

Effect of sublethal predation on reproductive output of the crown-of-thorns starfish *Acanthaster* sp., with an overview of arm damage

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ABSTRACT: The extreme reproductive potential of the crown-of-thorns starfish (CoTS) *Acanthaster* sp. is a key trait used to explain their population outbreaks. Despite their highly defended morphology, sublethal predation is prevalent, as documented here for 2 outbreak populations in the Great Barrier Reef: Davies Reef and Lynch's Reef (arm damage 73.0 and 58.3 %, respectively). It is not known how this trauma affects reproductive potential as a quantitative change in gonad production. We investigated the variability in gonad weight in the arms of uninjured CoTS. For CoTS with injured arms, we assessed the impact of arm injury and regeneration on gonad development at the level of the whole individual and among arms. The gonad index (GI) was lower in CoTS with 3 or more injured arms on Davies Reef, but not Lynch's Reef. At the level of individual arms, arm damage (25–100 % of individual arm lost at Davies Reef and 10–100 % at Lynch's Reef) resulted in a lower gonad weight compared to intact arms. Arms regenerating following total arm loss had a lower gonad weight than intact arms, even for arms that were 50–74 % (Davies Reef) and 75–99 % regenerated (Lynch's Reef). For uninjured CoTS, we show strong support for GI estimates based on extrapolation from one arm, and that inclusion of more than 4 arms resulted in marginal reduction in error. It is clear that sublethal injury can have a significant effect on gonad production in CoTS, with implications for population control given the reproductive potential of this species.

KEY WORDS: Outbreak population · Arm regeneration · Reproduction · Predator removal hypothesis · Great Barrier Reef

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1. INTRODUCTION

Coral reefs across the globe are facing a perilous future due to perturbations from climate change, overfishing, coastal development, shipping and coral predation by the crown-of-thorns starfish (CoTS) *Acanthaster* sp. As the ability to address global climate change is limited (Hughes et al. 2017a,b), there has been a focus on management of local stressors (Ban et al. 2014), such as outbreaks of CoTS. Through-

out the Indo-Pacific, this has been managed through CoTS removal and killing programs (Moran et al. 1988, Pratchett et al. 2017). These sea stars are key-stone predators (sensu Paine 1966) and are a major cause of coral loss throughout the Indo-Pacific, with outbreak populations dramatically altering coral reef ecosystems (Pearson & Endean 1969, Done 1985, Birkeland & Lucas 1990, De'ath et al. 2012).

The extreme reproductive potential of CoTS is key to explaining their population fluctuations and the

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initiation of outbreaks (Babcock & Mundy 1992, Uthicke et al. 2009, Caballes & Pratchett 2014, Pratchett et al. 2014, Babcock et al. 2016a). CoTS are likely the world's most fecund starfish, with the largest females estimated to produce more than 200 million eggs per season (Babcock et al. 2016a). Male CoTS also produce huge numbers of gametes (Babcock et al. 2016a). These starfish often aggregate before synchronous gamete release (Pearson & Endean 1969, Birkeland & Lucas 1990, Babcock & Mundy 1992, Yasuda et al. 2010), promoting fertilisation success (Babcock et al. 1994, Rogers et al. 2017). Fertilisation rates as high as 83% have been recorded during large spawning events (Babcock & Mundy 1992).

Despite their highly defended morphology, which includes a prominent cover of toxic spines (Shiomi et al. 1985), sublethal predation on CoTS is well documented (Pearson & Endean 1969, Nakamura 1986, McCallum et al. 1989, Stump 1996, De'ath & Moran 1998, Rivera-Posada et al. 2014, Messmer et al. 2017). One of the main hypotheses to explain the CoTS outbreak phenomenon, the predator removal hypothesis, posits that these sea stars have been released from predation due to overfishing of their predators (Endean 1969). This is supported by the observation that outbreaks are less frequent in reefs protected from fishing (Sweatman 2008, but see Sweatman & Cappo 2018). In a recent survey of reefs along the Great Barrier Reef (GBR), 20–80% of CoTS had injured arms (Messmer et al. 2017), with similar levels of injury reported for CoTS populations in the Philippines and Japan (Nakamura 1986, Rivera-Posada et al. 2014). As typical of many stellate echinoderms (Lawrence 2010, Byrne et al. 2019), CoTS have a great capacity to regenerate arms lost to predation or other misadventure (Birkeland & Lucas 1990). Though arm damage is common in CoTS populations, the cost of sublethal predation and subsequent regeneration in terms of reduced reproductive capacity is poorly understood.

In sea stars, arm loss incurs costs including the direct loss of the gonads and loss of the pyloric caeca (nutrient storage organs that are important to support gonad growth), as well as the loss of other arm components (e.g. skeleton, body wall) (Lawrence & Moran 1992, Lawrence & Vasquez 1996, Maginnis 2006, Byrne et al. 2019). Arm loss in sea stars also affects their ability to forage, which in turn affects growth (Diaz-Guisado et al. 2006, Barrios et al. 2008). In addition to the cost of injury, there is also a cost of arm regeneration which may divert energy away from reproduction (Lawrence & Vasquez 1996, Maginnis 2006, Lawrence 2010). This energetic cost may

result in a reduction in the total number, size and/or quality of eggs (Maginnis 2006). In a detailed study of arm regeneration in sea stars, King (1898) showed that while the regrowth of the arm skeleton can be prompt, there can be a considerable delay in organ regeneration (e.g. gonads, pyloric caeca).

Despite extensive research over many decades, there remain many unanswered questions on the biology of CoTS that need to be addressed to better understand the traits and mechanisms that drive population outbreaks (Pratchett et al. 2017). The relationship between arm injury, regeneration and gonad production has not yet been systematically studied in CoTS. We investigated the impact of sublethal injury in the form of damaged and regenerating arms on the gonad output of CoTS from 2 outbreak populations on the central GBR (Davies Reef, Lynch's Reef) just prior to the peak of spawning. In a comprehensive study of the relationship between arm trauma and gonad development in CoTS, we examined over 2000 arms from 148 starfish. Several studies have estimated the gonad index (GI) for an individual CoTS from samples of one or a few arms (Pearson & Endean 1969, Lucas 1973, Conand 1985, Kettle & Lucas 1987, Babcock et al. 2016a). Here, we used our empirical data to assess the precision of estimates of GI based on sampling different numbers of intact arms.

The CoTS group across the Indo-Pacific are now known to be a species complex with uncertain taxonomy (Haszprunar et al. 2017). Although the name 'solaris' is suggested as an available name for the '*Acanthaster* sp. Pacific clade' (Haszprunar et al. 2017 and others), the basis for this designation is uncertain as there are no independent (morphological) criteria or molecular verification data (C. Mah pers. comm.). Thus, we refer to this species as CoTS throughout.

