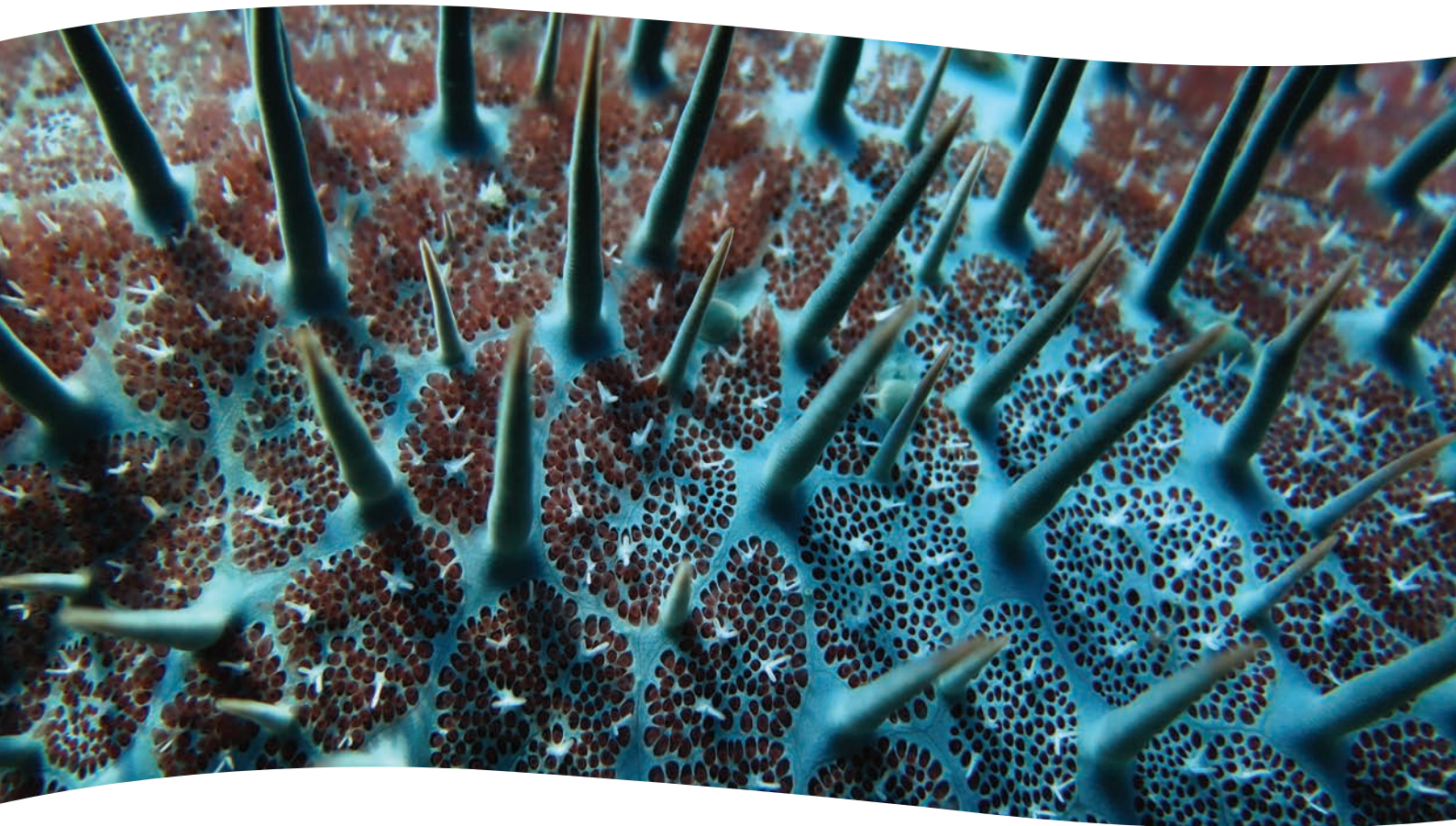


Inter-reef variation in the demography of Pacific crown-of-thorns starfish (*Acanthaster cf. solaris*) relative to marine reserves

Morgan S. Pratchett, Jennifer C. Wilmes, and Ciemon F. Caballes



Inter-reef variation in the demography of Pacific crown-of-thorns starfish (*Acanthaster cf. solaris*) relative to marine reserves

Morgan S. Pratchett¹, Jennifer C. Wilmes¹, and Ciemon F. Caballes¹

¹ ARC Centre of Excellence for Coral Reef Studies, James Cook University



Supported by the Australian Government's
National Environmental Science Program
Project 4.1 Crown-of-thorns starfish: surveillance and life history

© James Cook University, 2020



Creative Commons Attribution

Inter-reef variation in the demography of Pacific crown-of-thorns starfish (Acanthaster cf. solaris) relative to marine reserves is licensed by James Cook University for use under a Creative Commons Attribution 4.0 Australia licence. For licence conditions see: <https://creativecommons.org/licenses/by/4.0/>

National Library of Australia Cataloguing-in-Publication entry:
978-1-925514-64-3

This report should be cited as:

Pratchett, M. S., Wilmes, J. C., Caballes, C. F. (2020) *Inter-reef variation in the demography of Pacific crown-of-thorns starfish (Acanthaster cf. solaris) relative to marine reserves*. Report to the National Environmental Science Program. Reef and Rainforest Research Centre Limited, Cairns (30pp.).

Published by the Reef and Rainforest Research Centre on behalf of the Australian Government's National Environmental Science Program (NESP) Tropical Water Quality (TWQ) Hub.

The Tropical Water Quality Hub is part of the Australian Government's National Environmental Science Program and is administered by the Reef and Rainforest Research Centre Limited (RRRC). The NESP TWQ Hub addresses water quality and coastal management in the World Heritage listed Great Barrier Reef, its catchments and other tropical waters, through the generation and transfer of world-class research and shared knowledge.

This publication is copyright. The Copyright Act 1968 permits fair dealing for study, research, information or educational purposes subject to inclusion of a sufficient acknowledgement of the source.

The views and opinions expressed in this publication are those of the authors and do not necessarily reflect those of the Australian Government.

While reasonable effort has been made to ensure that the contents of this publication are factually correct, the Commonwealth does not accept responsibility for the accuracy or completeness of the contents, and shall not be liable for any loss or damage that may be occasioned directly or indirectly through the use of, or reliance on, the contents of this publication.

Cover photographs: (front) CoTS close up; (back) CoTS feeding. Images supplied by Morgan Pratchett.

This report is available for download from the NESP Tropical Water Quality Hub website:
<http://www.nesptropical.edu.au>

CONTENTS

Contents.....	i
List of Tables.....	ii
List of Figures.....	iii
Acronyms	iv
Acknowledgements	v
Executive Summary	1
1.0 Introduction	3
1.1 Cause(s) of population irruptions	4
1.2 Inter-reef differences in the incidence and severity of population irruptions.....	5
1.3 Study Objectives	6
2.0 Methods	7
2.1 Prevalence and severity of injuries.....	7
2.1.1 Adult crown-of-thorns starfish	7
2.1.2 Early-stage juvenile crown-of-thorns starfish	10
2.2 Recruitment and survival of early-stage juvenile crown-of-thorns starfish	11
3.0 Results and Discussion	13
3.1 Prevalence and severity of injuries.....	13
3.1.1 Adult crown-of-thorns starfish	13
3.1.2 Early-stage juvenile crown-of-thorns starfish	15
3.2 Recruitment and survival of early-stage juvenile starfish	17
4.0 Recommendations and ConclusionS.....	22
References.....	23

LIST OF TABLES

Table 1:	Extent of sampling conducted at reefs within different GBRMP management zones. Reefs within each zone are listed alphabetically with total number of starfish sampled from each reef and zone shown in brackets.	8
Table 2:	List of reefs (from north to south) from which juvenile <i>A. cf. solaris</i> were collected across contrasting GBRMP management zone. Adapted from Wilmes et al. 2019.	10
Table 3:	Variation in the size of crown-of-thorns starfish (<i>Acanthaster cf. solaris</i>) recorded during each of two distinct sampling occasions (June and November) in 2018 and 2019. Data was pooled across five mid-shelf reefs (n = 266 starfish); Kelso Reef, Little Kelso Reef, Rib Reef, Lodestone Reef and Keeper Reef. .	18
Table 4:	Density of crown-of-thorns starfish (<i>Acanthaster cf. solaris</i>) recorded at each of five mid-shelf reefs within contrasting spatial management zones.	19
Table 5:	Reported mean densities of starfish and estimated percentage of survival and mortality by year (based on changes in densities of starfish), reef and marine park zone.....	21

LIST OF FIGURES

Figure 1:	Marked variation in the size of arms of <i>Acanthaster cf. solaris</i> , where the smallest arm is likely to be regenerating from previous injuries, potentially caused by sub-lethal predation. Photograph: V. Messmer	9
Figure 2:	Frequency and density of the total number of arms recorded for 3,883 <i>Acanthaster cf. solaris</i> sampled on the Great Barrier Reef. The median number of arms was 15, but nearly as many starfish had 16 arms.	9
Figure 3:	Measuring radial extent for each arm of an early-stage juvenile crown-of-thorns starfish, whereby injured arms were defined as those that were >10% shorter than the longest arm (based on radial extent, not arm length). Figure from Wilmes et al. 2019.....	11
Figure 4:	Survey locations at five reefs in the central Great Barrier reef, Australia. Colours reflect Great Barrier Reef Marine Park zoning, where Marine National Park Zones are no-take areas and Habitat Protection Zones permit limited recreational and commercial fisheries activities. Map data © GBRMPA	12
Figure 5:	Prevalence (a; number of injured COTS: total number of COTS) and severity (b; number of injured arms: total number of arms) of injuries recorded for 5,238 crown-of-thorns starfish sampled across the GBRMP on reefs pooled across specific management zones (with increasing level of fisheries protection); Habitat Protection Zones (blue zones), Conservation Park Zones (yellow zones) and Marine National Park Zones (green zones). Letters indicate significantly different groups based on post hoc tests. Trends of prevalence (c) and severity (d) of injuries in relation to COTS size (measured as maximum diameter).	14
Figure 6:	Proportion of Pacific crown-of-thorns starfish (<i>A. cf. solaris</i>) sampled from reefs within three different management zones on the Great Barrier Reef (see Table 2) without injuries versus increasing number of arms injured.....	15
Figure 7:	Mean ($\pm$ SE) prevalence of injuries (proportion of individuals on each reef that had apparent injuries) recorded for 200 crown-of-thorns starfish sampled across the GBRMP on reefs (Table 2) from specific management zones (with increasing level of fisheries protection); Habitat Protection Zones (blue zones), Conservation Park Zones (yellow zones) and Marine National Park Zones (green zones). ...	16
Figure 8:	Severity of injuries in early-stage juvenile CoTS distinguishing between those starfish found feeding on coralline algae versus those (generally larger individuals) feeding on coral, and between those sampled from no-take marine reserves (Marine National Park Zones) and reefs where fishing was restricted (Habitat Protection Zones and Conservation Park Zones). Model data from Wilmes et al. 2019.....	17
Figure 9:	Boxplots showing diet-related size distribution of <i>Acanthaster cf. solaris</i> for each of two distinct sampling occasions (June and November) in 2018 and 2019. Data was pooled across five mid-shelf reefs (n = 266 starfish); Kelso Reef, Little Kelso reef, Rib Reef, Lodestone Reef and Keeper Reef.....	18
Figure 10:	Mean ($\pm$ SE) density of crown-of-thorns starfish (<i>Acanthaster cf. solaris</i>) recorded at each of five mid-shelf reefs (n ~ 60 quadrats) within contrasting spatial management zones (see Table 4). Sampling was conducted in approximately the same locations using haphazardly placed quadrats on each sampling occasion.	20

ACRONYMS

CoTS	Crown-of-thorns starfish
GBR	Great Barrier Reef
GBRMP	Great Barrier Reef Marine Park
JCU	James Cook University
LIRFF	Lizard Island Reef Research Foundation
LIRS	Lizard Island Research Station
NESP	National Environmental Science Program
TWQ	Tropical Water Quality

ACKNOWLEDGEMENTS

This research was supported by the Australian Government's National Environmental Science Program (NESP) Tropical Water Quality (TWQ) Hub, as well as the Ian Potter 50th Anniversary grants administered by the Lizard Island Reef Research Foundation (LIRRF). The authors are grateful to skipper Paul and crew of MV SeaEsta and staff at Lizard Island Research Station (LIRS) for logistic support. This work was conducted with assistance from Alexandre Siqueira, Vanessa Messmer, Cassandra Thompson, Deborah Burn, Alexander Buck, and Daniel Schultz. The authors also thank Vanessa Messmer and Maia Raymundo for helping with data analyses.

Data is publicly available on both [eAtlas](#) and via the [Tropical Data Hub](#) (Licenced under CC BY: Attribution 3.0 AU) or by direct request to the authors.

EXECUTIVE SUMMARY

Spatial and temporal stochasticity in the abundance and population dynamics of crown-of-thorns starfish (CoTS; *Acanthaster* spp.) highlights the critical need for improved knowledge of demographic variability within and among populations. This study explored variation in the demography of Pacific CoTS (*Acanthaster* cf. *solaris*) during the latest period of elevated CoTS densities (active population irruptions) in the central section of Australia's Great Barrier Reef. Specifically, we examined variation in i) the prevalence and severity of sub-lethal injuries among juvenile and adult CoTS, and ii) the recruitment, growth and survivorship of early-stage juvenile starfish, across different management zones where fishing is restricted (Habitat Protection Zone, Conservation Park Zone) versus effectively prohibited (Marine National Park Zone).

