an early warning system of future outbreaks (Chapter 2; Okaji et al., 2019). It is important therefore, to quantify changes in the abundance of herbivorous juvenile starfish over time across different reef habitats — beginning early following settlement — to establish i) whether and at what rate different year-class cohorts of visually-detectable herbivorous starfish may accumulate within settlement areas, and to quantify ii) the rate at which coral-feeding juvenile starfish populations build-up thereafter. Changes in the abundance of juvenile starfish also need to be related to benthic assemblages, such as coral prey, to explicitly examine how the size, structure and composition of coral communities constrains population replenishment of CoTS. Along with field and laboratory experimental studies, this could greatly enhance our understanding of the CoTS-coral interaction and its overall importance to the functioning of coral reef systems. Extending this research to other geographic locations and/or species of *Acanthaster* spp. will also be important to identify the intrinsic and extrinsic factors of the CoTS-coral system that are most influential in dictating variability in the severity and frequency of outbreaks.

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