2. MATERIALS AND METHODS

2.1. Specimen collection and dissection

A total of 148 CoTS were collected between 15 and 25 November 1991, at the time of peak gonad development for populations in the central GBR, and about 2 wk prior to the commencement of spawning (Babcock & Mundy 1992). All collected specimens had the colour typical of the Pacific variety of CoTS (see Haszprunar et al. 2017). In total, 96 starfish were collected from Lynch's Reef (18°46' S, 147°38' E), and 52 were collected from Davies Reef (18°50' S, 147°38' E). These reefs are located 2 km apart in the middle of the continental shelf (Fig. 1). At the time of collection,

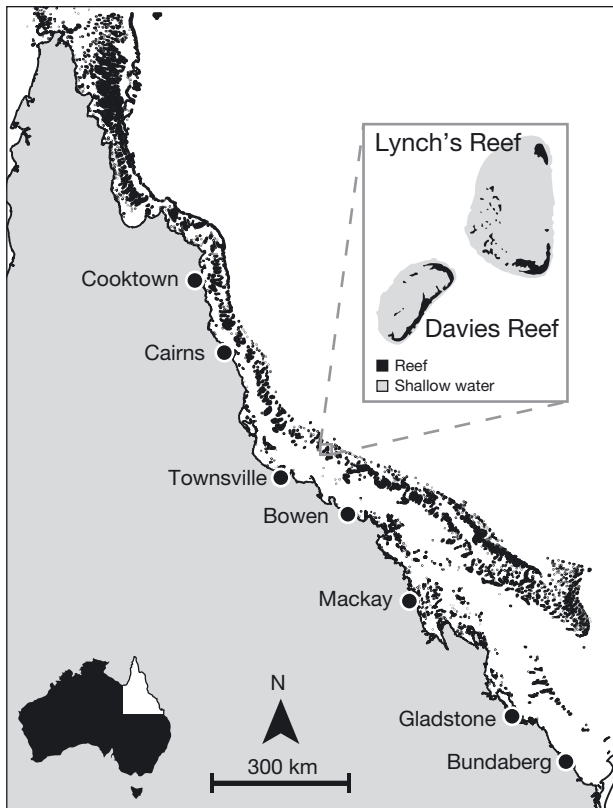


Fig. 1. Queensland (Australia), showing the location of Davies and Lynch's Reefs

Davies Reef was gazetted as a Marine National Park 'A' Zone and Lynch's Reef was General Use 'B' Zone. With this zoning fishing was allowed at both reefs. At the time of collection, these reefs were experiencing active sea star outbreaks, as indicated by the large numbers and high density of CoTS (I. Butler pers. obs.). The starfish were placed in a 1000 l tank with running seawater on board a ship.

Prior to dissection, each starfish was held up for about 3 s, shaken slightly to drain excess water and

then placed into a plastic tray. Their diameter (cm) was measured from arm tip to opposite arm tip across intact (uninjured) arms. Before dissection, a starting point was selected randomly, and the arms were numbered consecutively in a clockwise direction from this point for identification. The starfish were checked for injured and regenerating arms. An arm was considered to have been injured if it was obviously shorter than adjacent arms or if the starfish had a gap near the disc where an arm was missing completely (Fig. 2a,b). CoTS have their full set of arms within ~18 wk after metamorphosis (Yamaguchi 1973), so the presence of short and/or missing arms was attributed to sublethal predation. An arm was considered to be regenerating if there was obvious new growth, since regenerates have a thinner profile, lighter colour and finer, shorter spines compared with uninjured arms (Fig. 2c). Regenerating arms ranged from those with small, new growth buds extending from the original wound to longer, newly regenerated arms. The length of arms showing injury or regeneration was measured and recorded as a percentage with respect to of the length of the uninjured arms for each starfish. The amount of regeneration per arm was estimated.

2.2. GI calculations

All gonad material was removed from each arm. The sex was noted based on visual inspection, although the sex of one individual could not be determined. The gonads from each arm were then frozen and weighed separately (0.001 g accuracy). The somatic weight was obtained after dissection as the weight of all body structures without the gonads and coelomic fluid. Somatic weight and total gonad wet weight were summed to provide a total body weight. The somatic weights of 3 individuals were not recorded.

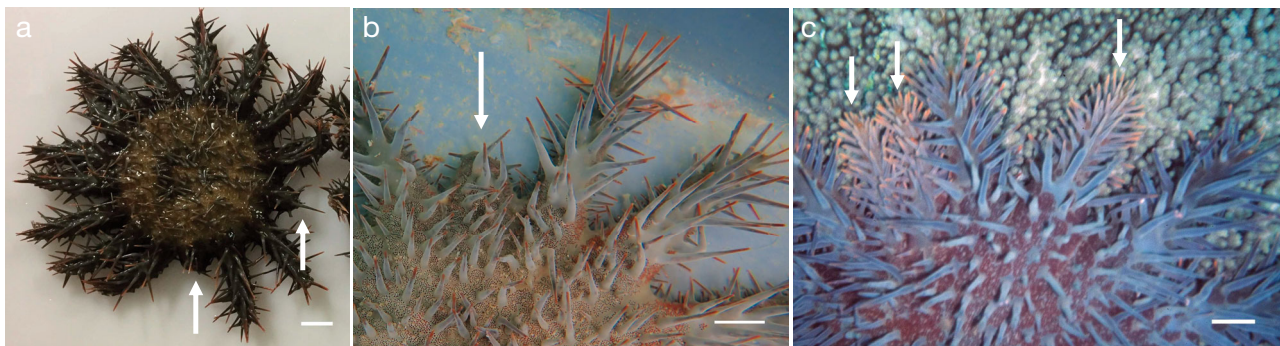


Fig. 2. Crown-of-thorns starfish (CoTS) (a,b) with short and missing arms (arrows) and (c) *in situ* with 3 regenerating arms (arrows). Scale bar: 20 mm

Total GI was calculated for each CoTS as the total gonad wet weight (from all arms) divided by total body weight (somatic weight + gonad wet weight) multiplied by 100. Several studies have used data from just one or a few arms to estimate the GI for the whole starfish (Pearson & Endean 1969, Lucas 1973, Conand 1985, Kettle & Lucas 1987, Babcock et al. 2016a). To test the validity of this approach, we also estimated the GI of uninjured starfish, using the gonad weights from successive, randomly selected arms. GI was calculated sequentially, first using one randomly selected arm, then using 2 randomly selected arms, and so on, until all arms were included ($n = 13\text{--}18 \text{ ind.}^{-1}$). Note that the maximum estimated GI using all arms is essentially the total empirically determined GI. Arms were randomly selected for each starfish using the 't(apply)' function in the 'base' package of R (R Core Team 2019).