On the Great Barrier Reef, apparent differences in the incidence of population irruptions of *A. cf. solaris* occur on reefs where fishing is permitted (but restricted) versus reefs where recreational and commercial fishing are prohibited. The most logical explanation for these differences are that higher densities of fisheries target species within no-take marine reserves may directly or indirectly regulate the local abundance of crown-of-thorns starfish by moderating their growth and survival, though this has never been tested. This study used incidence of injuries, which was measured for both early-stage juveniles, as well as larger and older *A. cf. solaris*, as a proxy for rates of predation, and compared among reefs within different management zones. The prevalence (proportion of individuals with injuries) was very high for early-stage juvenile starfish (91.0%, $n = 200$), compared to larger individuals (43.2%, $n = 5,238$). For early-stage juvenile *A. cf. solaris*, both the prevalence and severity of injuries varied with size of individuals, and did not differ with management zone. For larger individuals (50–600 mm diameter), however, there were significant differences in prevalence and severity of injuries among management zones, even after carefully accounting for the effects of body size. Importantly, both the prevalence and severity of sub-lethal injuries were significantly higher for CoTS collected from reefs with Marine National Park (*green*) Zones, versus Conservation Park (*yellow*) Zones or Habitat Protection (*blue*) Zones. This finding is consistent with the notion that predation rates on CoTS are higher within reef habitats where recreational and commercial fishing are prohibited, presumably due to the higher size or abundance of predators that feed on adult CoTS. It remains to be tested whether higher rates of predation within no-take areas also lead to higher rates of adult CoTS mortality, but even higher rates of sub-lethal predation may sufficiently constrain growth and reproduction to suppress densities of CoTS in reef habitats that are closed to fishing.

To explicitly test for variation in the growth and survivorship of early-stage juvenile *A. cf. solaris*, recurrent sampling was conducted from June 2018 to November 2019 at each of five reefs within contrasting management zones; Kelso Reef and Little Kelso Reef (Marine National Park Zone), Rib Reef, Lodestone Reef and Keeper Reef (Habitat Protection Zone). A total of 266 early-stage juvenile crown-of-thorns starfish were recorded across the five reefs, most of which (74.1%) were very small (4–19 mm) and found on coralline algae. Both highest and lowest densities of early-stage juvenile starfish were recorded at reefs (Lodestone Reef and Keeper Reef, respectively) where restricted fishing is permitted (Habitat Protection Zone). There were also no apparent differences in growth or survivorship among reefs with respect to fisheries management, though there was high inter-reef and inter-annual variability in vital rates. This

study shows that it is not only possible to detect recently settled CoTS within shallow reef habitats, but recurrent sampling across a broad range of locations could provide significant insights into the factors affecting early stage demography of *A. cf. solaris*.

This study adds to existing evidence that established networks of marine protected areas and differential fisheries management among reefs within the GBR may have important effects on the demography and therefore, local abundance of *A. cf. solaris*. Effects of marine protected areas were very specific and quite subtle, and it is unlikely that further restrictions in fisheries management will necessarily prevent future population irruptions of *A. cf. solaris*. However, the fisheries management may have an important role in mitigating effects of CoTS as part of increasing the general resilience of reefs across the GBR.

1.0 INTRODUCTION

Population outbreaks of crown-of-thorns starfish (*Acanthaster* spp.) are an enigmatic phenomenon (Moran 1986; Pratchett and Cumming 2019), which have significant influence on the health and condition of coral reef ecosystems throughout the Indo west-Pacific (e.g., Chesher 1969; Kayal et al. 2012). In French Polynesia, for example, recent population irruptions of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) killed >96% of corals around the entire circumference of the island of Moorea (Kayal et al. 2012). Population irruptions of crown-of-thorns starfish at Moorea (which occurred in 1980 and 2007) are the foremost cause of coral loss recorded since 1979 (Faurea 1989; Trapon et al. 2011), despite high frequency of other acute disturbances, including mass coral bleaching and severe tropical storms. Population irruptions of crown-of-thorns starfish are considered to be among the most significant causes of coral loss in many reef locations (Bruno and Selig 2007; Osborne et al. 2011; Mellin et al. 2019a), but have also attracted considerable and increasing attention because they are one of the few major causes of coral loss and reef degradation that may be amenable to direct and localised management interventions (De'ath et al. 2012; Anthony et al. 2015; Babcock et al. 2016a; Westcott et al. 2016).

Coral reefs, like many nearshore marine environments, are subject to extensive and escalating pressures and disturbances (Pandolfi et al. 2003; Hughes et al. 2017b; Bellwood et al. 2019; Darling et al. 2019), which have already caused sustained coral loss and fundamental shifts in habitat structure across a broad range of locations (Gardner et al. 2003; Graham et al. 2006; Alvarez-Filip et al. 2009; Norström et al. 2009; De'ath et al. 2012; Sheppard et al. 2020). The causes of coral loss vary regionally. However, there is often a mismatch between regional drivers of coral loss and reef degradation versus localised management priorities and actions (Hughes et al. 2017a; Bellwood et al. 2019). Long-term studies on changes in the structure and function of reef ecosystems highlight the critical influence of large-scale, but discrete (or acute) disturbances (Gardner et al. 2005; Adjeroud et al. 2009; Osborne et al. 2011; Trapon et al. 2011; Pisapia et al. 2016; Sheppard et al. 2020). However, contemporary coral reef management remains focussed on redressing perennial and pervasive human pressures, such as fisheries exploitation and land-based pollutants (Brodie and Pearson 2016; Aswani et al. 2018; Weijerman et al. 2018; Comeros-Raynal et al. 2019). Sustained degradation of coral reef ecosystems is at least partly attributable to persistent (or chronic) pressures (Anthony et al. 2015; Pratchett and Hoogenboom 2019), and corresponding impacts on the population dynamics of habitat-forming (Fabricius 2005; Browne et al. 2015) and functionally important reef species (Bellwood et al. 2012; Edwards et al. 2014). Reducing direct pressures on these groups of organisms may therefore, provide broad-scale ecosystem benefits, such as enhanced resilience (Bozec et al. 2016; Mellin et al. 2016; Steneck et al. 2018; Topor et al. 2019). Most notably, effective no-take marine reserves have been shown to enhance key ecosystem functions, which promote recovery of coral assemblages and maintenance of coral-dominated habitats in the aftermath of major disturbances (Mellin et al. 2016; Topor et al. 2019). Reduced fishing pressure and establishment of no-take marine reserves may also be effective in suppressing or preventing population irruptions of crown-of-thorns starfish (Dulvy et al. 2004; Sweatman 2008; Condie et al. 2018), which would greatly reduce coral loss (De'ath et al. 2012).

1.1 Cause(s) of population irruptions

Population irruptions of *Acanthaster* spp. are variously attributed to either; i) particular life-history characteristics (most obviously, their extreme levels of fecundity and variability in the extent to which reproductive capacity is realized) that predispose populations to marked fluctuations in abundance (Uthicke et al. 2009; Babcock et al. 2016a; Babcock et al. 2016b; Wilmes et al. 2020a), or ii) major changes in biological or environmental conditions that disrupt normal regulatory processes that otherwise constrain local densities of *Acanthaster* spp., such as predation (e.g., Endean 1969) or food-limitation (Antonelli and Kazarinoff 1984). While there is increasing recognition that early life-history stages are fundamental in understanding population dynamics (Wilmes et al. 2018, 2020a, 2020b), there is persistent controversy regarding the role of planktonic conditions (especially, availability of prey resources) in determining spatial and temporal fluctuations in larval supply, and if (or how) these processes are influenced by land run-off and nutrient inputs (Lucas 1982; Olson 1985; Brodie 1992; Brodie et al. 2005, 2017; Pratchett et al. 2014). While there have been numerous experimental tests of larval food-limitation for *Acanthaster* spp. (Lucas 1982; Ayukai 1994; Fabricius et al. 2010; Wolfe et al. 2015, 2017; Caballes et al. 2017; Pratchett et al. 2017a), there is yet to be effective sampling of larval abundance and condition showing explicit links to planktonic communities or nutrient availability in the wild, considered critical in resolving this debate (e.g., Babcock and Mundy 1993). More generally, understanding the cause(s) of population irruptions requires much greater sampling to document fine-scale spatial and temporal changes in the demography and population dynamics of crown-of-thorns starfish (Moran 1986), and corresponding sampling of relevant biological and environmental conditions (Babcock and Mundy 1993).

One of the foremost hypotheses that has been proposed to explain population irruptions of crown-of-thorns starfish is the predator removal hypothesis (Endean 1969). Endean (1969) argued that overfishing of the giant triton (*Charonia tritonis*) on the Great Barrier Reef (GBR) in the 1940s and 1950s contributed to the first documented population irruption of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) in the early 1960s. Reported catches of *C. tritonis* during the 1950s were >10,000 per annum (Endean 1973), and subsequent densities of giant triton on the GBR have been highly suppressed. Excessive removal of giant triton from reefs in the northern GBR was linked to increased abundance of large adult starfish capable of initiating outbreaks by virtue of their massive combined reproductive output (Endean 1969). While the role of giant triton in regulating abundances of crown-of-thorns starfish remains equivocal (Ormond et al. 1990), most of the contemporary studies of predatory regulation of crown-of-thorns starfish have focussed on reef fishes (Cowan et al. 2017b) and especially fishery target species (e.g., coral trout). Notably, Sweatman (2008) showed that the incidence of population irruptions of crown-of-thorns starfish was 3.75 times higher on GBR mid-shelf reefs that were open to fishing (e.g., Habitat Protection Zones) compared to no-take marine reserves (Marine National Park Zones). Observed differences in the incidence of population irruptions were attributed to trophic cascades arising due to fisheries-induced depletion of larger piscivorous fishes, such as coral trout (Sweatman 2008). There are, however, yet to be any detailed studies quantifying comparative rates of predation or mortality from *A. cf. solaris* inside versus outside of no-take marine reserves.

1.2 Inter-reef differences in the incidence and severity of population irruptions

On the GBR, reef-wide population irruptions of *A. cf. solaris* appear to originate on mid-shelf reefs in the vicinity of 14-15°S (Sweatman et al. 1998; Vanhatalo et al. 2016). In 1994, for example, population irruptions of *A. cf. solaris* were first recorded at Lizard Island and several other reefs within the immediate area, including Linnet, North Direction, and Rocky Islet (Sweatman et al. 1998). These initial population irruptions (primary outbreaks) then give rise to successive population irruptions (secondary outbreaks) that propagate predominantly southwards, but also northwards (Kenchington 1977; Reichelt et al. 1990; Moran et al. 1992; Vanhatalo et al. 2016). Consideration of the cause(s) of population irruptions on the GBR (e.g., Wooldridge and Brodie 2015; Babcock et al. 2016a; Pratchett et al. 2017b) focusses mainly on factors that lead to the initiation of population irruptions on northern reefs, whereas there are altogether different factors that might contribute to the propagation of secondary population irruptions (e.g., Hock et al. 2014; Brodie et al. 2017). Large-scale (GBR-wide) analyses of the incidence of population irruptions of *A. cf. solaris* tend to focus on overall patterns of initiation and spread (Moran et al. 1992; Vanhatalo et al. 2016), highlighting inherent connections and coupled oscillations in ecosystem state among closely-positioned reefs. However, the incidence and severity of population irruptions (both in terms of starfish densities and ecological impacts on coral assemblages) can vary among reefs (Vanhatalo et al. 2016), attributable to variation in cross-shelf position (e.g., proximity to coast) and inherent environmental conditions (Mellin et al. 2019b), connectivity to reefs with active population irruptions (Hock et al. 2017), and/ or fisheries management (Sweatman 2008).

The GBR comprises thousands of separate shallow, often emergent, reef systems (Pratchett et al. 2019), which are sometimes connected by very large continuous expanses of reef framework at greater depths (Beaman 2010). More importantly, closely positioned reefs are often highly connected by ocean currents that transport larval and dispersal stages of marine organisms (Hock et al. 2014, 2017) and have similar exposure to environmental pressures and large-scale disturbances (Mellin et al. 2019a). However, distinct reefs do vary in their size, shape, geomorphologic structure and maturity (Hopley et al. 2007), habitat (Emslie et al. 2010) and management (Day 2002). In terms of management, reefs are generally ascribed to one of several different management zones, including i) Preservation Zones (pink on zoning maps), which are no-access and the most restrictive of all zones; ii) Marine National Park Zones (green) which are no-take areas where all types of extractive activity are prohibited; iii) Conservation Park Zones (yellow) where only limited fishing is allowed; and iv) Habitat Protection Zones (blue) where recreational and commercial fisheries are permitted subject to certain conditions (Day 2002; Pratchett et al. 2019). Aside from demonstrated benefits for fisheries target species, which often extend (spill-over) beyond the boundaries of no-take areas (Williamson et al. 2004; Miller et al. 2012; Emslie et al. 2015; Carter et al. 2017), Preservation Zones and Marine National Park Zones have been shown to confer broader ecosystems benefits, such as ecosystem resilience (Sweatman 2008; McCook et al. 2010; Mellin et al. 2016). Explicitly testing for inter-reef differences in the demography of crown-of-thorns starfish with respect to contrasting management zones, may therefore provide important insights into the role of predators, but also alternative spatial management arrangements, in regulating populations and reducing the incidence and severity of population irruptions.

1.3 Study Objectives

The reported incidence of injuries among adult crown-of-thorns starfishes ranges from <5% (e.g., Ormond and Campbell 1971) to >65% (Rivera-Posada et al. 2014), and apparent injuries are widely attributed to sub-lethal predation (McCallum et al. 1989). If fisheries exploitation reduces predation pressure on these adult *Acanthaster* spp., we would expect to find lower incidence and severity of injuries among starfish located in reef habitats where fishing is permitted and higher incidence or severity of injuries in areas closed to fishing, as was shown in reefs in the Philippines (Rivera-Posada et al. 2014). Previously, Messmer et al. (2017) found no difference in the incidence or severity of injuries for *A. cf. solaris* among reefs where fishing is prohibited (Marine National Park) versus reefs where fishing is permitted (Conservation Park and Habitat Protection Zones) on the GBR. However, sampling across management zones was confounded by latitude, with most of the reefs within Marine National Park Zones sampled in the northern GBR, whereas reefs sampled in the south were exclusively Conservation Park and Habitat Protection Zones. Similarly, Wilmes et al. (2019) also did not find differences in the incidence and severity of injuries among early-stage juvenile starfish (5–45 mm diameter) across reefs where fishing is prohibited versus permitted. The present study builds on (and includes) results presented in Messmer et al. (2017) and Wilmes et al. (2019).

The objectives of this study were:

- i) To compare the prevalence (proportion of individuals with conspicuous injuries) and severity of injuries (extent of damage apparent on individual with injuries) for both adult and juvenile crown-of-thorns starfish among reefs within contrasting GBRMPA fisheries management zones, explicitly testing whether injuries are more prevalent or severe on reefs where fishing is permitted.
- ii) To explore spatiotemporal variation in the size and abundance of early-stage juvenile crown-of-thorns starfish between seasons in two successive years (2018 and 2019) and among reefs within contrasting GBRMPA fisheries management zones. By explicitly testing for changes in the size and abundance within fixed sampling locations, we test for variation in apparent growth and survivorship of crown-of-thorns starfish in the first year post-settlement, which may be critical in accounting for spatiotemporal variation in the abundance of these organisms (Wilmes et al. 2018, 2020b).

2.0 METHODS

2.1 Prevalence and severity of injuries

2.1.1 Adult crown-of-thorns starfish

A total of 5,238 *A. cf. solaris* (ranging in size from 50-600mm diameter) were sampled across 70 reefs in the Great Barrier Reef Marine Park between 2013 and 2018 (Table 1), building substantially on the sample ($n = 3,846$) of starfish analysed previously (Messmer et al. 2017). All starfish were carefully extracted from the reef matrix, using purpose-built large stainless-steel tongs or hooks, taking care not to damage the starfish. Starfish were then kept in mesh bags or perforated collection boxes for transport to support vessels. All starfish were processed within 3 hours of collection, except where we had access to holding facilities with large tanks and rapid exchange of fresh seawater (e.g., at Lizard Island Research Station) and could maintain the starfish for prolonged periods with limited adverse effects on individual condition.

The total diameter of individual starfish was measured by inverting starfish on a flat surface and measuring the distance between tips of opposite and undamaged arms. Measurements were taken (to the nearest mm) from the termination of the ambulacral grooves and ignoring the spines projecting from the tips of the arms. Where starfish were noticeably asymmetrical, the diameter was measured at least twice and then averaged. The underside (oral surface) of starfish was then examined to determine the number of arms and evidence of injuries, following Rivera-Posada et al. (2014). The total number of arms was counted based on the number of discrete ambulacral grooves extending directly from the oral cavity. Arms were considered to be damaged if they were less than 75% the length (Figure 1) of the other seemingly intact arms, or were conspicuously damaged, missing or regenerating. Recent injuries (e.g., fresh tears in the surface integument) were disregarded, as they likely occurred during collection. The incidence of injuries was determined based on the proportion of starfish with any evidence of injuries, whereas severity of injuries was estimated based on the proportion of an individual's arms that were injured. Where only the number of injured arms was recorded, this was expressed as a proportion, using the median number of arms (15) recorded for all *A. cf. solaris* where the number of arms was counted (Figure 2).

Variation in the incidence (modelled as presence/absence of injuries) and severity (modelled as proportion of arms damaged or missing on injured starfish) were compared among the three different management zones; i) Marine National Park Zones (green); ii) Conservation Park Zones (yellow); and iii) Habitat Protection Zones (blue), while also accounting for variation in the size (maximum diameter) of individual starfish. Differences among management zones (samples from individual reefs pooled across management zones) and with body size (maximum diameter) as an additive fixed effect were modelled using generalised linear model (GLM) with a binomial error distribution in R (R Core Team 2020). Analysis of deviance (likelihood ratio chi-square) on the models were done using the 'Anova' function within the 'car' package in R (Fox & Weisberg 2019). *Post hoc* pairwise comparisons of injury prevalence and severity among management zones were conducted using the 'emmeans' package in R (Lenth et al. 2017).

Table 1: Extent of sampling conducted at reefs within different GBRMP management zones. Reefs within each zone are listed alphabetically with total number of starfish sampled from each reef and zone shown in brackets.

Marine National Park Zone, aka <i>Green Zone</i> (n = 2,467)		
13-144 (3)	Hedley Reef (331)	Michaelmas Cay (5)
15-072 (20)	Heron Island 915)	Moore Reef (10)
Briggs Reef (208)	Lark Reef (20)	Nathan Reef (12)
Eagle Reef (23)	Lizard Island (642)	Norman Reef (16)
Endeavour Reef (349)	Low Isles (9)	North Direction Island (305)
Fairfax Island (13)	Martin Reef (31)	Stevens Reef (3)
Feather Reef (2)	MacGillivray Reef (336)	South Direction Island (257)
Green Island (29)	Mermaid Reef (1)	Taylor Reef (7)
Conservation Park Zone, aka <i>Yellow Zone</i> (n = 526)		
Boulder Reef (2)	Opal Reef (3)	Thetford Reef 10)
Davies Reef (3)	Pickersgill Reef (322)	Trunk Reef (42)
Elford Reef (99)	Sykes Reef (7)	Vlasoff Reef (20)
Habitat Protection Zone, aka <i>Blue Zone</i> (n = 2,245)		
15 044 (20)	Ellison Reef (3)	Otter Reef (3)
16-018 (10)	Emily Reef (348)	Pearl Reef (6)
17-060 (14)	Forrester Reef (20)	Potter Reef (10)
17-061 (8)	Gibson Reef (6)	Rib Reef (158)
22-143 (11)	Gilbey Reef (10)	Ribbon Reef No. 10 (20)
Adelaide Reef (12)	Hall-Thompson Reef (6)	Rudder Reef (10)
Arlington Reef (399)	Howie Reef (11)	Sandshoe Reef (5)
Batt Reef (30)	Irene Reef (10)	Spitfire Reef (300)
Bramble Reef (74)	Lodestone Reef (1)	Startle Reef (30)
Broadhurst Reef (19)	Mackay Reef (20)	Sudbury Reef (10)
Cayley Reef (10)	Maori Reef (37)	Sweetlip Reef (6)
Centipede Reef (5)	McCulloch Reef (312)	Tongue Reef (16)
Chinaman Reef (20)	Morning Reef (10)	Two Isles (20)
Coates Reef (3)	Musgrave Island (1)	Undine Reef (30)
Dicks Reef (94)	Noggin Reef (2)	Walker Reef (55)
Eddy Reef (8)	Noreaster Reef (27)	Wardle Reef (5)



Figure 1: Marked variation in the size of arms of *Acanthaster cf. solaris*, where the smallest arm is likely to be regenerating from previous injuries, potentially caused by sub-lethal predation. Photograph: V. Messmer

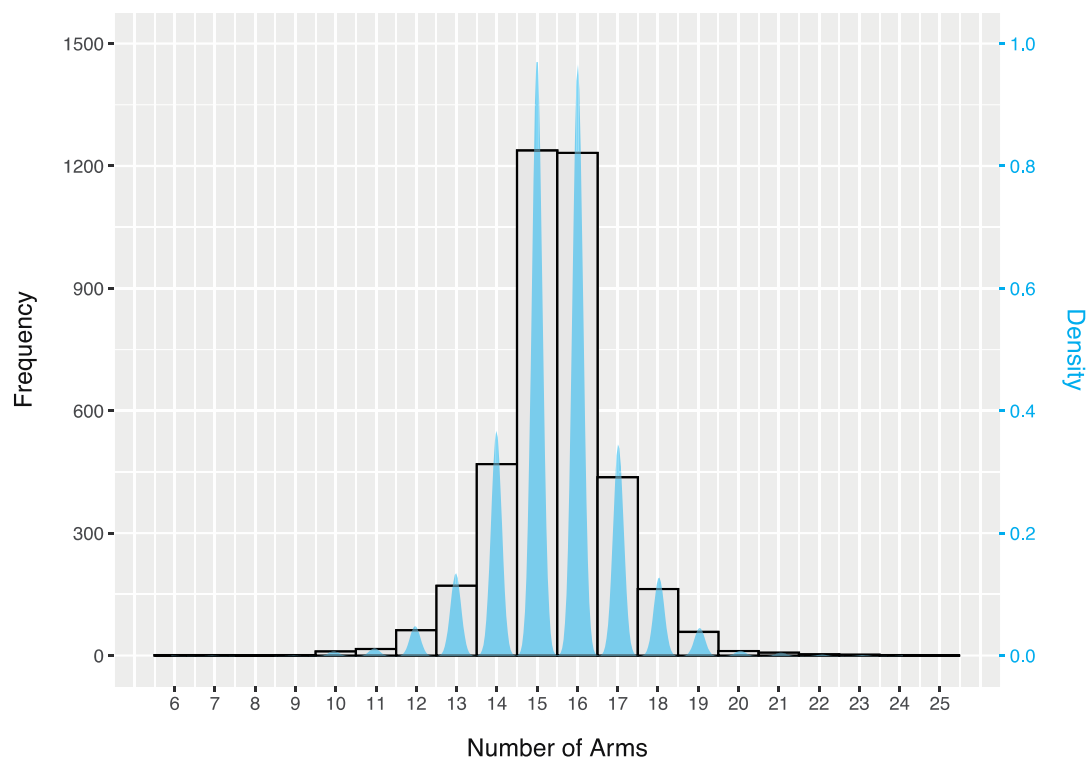


Figure 2: Frequency and density of the total number of arms recorded for 3,883 *Acanthaster cf. solaris* sampled on the Great Barrier Reef. The median number of arms was 15, but nearly as many starfish had 16 arms.

2.1.2 Early-stage juvenile crown-of-thorns starfish

Variation in the incidence and severity of injuries was also assessed for 200 early-stage juvenile *A. cf. solaris* (size range = 5–45 mm diameter) – presumed to be <1-year-old (Wilmes et al. 2016, 2019, 2020b). These early-stage juveniles were sampled from an extensive collection of early-stage juvenile starfish ($n = 3,532$) that had been collected on the GBR in 2015 (Wilmes and Schultz 2019). Sampling was in the present study intentionally biased towards the largest, and presumably oldest, individuals to avoid confusion between newly-forming versus regenerating arms (Wilmes et al. 2019). All starfish were collected on SCUBA (max depth = 15 m), during extensive searching in areas of unconsolidated coral rubble, interspersed with patches of consolidated carbonate and live corals (see Wilmes et al. 2019). Starfish were preserved in 95% ethanol following collection for later processing.

Table 2: List of reefs (from north to south) from which juvenile *A. cf. solaris* were collected across contrasting GBRMP management zone. Adapted from Wilmes et al. 2019.

Reef	Sample size	Percentage of starfish with injuries
Marine National Park Zone, aka Green Zone ($n = 76$)		
U/N Reef 15-072	3	100.00
U/N Reef 16-013a	4	100.00
Agincourt Reef No. 5	5	100.00
Hastings Reef	14	78.57
Upolo Reef	12	91.67
Green Island	30	90.91
Nathan Reef	8	87.50
Conservation Park Zone, aka Yellow Zone ($n = 17$)		
Oyster Reef	3	100.00
U/N Reef 16-044a	14	92.86
Habitat Protection Zone, aka Blue Zone ($n = 107$)		
Rosser Reef	3	100.00
Escape Reef	2	100.00
Morning Reef	11	90.91
Pretty Patches	22	90.91
Arlington Reef	36	91.67
Gibson Reef	11	90.91
Howie Reef	2	100.00
Gilbey Reef	12	91.67
Hall-Thompson Reef	1	100.00
Potter Reef No. 1	7	85.71

The aboral side of each of the 200 juvenile starfish selected for this study (Table 2) was photographed using an Olympus Om-D E-M5 camera. 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 (using ImageJ1, see Figure 3). Injured arms were defined as those that were >10% shorter than the radial extent of the longest arm, following Bos et al (2011).