2.3. Sublethal injury and the cost to reproduction

To characterise the incidence of sublethal predation at each reef, the proportion of starfish with injured arms was determined. For individuals with injured arms, the severity index of damage was calculated as the number of injured arms divided by the total number of arms as in Messmer et al. (2017). We also used the regeneration index of Rivera-Posada et al. (2014) to provide a comparative assessment. This index is the number of regenerating arms divided by the total number of injured arms in an individual.

The potential cost of arm injury in gonad production was analysed for individual arms and for whole starfish. At the starfish level, CoTS were separated into 4 categories based on the number of injured arms (0, 1–2, 3–4, 5+) for each population. For the analysis at the level of individual arms, injured arms were classified into 3 length categories (<50%, 50–74%, 75–99%) depending on the percentage of arm present, regardless of whether there was evidence of regeneration. Intact arms were included as a control.

The influence of arm regeneration on gonad weight was explored using a subset of cases where arms were regenerating following total arm loss ($n = 79$). The regenerating arms were classified into 3 length categories as above (<50%, 50–74%, 75–99%). Intact arms were included as a control.

2.4. Statistical analyses

For the entire sample population (injured and uninjured), size, GI and arm data for the 2 popula-

tions (Davies Reef, Lynch's Reef) were compared using a Student's *t*-test. The sex ratio of all CoTS and those with arm damage was analysed using a chi-squared goodness-of-fit test for deviation from the expected 1:1 ratio. Male and female reproductive investment were compared using a Student's *t*-test, and the influence of size on GI was examined with a linear correlation of total body weight and GI for each sex. We examined the variation between total GI (based on use of all gonads in each individual) and GIs extrapolated from incremental subsamples of gonads (from one arm to the maximum arm number) using linear regression models using the 'lm' function in the 'stats' package of R (R Core Team 2019). We also plotted the improvement in r^2 values with inclusion of additional arms to identify the number of arms from which there was a marginal gain with respect to estimation error. Incidence of injury in the 2 populations was compared using a 2-proportions *z*-test. The regeneration index for injured individuals in the 2 populations was compared using a Student's *t*-test. The GI of starfish at the 2 reefs were compared using a 2-way ANOVA with reef and number of injured arms as fixed factors. Tukey's HSD test was used for post hoc comparisons. To determine the effect of arm injury on the gonads, the weight data for these organs from injured arms were analysed using general linear mixed-effects models (GLMMs) fit by maximising the restricted log-likelihood (REML) using the 'nlme' package in R (Pinheiro et al. 2018). This method handles constraints of non-independence and accounts for spatial and temporal auto-correlation (Dormann et al. 2007). Similarly, the gonad weight data for arms that were regenerating after total arm loss were analysed using GLMMs. Models were fit with arm damage, total body weight, site (Davies and Lynch's Reefs) and sex (male, female) as fixed factors, treating CoTS and arm number as random factors to account for non-independence of multiple arms per starfish. Model selection was determined by comparing Akaike's information criterion values for small sample sizes (AIC_c) using the 'MuMIn' package in R (Barton 2019). Pairwise comparisons were performed using the 'emmeans' package when differences in gonad weight were detected (Lenth 2018). All percent data were log transformed before analysis and relevant assumptions and fit of data were explored using residual plots. Unless otherwise stated, all statistical modelling was performed using the 'stats' package in R (R Core Team 2019). Standard errors were calculated using the 'plotrix' package in R (Lemon 2006, Fox & Weisberg 2011).

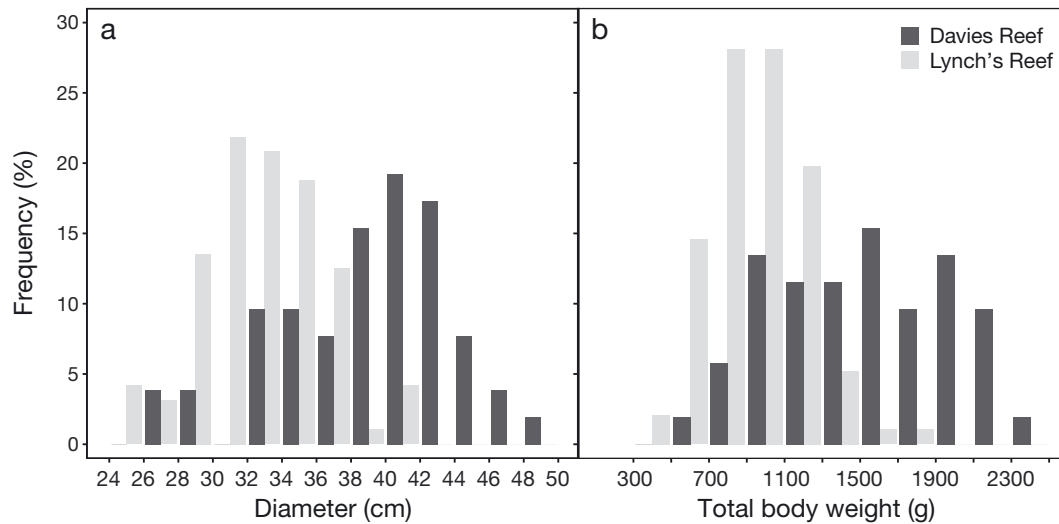


Fig. 3. Size distribution of crown-of-thorns starfish by (a) diameter and (b) total body weight at Davies ($n = 49$ –52) and Lynch's ($n = 96$) Reefs

3. RESULTS

3.1. Population biology and arm injury

CoTS from Davies and Lynch's Reefs differed significantly in diameter and weight, with a mean \pm SE diameter of 38.8 ± 0.7 cm ($n = 49$) and 32.3 ± 0.4 cm ($n = 96$) and mean \pm SE weights of 1425.7 ± 64.7 and 847.3 ± 25.4 g, respectively (t -test: diameter $t_{79.167} = 8.269$, $p < 0.001$; weight $t_{63.123} = 8.325$, $p < 0.001$) (Fig. 3). The mean \pm SE number of arms did not differ between the 2 reefs (16.0 ± 0.2 and 15.9 ± 0.1 , respectively; t -test: $t_{111.07} = 0.302$, $p = 0.763$).

Examples of arm injury and regeneration in CoTS are shown in Fig. 2. Some CoTS had gaps around the disc where an entire arm was missing and where the wound was sealed off by the body wall, while others had blunt ending arm stumps where part of the arm had been removed. In these cases, it is likely that the damage was recent as there was no evidence of regeneration. Regeneration was seen as a small arm bud or regrowth of the arm from the point of injury.