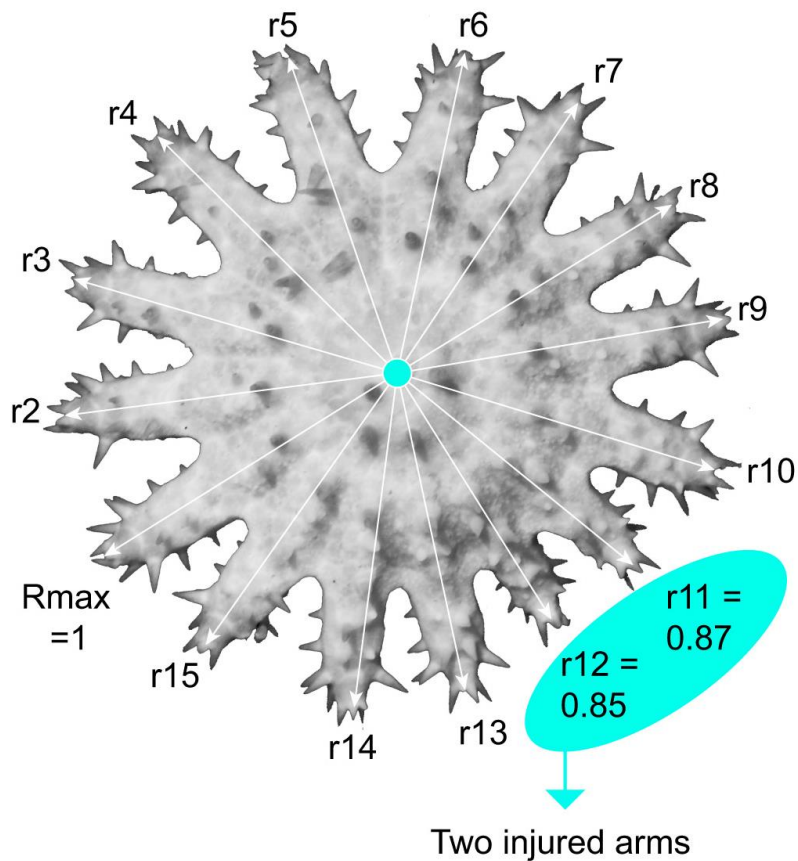


Figure 3: Measuring radial extent for each arm of an early-stage juvenile crown-of-thorns starfish, whereby injured arms were defined as those that were >10% shorter than the longest arm (based on radial extent, not arm length). Figure from Wilmes et al. 2019

Both the incidence (modelled as the presence/ absence of injuries) and severity (modelled as the proportion of injured arms) of injuries were related to size (maximum radius) of individual starfish – using generalised linear mixed effects model (glmmPQL function from the MASS package; Venables and Ripley 2002) with binomial error distribution in R (R Core Team 2020). Zoning was included as an additive fixed effect, with data pooled across Conservation Park and Habitat Protection Zones, to test for differences between no-take areas (Marine National Park Zones, $n = 76$) versus areas with restricted fishing ($n = 124$).

2.2 Recruitment and survival of early-stage juvenile crown-of-thorns starfish

Field studies were conducted in 2018 and 2019 at five mid-shelf reefs (Kelso Reef, Little Kelso reef, Rib Reef, Lodestone Reef and Keeper Reef) of the central GBR (Figure 4) to explore variation in recruitment and survival of early-stage juvenile crown-of-thorns starfish between reefs where fishing was permitted (Habitat Protection Zone; $n = 3$) versus those where fishing was prohibited (Marine National Park Zone; $n = 2$). Each reef was surveyed twice each year (June and November). Reefs were selected to represent contrasting GBRMPA management zones, at the time of active population irruptions. The specific study locations at each reef (see Figure 4) were chosen following extensive surveys at selected locations, which identified areas

with elevated densities of early-stage juvenile CoTS. The initial surveys in June 2018 were conducted at least 5 months after peak annual spawning and settlement (in late December and early January, respectively; Uthicke et al. 2019) as newly settled starfish are difficult to be visually detected prior to this time (Wilmes et al. 2016, 2020b).

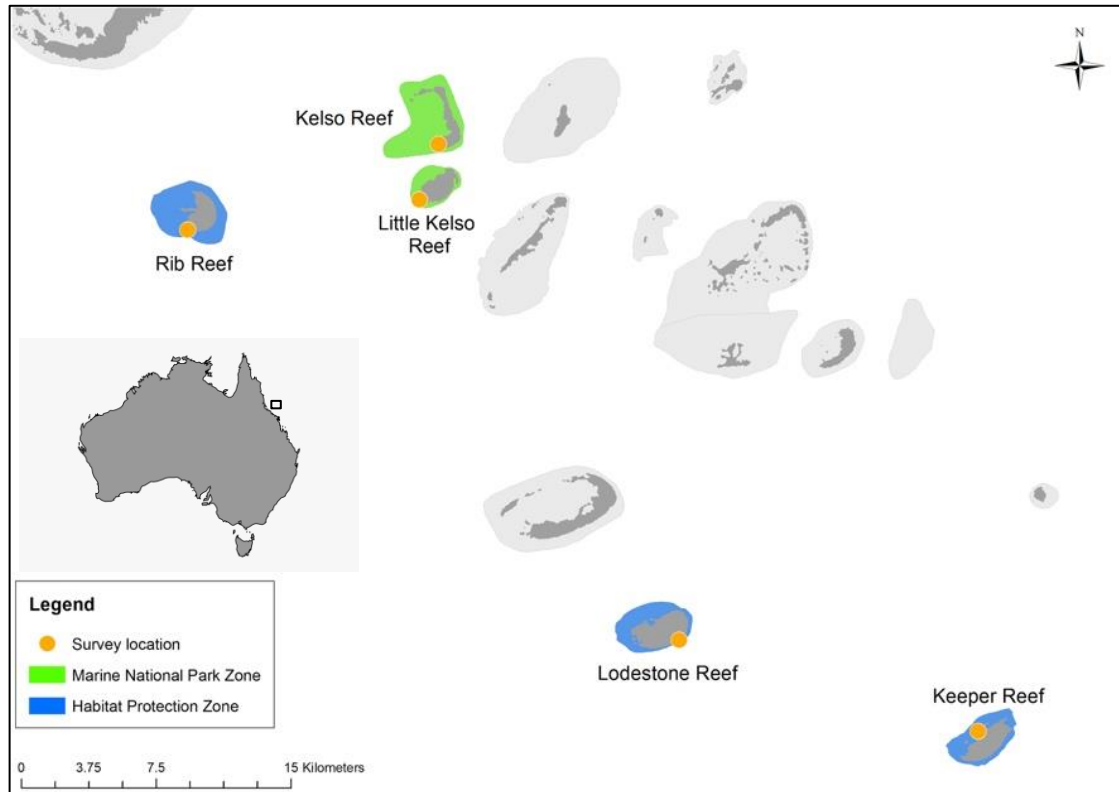


Figure 4: Survey locations at five reefs in the central Great Barrier reef, Australia. Colours reflect Great Barrier Reef Marine Park zoning, where Marine National Park Zones are no-take areas and Habitat Protection Zones permit limited recreational and commercial fisheries activities. Map data © GBRMPA

While study locations varied in their orientation to the prevailing south-east trade winds, they were all characterised by relatively steep slopes, enabling sampling of multiple depths (up to 15 m water depth). Surveys were conducted following an adapted version of Wilmes et al. (2020a), using 60 replicate 1m × 1m quadrats to survey each location. Replicate quadrats were placed haphazardly, working systematically from the bottom of the reef slope up to the reef crest and avoiding areas comprised mostly or entirely of sand. To maximize detection of early-stage juvenile starfish, the area encompassed within each quadrat was further divided into quadrants, which were thoroughly searched in turn (Wilmes et al. 2020a). All starfish detected (up to 200mm diameter) were measured *in situ*.

3.0 RESULTS AND DISCUSSION

3.1 Prevalence and severity of injuries

3.1.1 Adult crown-of-thorns starfish

2,264 out of 5,238 (43.22%) adult crown-of-thorns starfish sampled from across the GBR had evidence of injuries, whereby they had at least one arm that was missing or evidently shorter and thinner and generally covered in shorter and finer spines (Figure 1). This is very similar to overall prevalence of injuries (40%; $n = 276$) reported by McCallum et al (1989) on the GBR, though this is much lower than previous prevalence of injuries reported by Budden et al. (2019) from Davies Reef (73.0%; $n = 52$) and Lynch Reef (58.3%; $n = 96$) in the central GBR. While prevalence of injuries is known to vary among reefs (Messmer et al. 2017; Budden et al. 2019), we pooled data across reefs to explicitly test for variation in the incidence of prevalence relative to GBRMP management zones and size (Figure 5a, c).

Overall, zoning ($X^2=21.54$, $df=2$, $p<0.001$) had a significant effect on the prevalence of injuries. The overall prevalence of injuries was significantly higher for starfish sampled from reefs within Marine National Park Zone ('Green'; 49.00%: 1,209/2,467) compared to those sampled from Conservation Park Zones ($p=0.004$; 'Yellow'; 41.25%: 217/526) and Habitat Protection Zones ($p<0.001$; 'Blue'; 37.33%: 838/2,245). However, there was no statistical difference in prevalence of injuries recorded in Conservation Park Zones versus Habitat Protection Zones ($p=0.217$; Figure 5a). If the prevalence of injuries relates to incidence of sub-lethal predation and/or overall rates of predation (*sensu* McCallum et al. 1989) this would suggest predation rates increase with increasing levels of fisheries protection, as would be expected if fisheries target species do actually prey on crown-of-thorns starfish (Rivera-Posada et al. 2014). There is considerable evidence showing that coral trout are larger and more abundant in Marine National Park Zones across the GBRMP (Williamson et al. 2004; Miller et al. 2012; Emslie et al. 2015), at least in areas with moderate to high coral cover (e.g., in the early stages of population irruptions of crown-of-thorns starfish). Injury prevalence relative to CoTS size (Figure 5c) also showed a significant relationship with larger-sized CoTS exhibiting an overall lower injury prevalence ($X^2=22.43$, $df=1$, $p<0.001$). Data presented here provides one possible mechanism to explain lower incidence of population irruptions of *A. cf. solaris* within Marine National Park Zones (Sweatman 2008) suggesting that key fisheries species may be functionally important in regulating populations of crown-of-thorns starfish.

Beyond differences in the prevalence of injuries, we show that the severity (proportion of injured arms) also increases with increasing levels of fisheries protection (Figure 5b). For starfish with injuries, the median number of injured arms was 15 across all management zones (Figure 6). The average severity of injuries was significantly different between management zones ($X^2=21.74$, $df=2$, $p<0.001$), whereby severity was higher for starfish sampled from reefs within Marine National Park Zone (7.37% $\pm 0.21SE$) compared to those sampled from Conservation Park Zones ($p=0.005$; 6.31% $\pm 0.48SE$) and Habitat Protection Zones ($p<0.001$; 5.56% $\pm 0.20SE$). Variation in mean severity is mainly attributable to the lower incidence of injuries in Conservation Park Zones and Habitat Protection Zones. If we consider only those starfish with injuries, there are significant differences ($X^2=78.66$, $df=12$, $p<0.01$) in proportion of individuals with between 1 and >6 arms damaged (Figure 6), but there are more starfish with more severe injuries in Conservation Park Zones and Habitat Protection Zones. While not

considered in this study, McCallum et al. (1989) showed (based on the clustering of injured arms) that increasing severity of injuries rarely reflects cumulative impacts of multiple discrete injuries, but single large injuries caused by larger or more voracious and persistent predators. If so, this may suggest that there is higher abundance of opportunistic predators in areas that are closed to fishing (Marine National Park Zone), causing higher prevalence of injuries, but rarely killing these starfish outright. Conversely, the predators that do exist within areas where there is fishing permitted (though restricted) may be larger or more voracious. In addition, a significant decreasing trend in severity (Figure 5d) was observed with increasing body size ($X^2=96.93$, $df=1$, $p<0.001$).

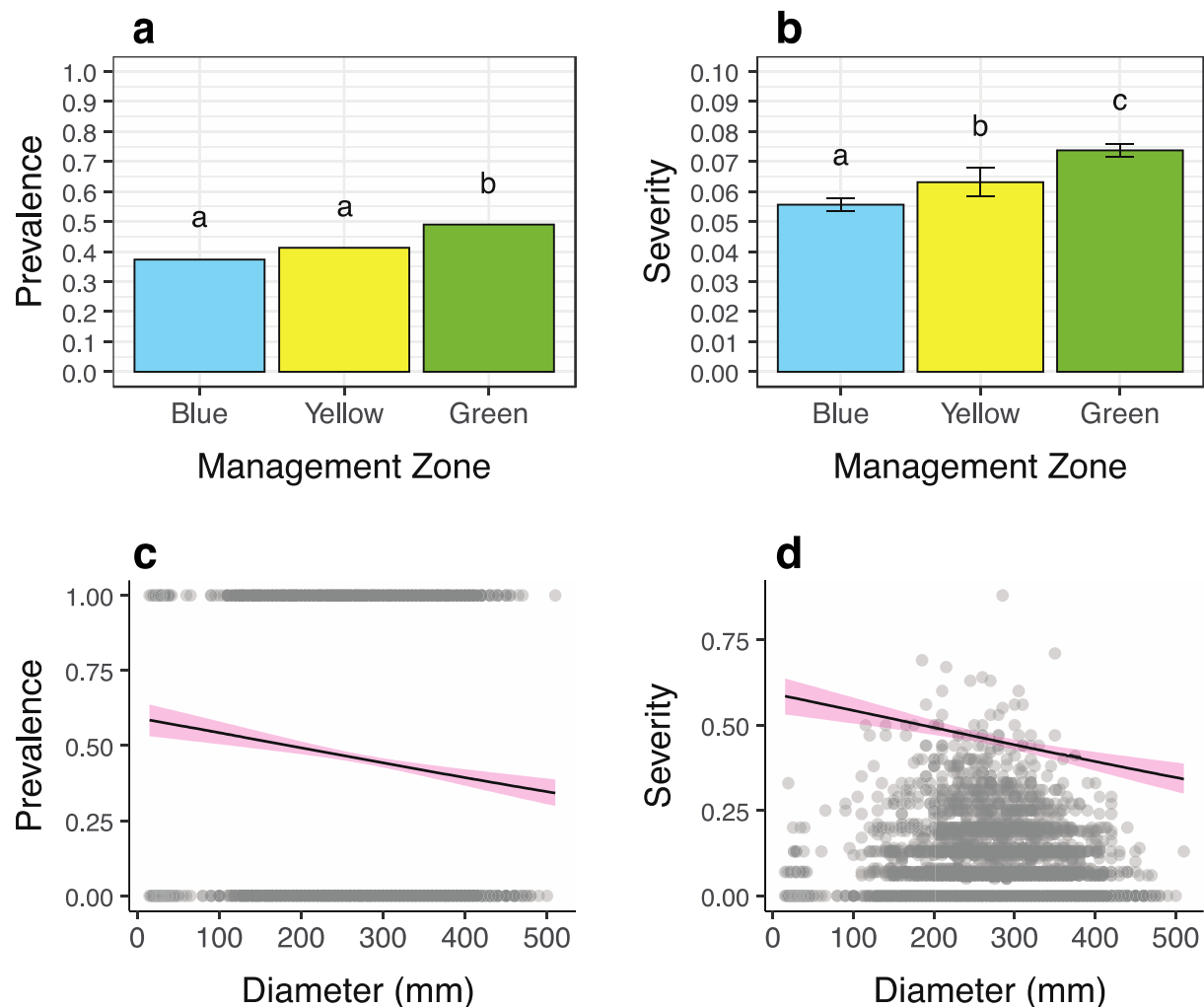


Figure 5: Prevalence (a; number of injured COTS: total number of COTS) and severity (b; number of injured arms: total number of arms) of injuries recorded for 5,238 crown-of-thorns starfish sampled across the GBRMP on reefs pooled across specific management zones (with increasing level of fisheries protection); Habitat Protection Zones (blue zones), Conservation Park Zones (yellow zones) and Marine National Park Zones (green zones). Letters indicate significantly different groups based on post hoc tests. Trends of prevalence (c) and severity (d) of injuries in relation to COTS size (measured as maximum diameter).