The incidence of arm injury was 73.0% ($n = 52$) at Davies Reef and 58.3% ($n = 96$) at Lynch's Reef, and this did not differ between the 2 reefs (2-tailed z -test: $z_1 = 0.390$, $p = 0.075$). Altogether, 63.5% of the starfish ($n = 148$) had arm injury, and the number of injured arms ranged from 1–7 ind.⁻¹ (Fig. 4). The mean \pm SE severity index did not differ between reefs (Davies Reef: $17.5 \pm 1.7\%$; Lynch's Reef: $14.4 \pm 1.2\%$; t -test: $t_{70.634} = 1.523$, $p = 0.132$). The mean \pm SE regeneration index did not differ between reefs (Davies Reef: $65.8 \pm 6.4\%$; Lynch's Reef: $49.0 \pm 5.7\%$; t -test: $t_{84.201} = 1.967$, $p = 0.053$).

3.2. Reproductive biology

The sex ratio of the CoTS from Davies Reef was close to 1:1, with 28 males and 24 females ($\chi^2_{(1)} = 0.308$, $p = 0.579$), while Lynch's Reef was significantly skewed towards males with 62 males and 33 females ($\chi^2_{(1)} = 8.853$, $p = 0.003$). The sex ratio of the CoTS with arm damage at each site was 1:1 at Davies Reef with 19 males and 19 females ($\chi^2_{(1)} = 0.0$, $p = 1.000$), and significantly skewed towards males at Lynch's Reef with 35 males and 20 females ($\chi^2_{(1)} = 4.091$, $p = 0.043$).

The GI for CoTS at Davies Reef (mean \pm SE $13.6 \pm 0.9\%$, $n = 49$) was greater than that for Lynch's Reef ($10.6 \pm 0.5\%$, $n = 95$), and this difference was significant (t -test: $t_{77.63} = 3.034$, $p = 0.003$). The

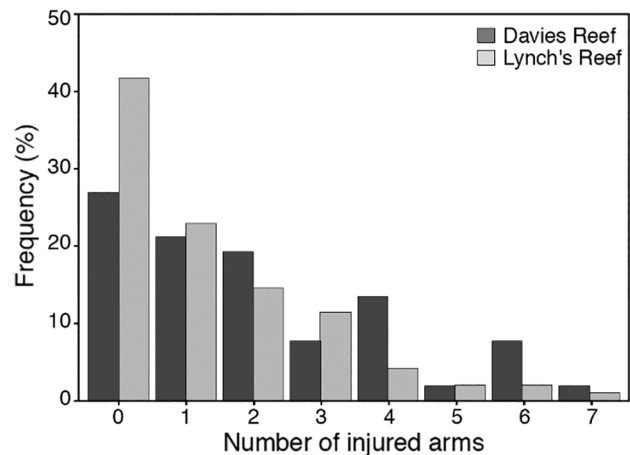


Fig. 4. Frequency distribution of the number of injured arms in crown-of-thorns starfish surveyed at Davies ($n = 52$) and Lynch's ($n = 96$) Reefs

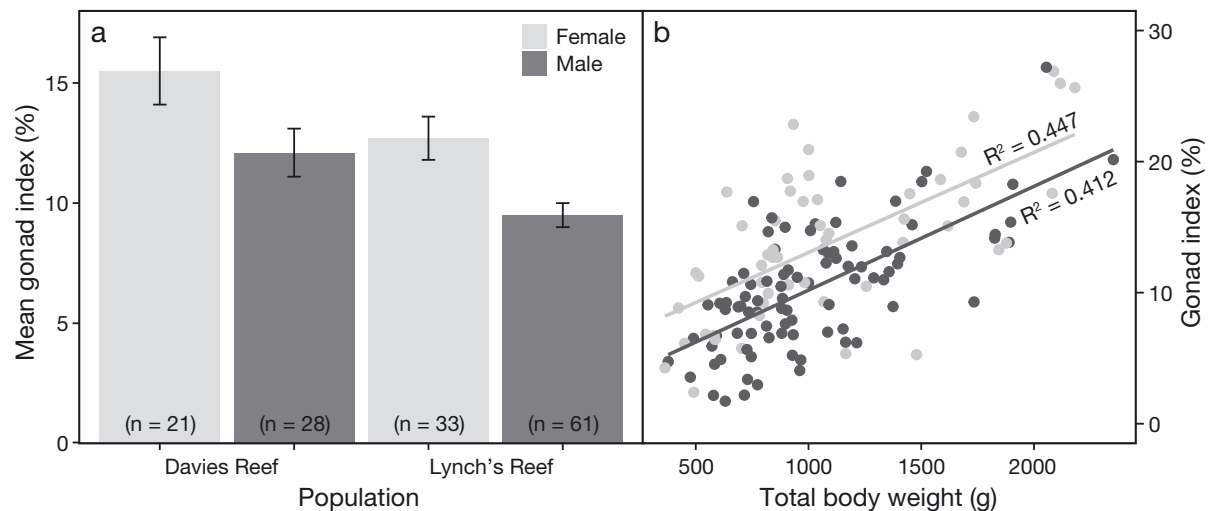


Fig. 5. (a) Mean (\pm SE) gonad index for male and female crown-of-thorns starfish at Davies and Lynch's Reefs, and (b) relationship between total body weight and gonad index for females and males

mean GI for the females and males from Davies Reef was 15.5 and 12.1%, respectively, while at Lynch's Reef mean GI was 12.7 and 9.5%, respectively (Fig. 5a). The highest individual GI was 26.9% for a female and 27.2% for a male. Overall, females ($13.8 \pm 0.8\%$) had a significantly higher GI than males ($10.3 \pm 0.5\%$) (t -test: $t_{94.00} = 3.768$, $p < 0.001$). Both sexes showed a positive linear relationship between total body weight and GI (females: $r = 0.65$, $p < 0.001$; males: $r = 0.67$, $p < 0.001$) (Fig. 5b).

For uninjured CoTS, estimated GIs calculated from individual arms varied in their proximation to the GI for the whole animal (Fig. 6a). Estimated values showed strong linear correlation with the total GI, which improved with increasing numbers of samples (Fig. 6b and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m629p103_suppl.pdf). For uninjured CoTS, estimation of the total GI based on the use of one randomly selected arm was supported ($r^2 = 0.828$), with improved precision as the number of arms used to calculate the estimate was increased (Figs. 6b & S1, Table 1). Confidence intervals were within 95% of the slope estimates when 4 or more arms were used in the GI cal-

culation, suggesting inclusion of >4 arms resulted in marginal gain with respect to decreasing measurement error.

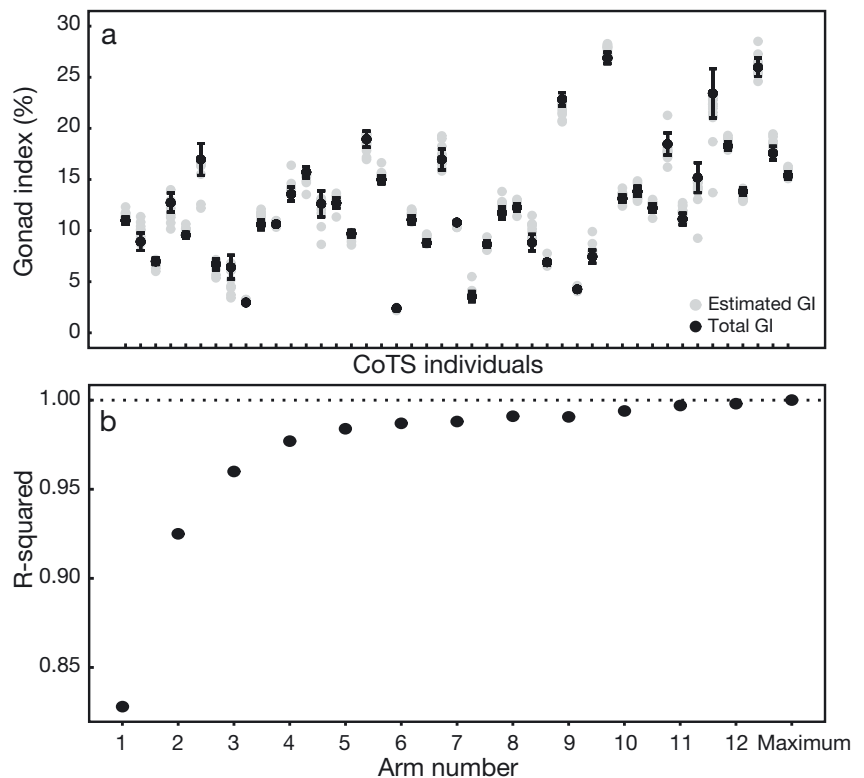


Fig. 6. Total and estimated gonad indices (GI) (a) for each individual crown-of-thorns starfish (CoTS) ($n = 45$), with estimates from randomly selected arms ($n = 13$ – 18 ind. $^{-1}$) relative to the total GI, and (b) R^2 values for linear regressions of estimated GI extrapolated using randomly selected arms vs. the total empirically determined GI from uninjured starfish ($n = 45$). Dotted line: perfect fit between estimated and total GI. Error bars in (a): SD from the total GI (note some error bars are small, not absent)

Table 1. Linear regression model results on the relationship between total and estimated gonad index (GI) in crown-of-thorns starfish, extrapolated using 1–12 randomly selected arms per starfish ($n = 45$, $df = 43$). Results for maximum number of arms ind.^{-1} ($n = 13$ –18) are shown, i.e. where estimated and total GI are the same

Number of arms used to estimate GI	<i>F</i>	<i>R</i> ²	Slope (estimate)	CI (2.5 %)	CI (97.5 %)
1	206.8	0.828	0.902	0.78	1.03
2	530.8	0.925	0.945	0.86	1.03
3	1044	0.960	0.977	0.92	1.04
4	1863	0.977	0.980	0.93	1.03
5	2679	0.984	0.978	0.94	1.02
6	3283	0.987	0.978	0.94	1.01
7	3616	0.988	0.981	0.95	1.01
8	4106	0.991	0.988	0.96	1.02
9	4640	0.991	0.975	0.95	1.00
10	6902	0.994	0.975	0.95	1.00
11	12 640	0.997	0.982	0.96	1.00
12	19 430	0.998	0.991	0.98	1.01
Maximum	1964 000	1.00	1.00	1.00	1.00

3.3. Cost of injury and regeneration on reproduction

The relationship between the GI and the number of damaged arms differed between the 2 reefs (2-way interaction, $F_{3,136} = 3.330$, $p = 0.022$) (Fig. 7, Table S1). On Davies Reef, starfish with 3–4 injured arms had a 39% decrease in GI compared with uninjured CoTS (GI = 10.1 vs. 16.6%, respectively), which was significant. At Lynch's Reef these values were 11.4 and 10.4%, respectively, and did not differ. There were no significant differences between the other 2 arm categories (1–2, 5+) with respect to the GI of uninjured CoTS for either reef. However, the sample size for the 5+ category was low ($n = 6$).

There was an effect of arm damage (i.e. arm length) on the gonad weight of CoTS (Table 2a) for both Davies and Lynch's Reef (Fig. 8a). Gonad weight in arms of <50% length (2.9 ± 0.4 g, $n = 10$) and 50–74% length (10.1 ± 1.5 g, $n = 24$) were significantly lower (80 and 29%, respectively) than that of intact arms (14.2 ± 0.4 g, $n = 683$) for CoTS at Davies Reef (Fig. 8a). Gonad weight in arms of <50% length (4.8 ± 0.6 g, $n = 19$) and 74–99% length (5.9 ± 0.6 g, $n = 47$) were significantly lower (23 and 5%, respectively) than that of intact arms (6.2 ± 0.1 g, $n =$

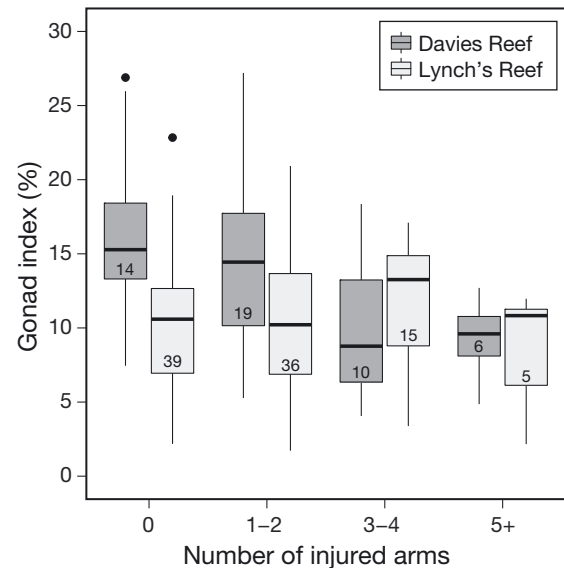


Fig. 7. Gonad index of crown-of-thorns starfish based on the number of injured arms for Davies and Lynch's Reefs. Lower and upper box boundaries: 25th and 75th percentiles, respectively; line inside box: median; whiskers: highest and lowest values within $1.5 \times$ interquartile range; filled circles: outliers. Numbers inside boxes indicate sample sizes

1349) for CoTS at Lynch's Reef (Fig. 8a). The model found that arm damage, total body weight and reef were important fixed effects (marginal $R^2 = 0.665$), with some of the variation explained by the random effect of CoTS individual (conditional $R^2 = 0.888$).