While some studies consider sub-lethal predation a proxy for overall rates of predation mortality, it seems likely that the predators that cause sub-lethal injuries (especially loss of individual arms) are different from those predators capable of killing crown-of-thorns (Cowan

et al. 2017b). Higher prevalence and severity of sub-lethal predation is nonetheless, likely to have significant impact on the individual fitness and population dynamics of crown-of-thorns starfish regardless of whether injuries are a valid proxy for overall predation and predation rates (Harris 1989; Zajac 1995; Budden et al. 2019; Wilmes et al. 2019). Budden et al. (2019), for example, showed that sublethal injuries can significantly reduce reproductive potential of *A. cf. solaris*. When coupled with high rates of self-recruitment (e.g., Wooldridge and Brodie et al. 2015) this would suggest that higher densities of putative predators, ranging from planktivorous fishes that feed on gametes and/ or larvae (Cowan et al. 2016a, 2017a) to larger benthic feeding fishes (Kroon et al. 2020) within no-take marine reserves, may serve to suppress populations and perhaps even prevent localized population irruptions. As such, high prevalence of sub-lethal predation may contribute to the lower incidence of population irruptions of *A. cf. solaris* recorded on reefs that are closed to fishing (Sweatman 2008).

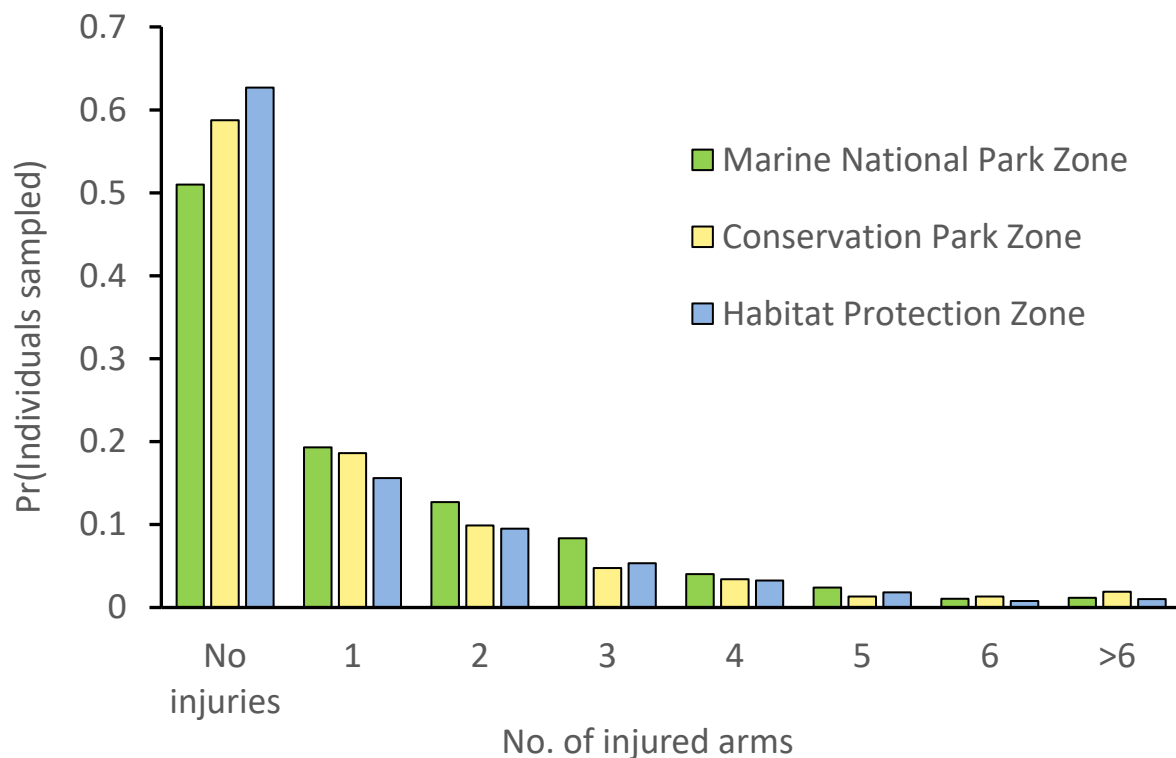


Figure 6: Proportion of Pacific crown-of-thorns starfish (*A. cf. solaris*) sampled from reefs within three different management zones on the Great Barrier Reef (see Table 2) without injuries versus increasing number of arms injured.

3.1.2 Early-stage juvenile crown-of-thorns starfish

Most (182 out of 200) early-stage juvenile CoTS sampled from across the GBR had evidence of injuries, whereby they had at least one arm for which the overall radial extent was >10% shorter than the longest arm (Figure 4). The prevalence of injuries (91.00%) for these small (up to 45mm diameter) starfish was much higher than was recorded for adult *A. cf. solaris* (43.22%; $n = 5,238$) considered in this study, but also much higher than has been recorded for crown-of-thorns starfish more broadly (reviewed by Cowan et al. 2017b). Vulnerability to predation is known to vary with size and ontogeny in many organisms (e.g., Scharf et al. 2000; Urban 2007). While size-based differences in the prevalence of injuries in early-stage juvenile starfish may be somewhat confounded by differences in their capacity for regeneration

(Wilmes et al. 2019), our results suggest that vulnerability to predation declines for crown-of-thorns starfish with increasing body size (also see Rivera-Posada et al. 2014, Messmer et al. 2017, Wilmes et al. 2019). Taken together with previous studies (e.g., Keesing and Halford 1992; Cowan et al. 2016b; Wilmes et al. 2019), our results suggest that smallest post-settlement stages of CoTS (e.g., settling larvae and newly-metamorphosed starfish) are most vulnerable to sub-lethal or lethal predatory attacks.

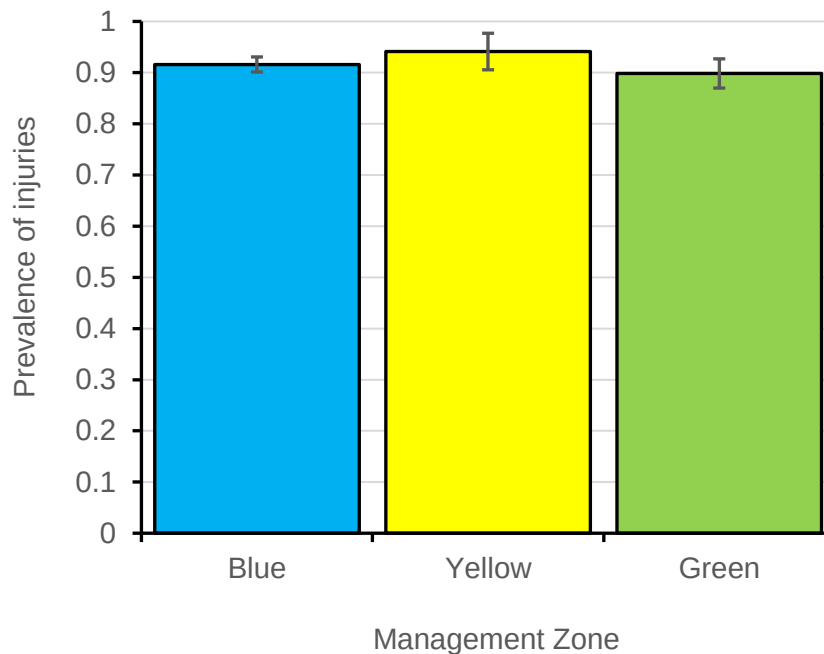


Figure 7: Mean ($\pm$ SE) prevalence of injuries (proportion of individuals on each reef that had apparent injuries) recorded for 200 crown-of-thorns starfish sampled across the GBRMP on reefs (Table 2) from specific management zones (with increasing level of fisheries protection); Habitat Protection Zones (blue zones), Conservation Park Zones (yellow zones) and Marine National Park Zones (green zones).

The proportion of injured early-stage juvenile crown-of-thorns starfish ranged from 78.57% to 100.00% among reefs (Table 2), with no apparent effect of management zone (Figure 7). Similarly, the severity (ratio between the number of injured arms and the total number of arms) of injuries did not vary between juveniles that were sampled from reefs where restricted fishing was permitted (Conservation Park and Habitat Protection Zones) versus no-take areas (Marine National Park Zones). The severity of injuries was negatively related to body size, and this was significant for coralline algal-feeding juveniles ($p < 0.05$, Figure 8 – Wilmes et al. 2019). After accounting for differences in size and ontogenetic stage, there was no difference in the severity of injuries for juvenile starfish from no-take and restricted fishing zones ($X^2 = 2.37$, $df = 4$, $p = 0.67$ – Wilmes et al. 2019).

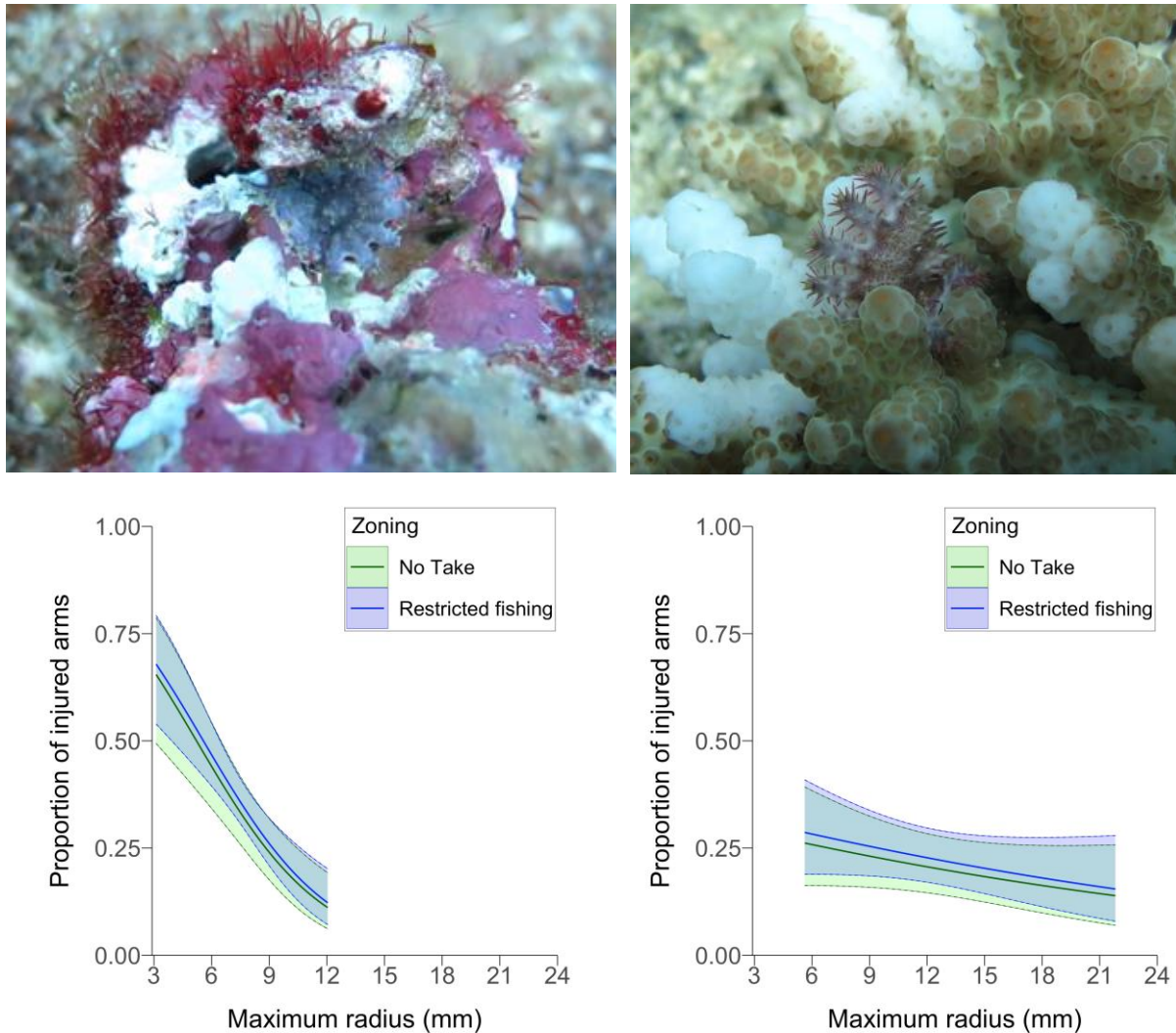


Figure 8: Severity of injuries in early-stage juvenile CoTS distinguishing between those starfish found feeding on coralline algae versus those (generally larger individuals) feeding on coral, and between those sampled from no-take marine reserves (Marine National Park Zones) and reefs where fishing was restricted (Habitat Protection Zones and Conservation Park Zones). Model data from Wilmes et al. 2019

3.2 Recruitment and survival of early-stage juvenile starfish

A total of 266 crown-of-thorns starfish (4–200 mm diameter) were recorded from June 2018 to November 2019 (Table 3). Most of these starfish (197 out of 266; i.e., 74.06%) were small (4–19 mm) and found associated with, and generally feeding on, coralline algae, while the remainder (69 individuals – 25.94%) had already shifted to feeding on scleractinian corals. In each sampling year (2018 and 2019), the initial (June) samples were clearly dominated by small (<20 mm diameter) algal-feeding individuals (Figure 9). However, by November (5 months later) there were relatively few individuals found on coralline algae, likely reflecting the ontogenetic shift in diet and habitat use, as well as growth and survivorship of these early-stage juvenile crown-of-thorns starfish (*sensu* Wilmes et al. 2020b). Though the transition from small algal-feeding individuals to larger coral feeding individuals was more apparent in 2018 than it was in 2019 (Figure 9).