There was an effect of regeneration (following total arm loss) on gonad weight (Table 2b) for both Davies and Lynch's Reefs (Fig. 8b). For Davies Reef, gonad

Table 2. Summary statistics for gonad weight of crown-of-thorns starfish by proportion of arm present for (A) damaged arms and (B) regenerating arms within Davies and Lynch's Reefs. Significant p-values in **bold**

Reef	Parameter	Value	SE	df	<i>t</i>	<i>p</i>
(a) Amount of arm present						
Davies	50–74% (intercept)	0.178	0.141	2050	1.26	0.207
	75–99%	0.088	0.077	2050	1.14	0.256
	Intact	0.143	0.054	2050	2.64	0.008
Lynch's	50–74%	0.370	0.100	140	3.69	<0.001
	75–99%	−0.177	0.099	2050	−1.80	0.073
	Intact	−0.149	0.068	2050	−2.20	0.028
(b) Regeneration						
Davies	<50% (intercept)	0.161	0.153	1956	2.09	0.292
	50–74%	−0.121	0.103	1956	−1.78	0.239
	75–99%	0.031	0.103	1956	0.30	0.761
	Intact	0.157	0.081	1956	1.95	0.051
Lynch's	<50%	0.315	0.143	140	2.20	0.029
	50–74%	0.173	0.151	1956	1.15	0.250
	75–99%	−0.174	0.153	1956	−1.13	0.258
	Intact	−0.093	0.122	1956	−0.76	0.446

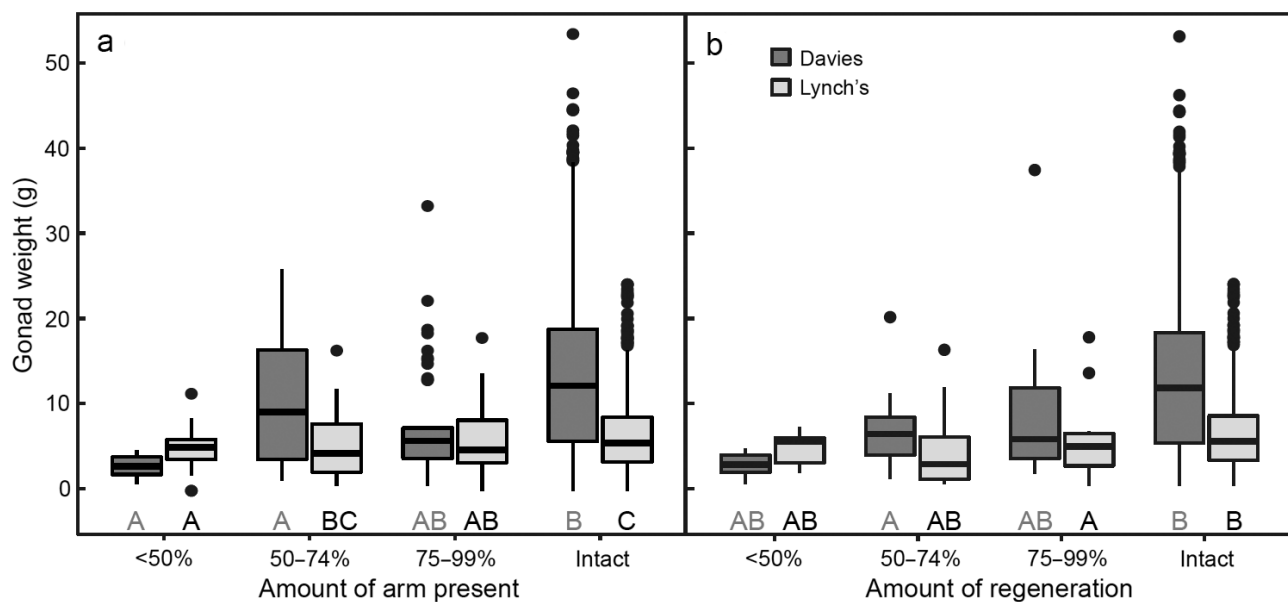


Fig. 8. Gonad weight of *Acanthaster* sp. by proportion of (a) arm damage and (b) regeneration following complete arm loss within Davies and Lynch's Reefs. Box/whisker parameters as in Fig. 7. Tukey's HSD tests within reef: similar uppercase letters indicate data that are not significantly different

weight of 50–74 % regenerated arms (7.0 ± 1.2 g, $n = 14$) was significantly lower (50 %) than for intact arms (14.2 ± 0.4 g, $n = 683$) (Fig. 8b). For Lynch's Reef, gonad weight in arms that were 75–99 % regenerated (5.6 ± 1.4 g, $n = 13$) was significantly lower (10 %) than for intact arms (6.2 ± 0.1 , $n = 1349$) (Fig. 8b). Reef, total body weight and proportion of regeneration were important fixed effects (marginal $R^2 = 0.675$), with some of the variation explained by the random effect of CoTS individual (conditional $R^2 = 0.897$).

4. DISCUSSION

Although arm damage in CoTS has been used as a metric to quantify sublethal predation (Table 3), this is the first study to explore the impact of such trauma on the reproductive capacity of CoTS. For individual arms that had lost 50 % or more of their length, the gonad weight of these injured arms was decreased by 80 and 23 % at Davies Reef and Lynch's Reef, respectively. Arms that had regenerated up to 75 % of their initial length following total arm loss on Davies Reef and ≥ 75 % on Lynch's Reef had a lower gonad weight than intact arms. The large number of arms and a body profile with a large disc to accommodate the large stomach are adaptations for predation as well as obtaining and storing energy (in the pyloric caecae), both of which are key to the enormous reproductive output of CoTS (Lawrence &

Moran 1992). Given the relationship between arm injury and reduced gonad size, sublethal predation may cause greater loss of reproductive capacity than has previously been thought.

The GI of the CoTS investigated here is similar to those reported in other studies of pre-spawning CoTS populations on the GBR, including for Davies Reef (Babcock & Mundy 1992, Stump 1994, Babcock et al. 2016a) and reefs elsewhere in the Indo-Pacific (Yamazato & Kiyon 1973, Conand 1985, Yokochi & Ogura 1987, Bos et al. 2013, Babcock et al. 2016a). GI was positively correlated with body weight, indicating that larger CoTS invest more energy in reproduction (see also Kettle & Lucas 1987, Stump 1994).

Despite the proximity of Davies and Lynch's reefs, there was a marked difference in their CoTS populations with respect to size and reproductive biology, as also noted for other reefs on the GBR (MacNeil et al. 2017). The presence of larger CoTS at Davies Reef may be due to differences in age/recruitment history. Differences in environmental conditions such as diet (Dana et al. 1972, Branham 1973, Lucas 1984), wave exposure or tidal currents (Kenchington 1977) are also known to influence growth rate of CoTS. When fed their preferred diet (e.g. *Acropora*), CoTS develop larger gonads than those fed their less preferred diet (e.g. *Porites*) (Caballes et al. 2016). However, attempts to determine the age of individual CoTS have had mixed and equivocal results (Souter et al. 1997, Stump & Lucas 1999, MacNeil et al. 2017).