Table 3: Variation in the size of crown-of-thorns starfish (*Acanthaster cf. solaris*) recorded during each of two distinct sampling occasions (June and November) in 2018 and 2019. Data was pooled across five mid-shelf reefs (n = 266 starfish); Kelso Reef, Little Kelso Reef, Rib Reef, Lodestone Reef and Keeper Reef.

Sampling time	Substrate	Diameter (in mm)				Sample size (n)
		mean	SE	min	max	
Jun-18	Coral	63.29	12.98	20	120	7
	Coralline algae	8.93	0.23	4	18	135
Nov-18	Coral	44.06	6.91	15	200	34
	Coralline algae	11.00	1.73	6	14	4
Jun-19	Coral	84.21	6.48	10	130	19
	Coralline algae	9.78	0.48	4	17	45
Nov-19	Coral	81.33	10.54	22	135	9
	Coralline algae	11.46	0.89	8	19	13

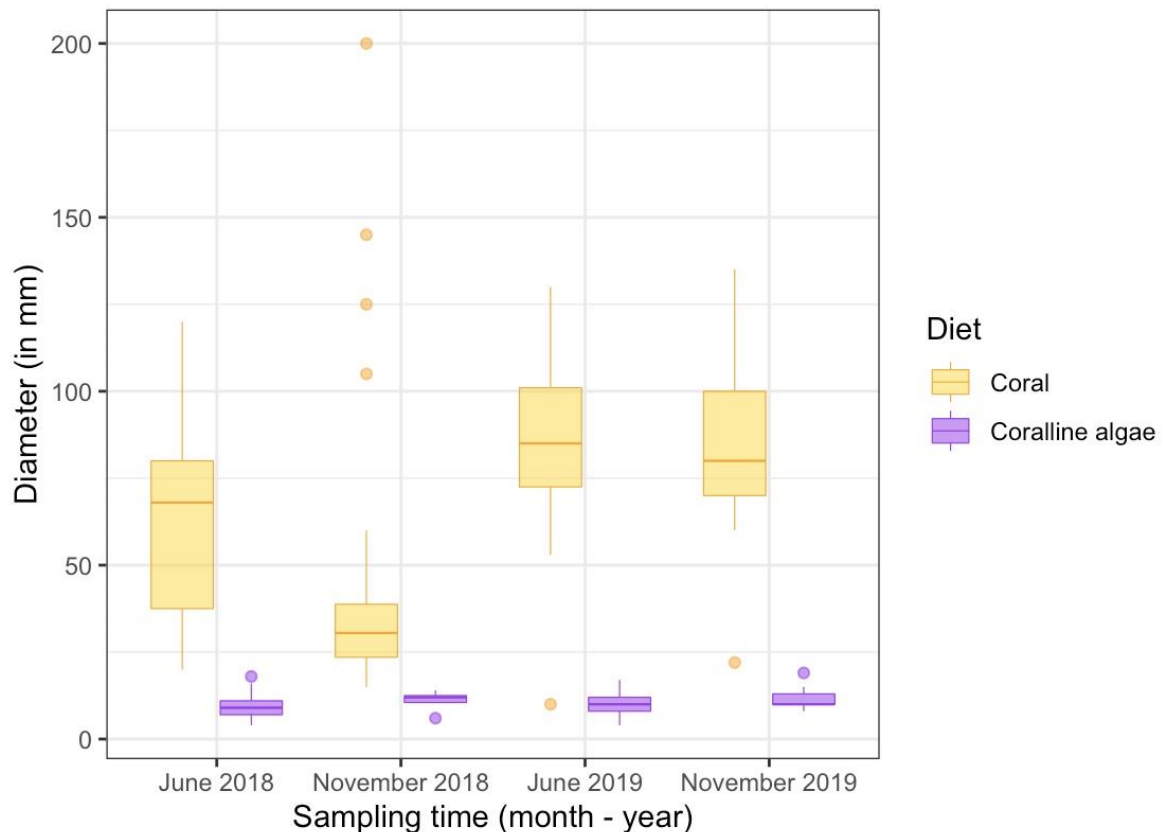


Figure 9: Boxplots showing diet-related size distribution of *Acanthaster cf. solaris* for each of two distinct sampling occasions (June and November) in 2018 and 2019. Data was pooled across five mid-shelf reefs (n = 266 starfish); Kelso Reef, Little Kelso reef, Rib Reef, Lodestone Reef and Keeper Reef.

Average densities of juvenile crown-of-thorns starfish ranged from 0.32–0.58 individuals m^{-2} across sampling locations in June 2018 (Table 4; Figure 10), with both highest and lowest densities recorded at reefs (Lodestone Reef and Keeper Reef, respectively) where restricted fishing is permitted (Habitat Protection Zone). These densities lie within the upper range of

densities of early-stage juvenile starfish (i.e., 0.00–0.77 individuals m^{-2}), recorded previously in 2017 by Wilmes et al. (2020a). In November 2018, densities of crown-of-thorns starfish recorded at reefs closed to fishing (Kelso and Little Kelso Reefs) were higher than those recorded at reefs where restricted fishing is permitted.

In June 2019 average densities of crown-of-thorns starfish were substantially lower than in June 2018, ranging from 0.05–0.30 individuals m^{-2} across sampling locations (Table 4; Figure 10). Highest averaged densities (0.22–0.30 individuals m^{-2}) were recorded at both, reefs where restricted fishing is permitted (Rib, Lodestone and Keeper Reef) and a no-take reef (Little Kelso Reef). By contrast, starfish occurred in June 2019 at the lowest density (0.05 individuals m^{-2}) at Kelso Reef (no-take). Densities of early-stage juvenile starfish recorded in June 2019 were lower than in the preceding year, but still remained within the upper range (mean = 0.11 starfish m^{-2} , median = 0.07 starfish m^{-2} , IQR = 0.01–0.13 starfish m^{-2}) of those recorded by Wilmes et al. (2020a) in 2017. In November 2019, densities of crown-of-thorns starfish recorded at reefs closed to fishing (Kelso and Little Kelso Reefs) did not seem to differ from those recorded at reefs where restricted fishing is permitted (Table 4; Figure 10).

Table 4: Density of crown-of-thorns starfish (*Acanthaster cf. solaris*) recorded at each of five mid-shelf reefs within contrasting spatial management zones.

GBRMP Zoning	Reef	Sampling time (month-year)	Mean density (ind. m^{-2})	Standard error (se)	Sample size (n)
Habitat Protection Zone	Rib	Jun-18	0.40	0.10	60
		Nov-18	0.08	0.04	60
		Jun-19	0.30	0.07	60
		Nov-19	0.18	0.06	60
	Lodestone	Jun-18	0.58	0.13	57
		Nov-18	0.05	0.03	60
		Jun-19	0.22	0.06	60
		Nov-19	0.08	0.04	60
	Keeper	Jun-18	0.32	0.09	60
		Nov-18	0.11	0.05	61
		Jun-19	0.25	0.08	60
		Nov-19	0.00	NA	60
Marine National Park Zone	Kelso	Jun-18	0.57	0.12	60
		Nov-18	0.18	0.05	61
		Jun-19	0.05	0.03	60
		Nov-19	0.00	NA	60
	Little Kelso	Jun-18	0.53	0.13	60
		Nov-18	0.20	0.06	60
		Jun-19	0.25	0.07	60
		Nov-19	0.10	0.05	60

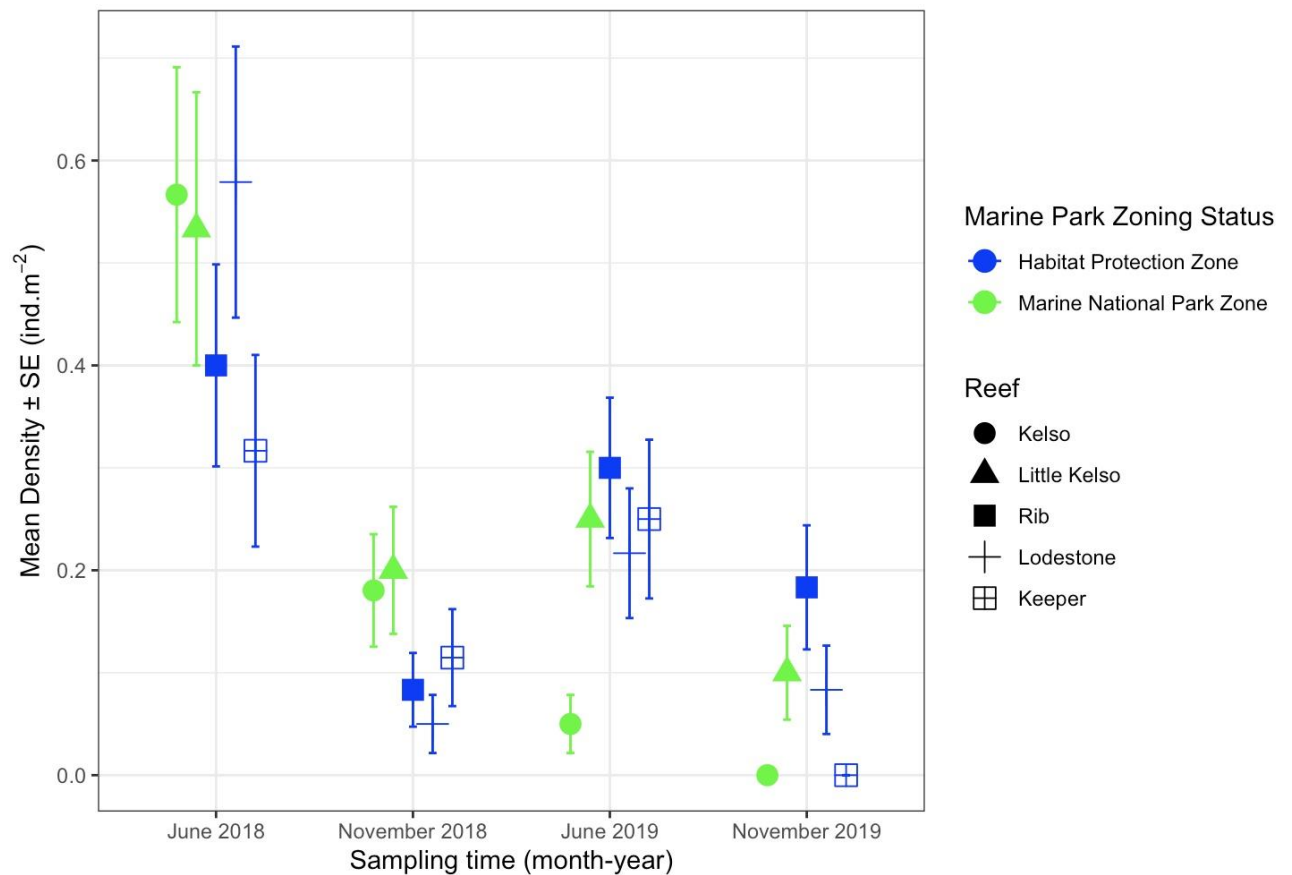


Figure 10: Mean ($\pm$ SE) density of crown-of-thorns starfish (*Acanthaster cf. solaris*) recorded at each of five mid-shelf reefs ($n \sim 60$ quadrats) within contrasting spatial management zones (see Table 4). Sampling was conducted in approximately the same locations using haphazardly placed quadrats on each sampling occasion.

When considering all locations and all sampling occasions, there are no consistent differences in densities of starfish with respect to spatial management zones (Table 4; Figure 10). Given the small sample size of sampling locations in each group of the GBRMP zone (Habitat Protection Zone, $n = 3$; Marine National Park Zone, $n = 2$), differences in mean densities of starfish, could not be statistically tested in relation to the GBRMP management zone.

Survival of starfish was estimated for each reef and year as the ratio between the mean density of starfish recorded in November and the mean density of starfish recorded in June, and then expressed as a percentage (Table 5). In 2018, estimated survivorship of starfish ranged between 8.64–37.50%, with highest survival rates recorded at Little Kelso (37.5%), followed by Keeper (36.24%), Kelso (31.82%), Rib (20.83%) and Lodestone Reef (8.64%). By contrast, in 2019 estimated survivorship ranged between 0.00–61.00%. When considering all locations and all sampling occasions, there are no consistent differences in survivorship of starfish with respect to spatial management zones.

Table 5: Reported mean densities of starfish and estimated percentage of survival and mortality by year (based on changes in densities of starfish), reef and marine park zone

GBRMP Zoning	Reef	Mean density in individuals m ⁻² (by sampling month-year)				Estimated survival (%) by year		Estimated mortality (%) by year	
		June	Nov 201	June	Nov	2018	2019	2018	2019
Habitat Protection Zone	Rib	0.40	0.08	0.3	0.1	20.83	61.11	79.17	38.89
	Lodest	0.58	0.05	0.2	0.0	8.64	38.46	91.36	61.54
	Keeper	0.32	0.11	0.2	0.0	36.24	0.00	63.76	100.00
Marine National Park Zone	Kelso	0.57	0.18	0.0	0.0	31.82	0.00	68.18	100.00
	Little Kelso	0.53	0.20	0.25	0.10	37.50	40.00	62.50	60.00

4.0 RECOMMENDATIONS AND CONCLUSIONS

The significant research and management interest in crown-of-thorns starfish directly stems from their propensity to undergo population irruptions, and their corresponding effects on coral assemblages and reef habitats (Westcott et al. 2020). Understanding population dynamics and population irruptions of *Acanthaster* spp. is currently constrained by limited knowledge of early life-history processes and vital rates (Wilmes et al. 2018) and how these vary among management zones. The present study presents the first attempt at explicitly comparing growth and survivorship of early-stage juvenile *A. cf. solaris* among reefs with contrasting management zones, based on intensive and recurrent sampling at five distinct sites. The results suggest high inter-reef and annual variability in recruitment rates of early-stage juvenile crown-of-thorns starfish. However, due to the limited number of survey sites across different zones (Habitat Protection Zone, $n = 3$; Marine National Park Zone, $n = 2$), the results are inconclusive with respect to differences in demographic rates of early-stage juveniles in relation to management zone. It is critical therefore, that further and increased research be undertaken to explicitly quantify spatiotemporal variation in demographic rates of crown-of-thorns starfish and across all life-stages.

Data pertaining to the incidence and severity of injuries for both juvenile and adult crown-of-thorns starfish adds to the considerable weight of evidence showing that *Acanthaster* spp. are extremely vulnerable to predation (Endean 1969; McCallum et al. 1989; Ormond et al. 1990; Bos et al. 2008; Rivera-Posada et al. 2014; Cowan et al. 2016a, 2017b; Wilmes et al. 2019; Kroon et al. 2020). Predation and predators may therefore, play a significant role in regulating local populations of crown-of-thorns, potentially dampening fluctuations in their local abundance and greatly reducing the likelihood of population irruptions (Ormond et al. 1990; Babcock et al. 2016a; Cowan et al. 2016a; Messmer et al. 2017). Importantly, the high prevalence, and sometimes high severity, of injuries apparent across juvenile and adult starfish are likely to impact on subsequent growth and survivorship, as well as reproductive capacity (Budden et al. 2019). There remains, however, a definite need to quantify rates of predation and mortality of crown-of-thorns starfish to better understand the specific role of reef predators on the population regulation of *Acanthaster* spp.

Maximising the number and diversity of potential predatory species (e.g., through the increased establishment no-take marine reserves and/ or increased fisheries regulation) is a *no regrets* strategy to minimise the risk of future population irruptions, given that it would also increase the resilience of coral reef ecosystems (Condie et al. 2018). However, explicit research is required to establish the relative importance of different predatory species and at different life-stages, based on their capacity to regulate larval supply, settlement, and post-settlement survivorship of *Acanthaster* spp. Rates of pre- and post-settlement predation should then be related to the local abundance of different predators to test whether changes in the functional diversity and composition of coral reef assemblages (e.g., inside and outside of no-take marine reserves) have measurable effects on the demography and population dynamics of crown-of-thorns starfish (Cowan et al. 2016a). Importantly, new technologies provide much improved opportunities to identify potential predators (Kroon et al. 2020), while increased potential to tag and track benthic species within reef environments (Pratchett et al. 2020; Schlaff et al. 2020) pave the way for much greater insights into predator-prey dynamics.

REFERENCES

- Adjeroud M, Michonneau F, Edmunds PJ, Chancerelle Y, De Loma TL, Penin L, Thibaut L, Vidal-Dupiol J, Salvat B, Galzin R (2009) Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef. *Coral Reefs* 28(3):775-80
- Alvarez-Filip L, Dulvy NK, Gill JA, Co  te IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences* 276(1669):3019-3025
- Antonelli PL, Kazarinoff ND (1984) Starfish predation of a growing coral reef community. *Journal of Theoretical Biology* 107: 667-684
- Aswani S, Basurto X, Ferse S, Glaser M, Campbell L, Cinner JE, Dalton T, Jenkins LD, Miller ML, Pollnac R, Vaccaro I (2018) Marine resource management and conservation in the Anthropocene. *Environmental Conservation* 45(2):192-202
- Anthony KR, Marshall PA, Abdulla A, Beeden R, Bergh C, Black R, Eakin CM, Game ET, Gooch M, Graham NAJ, Green A, Heron SF, van Hooidonk R, Knowland C, Mangubhai S, Marshal N, Maynard JA, McGinnity P, McLeod E, Mumby PJ, Nystrom M, Obura D, Oliver J, Possingham HP, Pressey RL, Rowlands GP, Tamelander J, Wachenfeld D, Wear S (2015) Operationalizing resilience for adaptive coral reef management under global environmental change. *Global Change Biology* 21(1):48-61
- Ayukai T (1994) Ingestion of ultraplankton by the planktonic larvae of the crown-of-thorns starfish, *Acanthaster planci*. *The Biological Bulletin* 186(1):90-100
- Babcock RC, Mundy CN (1993) Seasonal changes in fertility and fecundity in *Acanthaster planci*. pp13-20 In: Engelhardt U, Lassig B (eds) *The Possible Causes and Consequences of Outbreaks of Crown-of-Thorns Starfish*. Workshop Series No. 18, Great Barrier Reef Marine Park Authority, Australia
- Babcock RC, Dambacher JM, Morello EB, Plaganyi EE, Hayes KR, Sweatman HP, Pratchett MS (2016a) Assessing different causes of crown-of-thorns starfish outbreaks and appropriate responses for management on the Great Barrier Reef. *PLoS One*. 11(12):e0169048
- Babcock RC, Milton DA, Pratchett MS (2016b) Relationships between size and reproductive output in the crown-of-thorns starfish. *Marine Biology* 163(11):234
- Beaman RJ (2010) Project 3D-GBR: A high-resolution depth model for the Great Barrier Reef and Coral Sea. Marine and Tropical Sciences Research Facility (MTSRF) Project 2.5i.1a Final Report, MTSRF, Cairns, Australia, pp. 13 plus Appendix 1.
- Bellwood DR, Hoey AS, Hughes TP (2012) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B: Biological Sciences* 279(1733):1621-1629
- Bellwood DR, Pratchett MS, Morrison TH, Gurney GG, Hughes TP,   lvarez-Romero JG, Day JC, Grantham R, Grech A, Hoey AS, Jones GP (2019) Coral reef conservation in the Anthropocene: Confronting spatial mismatches and prioritizing functions. *Biological Conservation* 236:604-615

- Bos AR, Gumanao GS, Salac FN (2008) A newly discovered predator of the crown-of-thorns starfish. *Coral Reefs*. 2008 27(3):581
- Bos AR, Gumanao GS, van Katwijk MM, Mueller B, Saceda MM, Tejada RLP (2011) Ontogenetic habitat shift, population growth, and burrowing behavior of the Indo-Pacific beach star, *Archaster typicus* (Echinodermata; Asteroidea). *Marine Biology* 158:639–648
- Bozec YM, O'Farrell S, Bruggemann JH, Luckhurst BE, Mumby PJ (2016) Tradeoffs between fisheries harvest and the resilience of coral reefs. *Proceedings of the National Academy of Sciences* 113(16):4536-4541
- Brodie JE (1992) Enhancement of larval and juvenile survival and recruitment in *Acanthaster planci* from the effects of terrestrial runoff: a review. *Marine and Freshwater Research*. 43(3):539-553
- Brodie J, Fabricius K, De'ath G, Okaji K (2005) Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. *Marine Pollution Bulletin* 51(1-4):266-278
- Brodie J, Pearson RG (2016) Ecosystem health of the Great Barrier Reef: time for effective management action based on evidence. *Estuarine, Coastal and Shelf Science* 183:438-451
- Brodie J, Devlin M, Lewis S (2017) Potential enhanced survivorship of crown of thorns starfish larvae due to near-annual nutrient enrichment during secondary outbreaks on the central mid-shelf of the Great Barrier Reef, Australia. *Diversity* 9(1):17
- Browne NK, Tay JK, Low J, Larson O, Todd PA (2015) Fluctuations in coral health of four common inshore reef corals in response to seasonal and anthropogenic changes in water quality. *Marine Environmental Research* 105:39-52
- Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One* 2(8):e711
- Budden C, Butler I, Wolfe K, Deaker D, Sweatman H, Byrne M (2019) Effect of sublethal predation on reproductive output of the crown-of-thorns starfish *Acanthaster* sp., with an overview of arm damage. *Marine Ecology Progress Series* 629:103-116
- Caballes CF, Pratchett MS, Buck AC (2017) Interactive effects of endogenous and exogenous nutrition on larval development for crown-of-thorns starfish. *Diversity* 9(1): 15
- Carter AB, Davies CR, Emslie MJ, Mapstone BD, Russ GR, Tobin AJ, Williams AJ (2017) Reproductive benefits of no-take marine reserves vary with region for an exploited coral reef fish. *Scientific Reports* 7(1):9693
- Chesher RH (1969) Destruction of Pacific corals by the sea star *Acanthaster planci*. *Science* 165(3890):280-283
- Comeros-Raynal MT, Lawrence A, Sudek M, Vaeoso M, McGuire K, Regis J, Houk P (2019) Applying a ridge-to-reef framework to support watershed, water quality, and community-based fisheries management in American Samoa. *Coral Reefs* 38(3):505-520
- Condie SA, Plagányi EE, Morello EB, Hock K, Beeden R (2018) Great Barrier Reef recovery through multiple interventions. *Conservation Biology* 32(6):1356-1367.

- Cowan ZL, Dworjanyn SA, Caballes CF, Pratchett MS (2016a) Predation on crown-of-thorns starfish larvae by damselfishes. *Coral Reefs* 35:1253-1262
- Cowan ZL, Dworjanyn SA, Caballes CF, Pratchett MS (2016b) Benthic predators influence microhabitat preferences and settlement success of crown-of-thorns starfish (*Acanthaster cf. solaris*). *Diversity* 8(4): 27
- Cowan Z, Ling SD, Dworjanyn SA, Caballes CF, Pratchett MS (2017a) Interspecific variation in potential importance of planktivorous damselfishes as predators of *Acanthaster* sp. eggs. *Coral Reefs* 36(2): 653-661
- Cowan Z, Pratchett MS, Messmer V, Ling S (2017b) Known predators of crown-of-thorns starfish (*Acanthaster* spp.) and their role in mitigating, if not preventing, population outbreaks. *Diversity* 9(1):7
- Darling ES, McClanahan TR, Maina J, Gurney GG, Graham NA, Januchowski-Hartley F, Cinner JE, Mora C, Hicks CC, Maire E, Puotinen M (2019) Social–environmental drivers inform strategic management of coral reefs in the Anthropocene. *Nature Ecology & Evolution* 3(9):1341-1350
- Day JC (2002) Zoning - lessons from the Great Barrier Reef marine park. *Ocean and Coastal Management* 45(2-3):139-156
- De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27–year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences* 109(44):17995-17999
- Dulvy NK, Freckleton RP, Polunin NV (2004) Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters* 7(5):410-416
- Edwards CB, Friedlander AM, Green AG, Hardt MJ, Sala E, Sweatman HP, Williams ID, Zgliczynski B, Sandin SA, Smith JE (2014) Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proceedings of the Royal Society B: Biological Sciences* 281(1774):20131835
- Emslie MJ, Pratchett MS, Cheal AJ, Osborne K (2010) Great Barrier Reef butterflyfish community structure: the role of shelf position and benthic community type. *Coral Reefs* 29(3):705-715
- Emslie MJ, Logan M, Williamson DH, Ayling AM, MacNeil MA, Ceccarelli D, Cheal AJ, Evans RD, Johns KA, Jonker MJ, Miller IR (2015) Expectations and outcomes of reserve network performance following re-zoning of the Great Barrier Reef Marine Park. *Current Biology* 25(8):983-992
- Endean R (1969) Report on investigations made into aspects of the current *Acanthaster planci* (crown-of-thorns) infestations of certain reefs of the Great Barrier Reef. Queensland Department of Primary Industries (Fisheries Branch), Australia.
- Endean R (1973) Population explosions of *Acanthaster planci* and associated destruction of hermatypic corals in the Indo-West Pacific region. pp 389–438 In: Jones OA, Endean R (ed) *Biology and Geology of Coral Reefs*. Academic Press, New York
- Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50(2):125-146