Table 3. Studies reporting the proportion of adult and juvenile crown-of-thorns starfish (CoTS) with arm damage (includes regenerating and non-regenerating arms) and regenerating arms in Indo-Pacific Reefs. Definitions of missing, damaged and regenerating arms are also shown

Location	CoTS diameter (cm)	Proportion with arm damage	Proportion with regenerating arms	Definitions	Reference
Holbourne Island, Great Barrier Reef (Feb–May 1987)	Adult (20–75)	39.8 % (n = 263)	Not reported	Regenerating: arm obviously shorter than arms on either side of the injury Missing: no evidence of regeneration	McCallum et al. (1989)
15 reefs, Great Barrier Reef (2012–2015)	Juvenile to adult (6–51)	Range from 31.7–83.1 % across 15 reefs for samples n ≥ 36	Not reported	Arm damage: less than 75 % the length of adjacent arms Missing: ambulacral groove terminated at the edge of the oral disk	Messmer et al. (2017)
Philippines (2012)	Juvenile to adult (4.4–29.7)	Tandayag Marine Sanctuary: 67 % (n = 100) Tandayag Reef: 53 % (n = 132) Mactan: 62 % (n = 78)	Not reported	Arm damage: fresh injuries, missing arms, regenerating arms	Rivera-Posada et al. (2014)
Hawaii (1969–1970)	Juvenile to adult (8–33)	Not reported	Approx. 60 % (n = 1855)	Regenerating: small arm size	Branham et al. (1971), Branham (1973)
Guam (1991)	Not reported	Not reported	59 % (n = 83)	Regenerating: not defined	Lawrence (1992)
Local Island (Port Moresby), Papua New Guinea (1970)	Not reported	Not reported	> 50 % (n = 47)	Definite signs of regeneration	Pyne (1970)
Lizard Island, Great Barrier Reef (1994)	Adult (> 25)	49.5 % (n = 169)	Not reported	Arm damage: not defined	Stump (1996)
Ryukyu Islands (1984–1986)	Juvenile to adult (8–35)	Amami-oshima: 20.4 % (n = 162) Sesoko (1984): 19.8 % (n = 484) Sesoko (1985): 32.3 % (n = 192) Sesoko (1986): 33.3 % (n = 135) Tonaki: 34.7 % (n = 101) Hamashima: 45.7 % (n = 164)	Not reported	Injury scars and regeneration of discs and arms	Nakamura (1986)
Piti Bay, Guam (Jan–Jun 1981)	Not reported	43 % (n = 54)	Not reported	Gross deformities: arm stubs and missing arm tips, offset madreporites and disc clefts	Glynn (1982)
Uva Island, Panama (Jan–Jun 1980–1981)	Not reported	17 % (n = 70)	Not reported	Gross deformities: arm stubs and missing arm tips, offset madreporites and disc clefts	Glynn (1982)
Great Barrier Reef (14–46) (1967–1968)	Juvenile to adult	33.5 % (n = 346)	Not reported	Arm damage: rays less than half normal size	Pearson & Endeane (1969)
15 reefs, Great Barrier Reef (Jun 1986–Dec 1987)	Juveniles (<25); adults (≥25)	24.9 % (n = 1434)	Not reported	Damage: regenerating arms and missing body parts	De'ath & Moran (1998)
Southeastern Polynesia (1970–1971)	Adult (32–48)	Not reported	39.1 % (n = 46)	Regenerating: not defined	Devaney & Randall (1973)

The sex ratio at Davies Reef was 1:1, similar to that reported for other locations in the GBR (Pearson & Endean 1969). In contrast, the population at Lynch's Reef was skewed towards males. Male-dominant CoTS populations have also been reported elsewhere on the GBR (Pratchett et al. 2014), in the Ryukyu Islands (Nakamura 1986) and in Guam (Caballes 2017). It has been suggested that the number of females in outbreak populations decreases due to the lower survival of females after spawning as they invest more into reproduction than males (Stump 1994). As the females have larger gonads, they may also present as a more attractive nutritive resource to predators than testes, which may influence natural sex ratios towards males. However, in the present study, the total predation rate (i.e. incidence of arm injury) on females (68.4 %) and males (60.0 %) across both reefs did not differ significantly.

The GI of CoTS is often estimated based on the weight of the gonads from 1 (Pearson & Endean 1969, Lucas 1973) or 3 arms (Conand 1985, Kettle & Lucas 1987, Babcock et al. 2016a, Caballes et al. 2016). We found a strong relationship between the whole-animal GI and that extrapolated from just 1 arm ($r^2 = 0.828$), with improved precision as the number of arms increased. The linear fit of our extrapolation using 3 randomly selected arms from a pool where all arms were available to use for the model ($r^2 = 0.960$) was similar to that in Babcock et al. (2016a) ($r^2 = 0.9459$), who compared estimates of GI from 3 dissected arms per individual. While determination of GI based on dissection of 1–3 arms is less accurate than using all arms (Kettle 1990), we found that inclusion of >4 arms resulted in just a marginal gain with respect to effort and error. Certainly, the whole animal does not need to be sampled to achieve confidence in the GI estimate.

The incidence of arm injury was high in both populations (Davies Reef: 73.0 %; Lynch's Reef: 58.3 %). The high incidence of injury noted here is similar to that reported in a recent survey (2012–2015) of CoTS on 15 other reefs on the GBR (31.7–83.1 % injury), where a large number of CoTS ($n \geq 36$ reef⁻¹) were sampled (Messmer et al. 2017). In reports where the incidence of arm injury was aggregated across reefs, injury rates of 24.9 % (De'ath & Moran 1998) and 33.5 % (Pearson & Endean 1969) were reported for the GBR. Thus, in studies spanning over 20 yr, arm injury is a conspicuous and consistent feature of CoTS on the GBR, at least for outbreaking populations. In the Philippines, CoTS similar in size to those investigated here (≥ 24 cm diameter) had an incidence of injury of 45 % (Rivera-Posada et al. 2014).

With respect to the size of CoTS, there is uncertainty regarding the incidence of arm injury in juveniles and sub-adults. Messmer et al. (2017) reported a higher level of damage (>60 %) for this size class (<12.5 cm), while Rivera-Posada et al. (2014) reported lower rates of arm injury (27 % for CoTS ≤ 10 cm). However, both studies noted their low sample sizes and the difficulty of finding small CoTS in the field. Juvenile CoTS are cryptic during the day and have been observed to feed nocturnally, a behavioural adaptation which may help them avoid day-active visual predators (Keesing 1995). However, sublethal predation on juvenile CoTS is not a good proxy for overall predation rates, as predation on small individuals is more likely to be lethal than sublethal (Rivera-Posada et al. 2014, Wilmes et al. 2018). Overall, it appears that larger CoTS are less vulnerable to injury (Rivera-Posada et al. 2014, Messmer et al. 2017).