- Fabricius KE, Okaji K, De'Ath G (2010) Three lines of evidence to link outbreaks of the crown-of-thorns seastar *Acanthaster planci* to the release of larval food limitation. *Coral Reefs*. 29(3):593-605
- Faurea G (1989) Degradation of coral reefs at Moorea Island (French Polynesia) by *Acanthaster planci*. *Journal of Coastal Research* 1:295-305
- Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA.
- Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301(5635):958-960
- Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2005) Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline. *Ecology* 86(1):174-184
- Graham NA, Wilson SK, Jennings S, Polunin NV, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences, USA* 103(22):8425-8429
- Harris RN (1989) Nonlethal injury to organisms as a mechanism of population regulation. *American Naturalist* 134:835–847
- Hock K, Wolff NH, Condie SA, Anthony KR, Mumby PJ (2014) Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef. *Journal of Applied Ecology* 51(5):1188-1196
- Hock K, Wolff NH, Ortiz JC, Condie SA, Anthony KR, Blackwell PG, Mumby PJ (2017) Connectivity and systemic resilience of the Great Barrier Reef. *PLoS Biology* 15(11):e2003355
- Hopley D, Smithers SG, Parnell KE (2007) *The geomorphology of the Great Barrier Reef; Development Diversity and Change*. Cambridge University Press, Cambridge
- Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JB, Kleypas J, Van De Leemput IA, Lough JM, Morrison TH, Palumbi SR (2017a) Coral reefs in the Anthropocene. *Nature* 546(7656):82-90
- Hughes TP, Kerry JT, Alvarez-Noriega M, Alvarez-Romero JC, Anderson KD, et al. (2017b) Global warming and recurrent mass bleaching of corals. *Nature* 543: 373-377
- Kayal M, Vercelloni J, De Loma TL, Bosserelle P, Chancerelle Y, Geoffroy S, Stievenart C, Michonneau F, Penin L, Planes S, Adjeroud M (2012) Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. *PloS One* 7(10):e47363
- Keesing J, Halford A (1992) Field measurement of survival rates of juvenile *Acanthaster planci*, techniques and preliminary results. *Marine Ecology Progress Series* 85:107-114
- Kenchington RA (1977) Growth and recruitment of *Acanthaster planci* (L.) on the Great Barrier Reef. *Biological Conservation* 11(2):103-118
- Kroon FJ, Lefèvre CD, Doyle JR, Patel F, Milton G, Severati A, Kenway M, Johansson CL, Schnebert S, Thomas-Hall P, Bonin MC (2020) DNA-based identification of predators of the corallivorous Crown-of-Thorns Starfish (*Acanthaster cf. solaris*) from fish faeces and gut contents. *Scientific Reports* 10(1):8184

- Lenth, R. Love, J., & Hervé, M. (2017). Package 'emmeans'. Underst Stat, 34, 216-21.
- Lucas JS (1982) Quantitative studies of feeding and nutrition during larval development of the coral reef asteroid *Acanthaster planci* (L.). Journal of Experimental Marine Biology and Ecology 65(2):173-193
- McCallum HI, Endean R, Cameron AM (1989) Sublethal damage to *Acanthaster planci* as an index of predation pressure. Marine Ecology Progress Series 56:29-36
- McCook LJ, Ayling T, Cappo M, Choat JH, Evans RD, De Freitas DM, Heupel M, Hughes TP, Jones GP, Mapstone B, Marsh H, Mills M, Molloy FJ, Pitcher CR, Pressey RL, Russ GR, Sutton S, Sweatman HPA, Tobin R, Wachenfeld DR, Williamson DH (2010) Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. Proceedings of the National Academy of Sciences, USA 107(43):18278-18285
- Miller I, Cheal AJ, Emslie MJ, Logan M, Sweatman H (2012) Ongoing effects of no-take marine reserves on commercially exploited coral trout populations on the Great Barrier Reef. Marine Environmental Research 79:167-170
- Mellin C, MacNeil AM, Cheal AJ, Emslie MJ, Caley JM (2016) Marine protected areas increase resilience among coral reef communities. Ecology Letters 19(6):629-637
- Mellin C, Matthews S, Anthony KR, Brown SC, Caley MJ, Johns KA, Osborne K, Puotinen M, Thompson A, Wolff NH, Fordham DA (2019a) Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts. Global Change Biology 25(7):2431-2445
- Mellin C, Thompson A, Jonker MJ, Emslie MJ (2019b) Cross-shelf variation in coral community response to disturbance on the Great Barrier Reef. Diversity 11(3):38
- Messmer V, Pratchett MS, Chong-Seng K (2017) Variation in incidence and severity of injuries among crown-of-thorns starfish (*Acanthaster cf. solaris*) on Australia's Great Barrier Reef. Diversity 9(1):12
- Moran PJ (1986) The *Acanthaster* phenomenon. Oceanography and Marine Biology: An Annual Review 24:379-480
- Moran PJ, De'Ath G, Baker VJ, Bass DK, Christie CA, Miller IR, Miller-Smith BA, Thompson AA (1992) Pattern of outbreaks of crown-of-thorns starfish (*Acanthaster planci* L.) along the Great Barrier Reef since 1966. Marine and Freshwater Research 43(3):555-567
- Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. Marine Ecology Progress Series 376:295-306
- Olson RR (1985) *In situ* culturing of larvae of the crown-of-thorns starfish *Acanthaster planci*. Marine Ecology Progress Series 25:207-210
- Ormond RT, Campbell AC (1971) Observations on *Acanthaster planci* and other coral reef echinoderms in the Sudanese Red Sea. Symposia of the Zoological Society of London 1971 28(433-454):3-4.
- Ormond R, Bradbury R, Bainbridge S, Fabricius K, Keesing J, de Vantier L, Medlay P, Steven A (1990) Test of a model of regulation of crown-of-thorns starfish by fish predators. pp 189-207 In: Bradbury R (ed) *Acanthaster* and the Coral Reef: A Theoretical Perspective. Springer, Berlin

- Osborne K, Dolman AM, Burgess SC, Johns KA (2011) Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995–2009). *PloS One* 6(3):e17516
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJ, Paredes G, Warner RR (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301(5635):955-958.
- Pearson RG, Endean R (1969) A preliminary study of the coral predator *Acanthaster planci* (L.) (Asteroidea) on the Great Barrier Reef. *Fisheries Notes, Queensland Dept of Harbours and Marine* 3:27–55
- Pisapia C, Burns D, Yoosuf R, Najeeb A, Anderson KD, Pratchett MS (2016) Coral recovery in the central Maldives archipeligo since the last major mass-bleaching, in 1999. *Scientific Reports* 6:34720
- Pratchett MS, Cumming GS (2019) Managing cross-scale dynamics in marine conservation: Pest irruptions and lessons from culling of crown-of-thorns starfish (*Acanthaster* spp.). *Biological Conservation* 23:108211
- Pratchett MS, Hoogenboom MO (2019) Disturbances and pressures on coral reefs. pp 131-141 In: Hutchings P, Kingsford M (eds) *The Great Barrier Reef*. Springer
- Pratchett MS, Caballes CF, Rivera-Posada JA, Sweatman HPA (2014) Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster* spp.). *Oceanography and Marine Biology: An Annual Review* 52:133–200
- Pratchett MS, Dworjanyn SA, Mos B, Caballes CF, Thompson CA, Blowes S (2017a) Larval survivorship and settlement of crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at varying algal cell densities. *Diversity* 9(1):2
- Pratchett MS, Caballes CF, Wilmes JC, Matthews S, Mellin C, Sweatman HPA, Nadler LE, Brodie J, Thompson CA, Hoey J, Bos AR, Byrne M, Messmer V, Fortunato SAV, Chen CMN, Buck ACE, Babcock RC, Uthicke S (2017b) 30 years of research on crown-of-thorns starfish (1986-2016): Scientific advances and emerging opportunities. *Diversity* 9(4):41
- Pratchett MS, Bridge TC, Brodie J, Cameron DS, Day JC, Emslie MJ, Grech A, Hamann M, Heron SF, Hoey AS, Hoogenboom MO (2019) Australia's Great Barrier Reef. pp 333-362 In: Sheppard C (ed) *World Seas: an Environmental Evaluation*. Academic Press, London
- Pratchett MS, Caballes CF, Messmer V, Fletcher CS, Westcott DA (2020) Movement patterns of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) linked to habitat structure and prey availability. Report to the National Environmental Science Program. Reef and Rainforest Research Centre Limited, Cairns. 47pp
- R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rivera-Posada J, Caballes CF, Pratchett MS (2014) Size-related variation in arm damage frequency in the crown-of-thorns sea star, *Acanthaster planci*. *Journal of Coastal Life Medicine* 2:187-195
- Reichelt RE, Bradbury RH, Moran PJ (1990) Distribution of *Acanthaster planci* outbreaks on the Great Barrier Reef between 1966 and 1989. *Coral Reefs* 9(3):97-103

- Scharf FS, Juanes F, Rountree RA (2000) Predator size-prey size relationships of marine fish predators: Interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series* 208:229-248
- Schlaff A, Menéndez P, Hall M, Heupel M, Armstrong T, Motti C (2020) Acoustic tracking of a large predatory marine gastropod, *Charonia tritonis*, on the Great Barrier Reef. *Marine Ecology Progress Series* 642:147-161
- Sheppard C, Sheppard A, Fenner D (2020) Coral mass mortalities in the Chagos Archipelago over 40 years: Regional species and assemblage extinctions and indications of positive feedbacks. *Marine Pollution Bulletin* 154:111075
- Steneck RS, Mumby PJ, MacDonald C, Rasher DB, Stoye G (2018) Attenuating effects of ecosystem management on coral reefs. *Science Advances* 4(5):eaao5493
- Sweatman HPA, Bass DK, Cheal AJ, Coleman G, Miller IR, Ninio R, Osborne K, Oxley WG, Ryan DAJ, Thompson AA, Tomkins P (1998) Long-term monitoring of the Great Barrier Reef. Status Report No. 3. Australian Institute of Marine Science, Townsville
- Sweatman HPA (2008) No-take reserves protect coral reefs from predatory starfish. *Current Biology* 18(14):R598- R599
- Topor ZM, Rasher DB, Duffy JE, Brandl SJ (2019) Marine protected areas enhance coral reef functioning by promoting fish biodiversity. *Conservation Letters* 12(4):e12638
- Trapon ML, Pratchett MS, Penin L (2011) Comparative effects of different disturbances in coral reef habitats in Moorea, French Polynesia. *Journal of Marine Biology* 2011:807625
- Urban MC (2007) Predator size and phenology shape prey survival in temporary ponds. *Oecologia* 154(3):571-580
- Uthicke S, Schaffelke B, Byrne M (2009) A boom–bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecological Monographs* 79(1):3-24
- Uthicke S, Fisher EE, Patel F, Diaz-Guijarro B, Doyle JR, Messmer V, Pratchett MS (2019) Spawning time of *Acanthaster* cf. *solaris* on the Great Barrier Reef inferred using qPCR quantification of embryos and larvae: do they know it's Christmas?. *Marine Biology* 166(10):133
- Vanhatalo J, Hosack GR, Sweatman H (2017) Spatiotemporal modelling of crown-of-thorns starfish outbreaks on the Great Barrier Reef to inform control strategies. *Journal of Applied Ecology* 54(1):188-197
- Venables WN, Ripley BD (2002) Modern Applied statistics with S. Springer, New York
- Weijerman M, Gove JM, Williams ID, Walsh WJ, Minton D, Polovina JJ (2018) Evaluating management strategies to optimise coral reef ecosystem services. *Journal of Applied Ecology*. 55(4):1823-1833
- Westcott DA, Fletcher CS, Babcock R, Plaganyi-Lloyd E (2016) A Strategy to Link Research and Management of Crown-of-Thorns Starfish on the Great Barrier Reef: An Integrated Pest Management Approach, Report to the National Environmental Science Programme, Reef and Rainforest Research Centre Limited, Cairns, Australia 77pp
- Westcott DA, Fletcher CS, Kroon FJ, Babcock RC, Plagányi EE, Pratchett MS, Bonin MC. Relative efficacy of three approaches to mitigate crown-of-thorns starfish outbreaks on Australia's Great Barrier Reef. *Scientific Reports* 10(1):12594.

- Williamson DH, Russ GR, Ayling AM (2004) No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environmental Conservation* 1:149-159
- 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.
- Wilmes JC, Caballes CF, Cowan ZL, Hoey AS, Lang BJ, Messmer V, Pratchett MS (2018) Contributions of pre-versus post-settlement processes to fluctuating abundance of crown-of-thorns starfishes (*Acanthaster* spp.). *Marine Pollution Bulletin* 135:332-345
- Wilmes JC, Hoey AS, Messmer V, Pratchett MS (2019) Incidence and severity of injuries among juvenile crown-of-thorns starfish on Australia's Great Barrier Reef. *Coral Reefs* 38:1187-1195
- Wilmes JC, Schultz DJ (2019) Size and diet of newly settled crown-of-thorns starfish from Australia's Great Barrier Reef. James Cook University (dataset). doi:10.25903/5da3d2eb955fb.
- Wilmes JC, Hoey AS, Pratchett MS (2020a) Contrasting size and fate of crown-of-thorns starfish linked to ontogenetic diet shifts. *Proc R Soc B* 287: 20201052. doi: 10.1098/rspb.2020.1052.
- Wilmes JC, Schultz DS, Hoey AS, Messmer V, Pratchett MS (2020b) 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.
- Wolfe K, Graba-Landry A, Dworjanyn SA, Byrne M (2015) Larval starvation to satiation: Influence of nutrient regime on the success of *Acanthaster planci*. *PLoS One*10(3):e0122010
- Wolfe K, Graba-Landry A, Dworjanyn SA, Byrne M (2017) Superstars: Assessing nutrient thresholds for enhanced larval success of *Acanthaster planci*, a review of the evidence. *Marine Pollution Bulletin* 116(1-2):307-314
- Wooldridge SA, Brodie JE (2015) Environmental triggers for primary outbreaks of crown-of-thorns starfish on the Great Barrier Reef, Australia. *Marine Pollution Bulletin* 101(2):805-815
- Zajac RN (1995) Sublethal predation on *Polydora cornuta* (Polychaeta, Spionidae) - Patterns of tissue loss in a field population, predator functional response and potential demographic impacts. *Marine Biology* 123:531-541