Most of the injured CoTS at Davies and Lynch's reefs had damage to just 1 or 2 arms, as reported for other populations (McCallum et al. 1989, Messmer et al. 2017). Similarly, the severity indices of injuries (mean: Davies Reef, 17.6 %; Lynch's Reef, 14.4 %) were within the range reported by Messmer et al. (2017) of 10.9–21.8 %. With respect to the details of arm injury and regeneration, it is difficult to compare among studies due to differences in how arm injury is reported in CoTS (reviewed in Rivera-Posada et al. 2014). Most studies report on all arm injury (e.g. McCallum et al. 1989, Rivera-Posada et al. 2014, Messmer et al. 2017), while others just report on regenerating arms (e.g. Pyne 1970, Branham 1973, Lawrence 1992). There are also different characterisations of injury, with some studies only reporting on arms less than 75 or 50 % normal length (e.g. Pearson & Endean 1969, Messmer et al. 2017). Disc injury is also reported to occur in CoTS (Glynn 1982, Nakamura 1986), but was not observed in this study.

Our study is one of few to make the distinction between injured arms with no regeneration evident and regenerating arms in CoTS and the first we are aware of to quantify the degree of arm injury. Across both populations we found that 56 % of injured arms were regenerating. In a study of similarly sized CoTS in the Philippines, 65 % of injured arms were regenerating (Rivera-Posada et al. 2014). The presence of regenerating and non-regenerating arms in the CoTS populations indicates that the occurrence of arm damage is temporally dynamic. It is likely that the complete absence of arms and arm stumps with no regeneration evident indicate more recent trauma than for arms with substantial regeneration evident.

Since the gonads and nutrient storage organs (pyloric caeca) are located in the sea stars' arms, injury and complete loss of arms (including substantial investment in body wall skeleton) are energetically costly, with negative impacts on reproduction (Lawrence & Moran 1992, Lares & Lawrence 1994, Bingham et al. 2000). This is demonstrated here for CoTS, with a reduced gonad weight of ~30 % in injured arms 50–74 % length on Davies Reef. A smaller effect was observed on Lynch's Reef, with a reduced gonad weight of ~25 % in injured arms <50 % length and ~5 % in injured arms 75–99 % length. Lynch's Reef had a distinctly different CoTS population with a smaller gonad weight. This effect has been noted for other asteroids. In *Leptasterias hexactis*, arm loss resulted in a 44–69 % drop in egg production even after 7 mo post-injury (Bingham et al. 2000). Barrios et al. (2008) reported a marked decrease in the energy content of the gonads of *Heliaster helianthus* that had undergone autotomy. Lares & Lawrence (1994) reported that the ovaries of regenerating arms of *Echinaster paucispinus* had a significantly lower dry weight compared to intact arms, although there was no significant difference for the testes. In stellate (narrow armed) asteroids (e.g. *Asterias* spp.), arm loss is associated with basal constriction and clean separation of the arm at a specialised autotomy plane designed to reduce soft tissue trauma and to facilitate efficient regeneration (Lawrence 1992, Wilkie 2001, Byrne et al. 2019). It is not known if arm loss in CoTS is also associated with a specialised autotomy plane. The irregular appearance of some damaged arms (M. Byrne pers. obs.) suggests tearing rather than autotomy.

In one of the most detailed studies of arm regeneration in asteroids following autotomy, King (1898) described the stages of regrowth of the arm and internal organs in *Asterias rubens*. While the regrowing arm was evident externally, there was a considerable delay in gonad regeneration. The gonads were the last organ to regenerate following arm loss. In addition, the timing of the appearance of the gonad was not related to the length of the new arm. This also seems to be the case for CoTS, as even arms that had regenerated more than 75 % of their length on Lynch's Reef, and up to 75 % on Davies Reef, had a lower (10 and 52 %, respectively) gonad weight than intact arms. There was no effect observed for arms <50 % regenerated, but this may be due to small sample sizes ($n < 10$) in this arm length category. This suggests that gonad regeneration follows formation of the arm skeleton as a supportive scaffold and does not return to its full weight until the arm approaches its full length.

The 'predator removal hypothesis' posits that, in the absence of human influences, CoTS populations are regulated by predation, and a reduction in predation pressure through overfishing can result in population outbreaks (Endean 1969). Evidence for this hypothesis largely comes from studies that have linked CoTS density with level of fishing activity and/or predator density (Ormond et al. 1990, Dulvy et al. 2004, Sweatman 2008, but see Sweatman & Cappo 2018). Protected reefs, which would be expected to have a more natural diversity across the fish guild from small planktivores to benthic foragers and large predatory fishes, are less prone to CoTS outbreaks (Sweatman 2008). There is a growing list of predators observed to prey on CoTS in aquaria or in the field (Cowan et al. 2017). Several planktivorous damselfishes prey on CoTS larvae and may reduce starfish recruitment (Cowan et al. 2016). Predators of early juvenile CoTS include the harlequin shrimp *Hymenocera* sp. and probably also include other crustaceans and polychaetes (Keesing & Halford 1992a,b, Keesing et al. 2018). However, it is unlikely that known predators can consume CoTS in sufficient quantities to prevent the initiation of CoTS outbreaks (Cowan et al. 2017), although predation may interact with other factors to regulate CoTS populations (Babcock et al. 2016b).

The other major hypothesis proposed to explain CoTS outbreaks, and which has achieved the greatest traction, is the enhanced nutrient–terrestrial runoff hypothesis, which posits that increased phytoplankton food resulting from eutrophication from land runoff enhances larval survival and success, thereby driving outbreaks (Birkeland 1982, Pratchett et al. 2014). However, support for this hypothesis is equivocal, with recent research pointing to the phenotypic plasticity of CoTS larvae and their inherent resilience to the oligotrophic conditions characteristic of coral reef waters (Wolfe et al. 2015a,b, 2017) and that CoTS outbreaks occur at great distances away from sources of enhanced nutrients (Pratchett et al. 2014). Moreover, recent studies have shown the ability of CoTS larvae to clone (Allen et al. 2019) and the potential presence of associated photobacteria (Carrier et al. 2018), emphasising that we need a greater understanding of the larval biology of this species to determine the application of hypotheses based on the larval stage.

To date, population modelling for CoTS has focussed on lethal predation (McCallum 1987, Ormond et al. 1990, Morello et al. 2014), while the potential role of sublethal predation in regulating CoTS populations has not been considered. Since arm injury

impairs gonad development, sublethal predation may have a significant influence on population dynamics (Harris 1989). Thus, reduced gonad development due to sublethal predation should be considered as one of the contributing factors that regulate CoTS population numbers. Further investigation of the conditions under which arm injury affects gonad production in CoTS, including food availability (Lawrence et al. 1986, Lawrence & Ellwood 1991) and timing of injury with respect to the breeding cycle (Pomory & Lawrence 2001), would shed light on the importance of sublethal predation in regulating CoTS populations. This has implications for modelling of CoTS populations, larval output and culling programs.

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