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REPORT

Interspecific variation in potential importance of planktivorous damselfishes as predators of *Acanthaster* sp. eggs

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Abstract Coral-eating crown-of-thorns starfish (*Acanthaster* sp.) often exhibit dramatic population outbreaks, suggesting that their local abundance may be relatively unchecked by predators. This may be due to high concentrations of anti-predator chemicals (saponins and plancitoxins), but the effectiveness of chemical deterrents in protecting *Acanthaster* sp., especially spawned eggs, from predation remains controversial. We show that planktivorous damselfishes will readily consume food pellets with low proportions ($\leq 80\%$) of eggs of crown-of-thorns starfish. However, all fishes exhibited increasing rejection of food pellets with higher proportions of starfish eggs, suggesting that chemicals in eggs of crown-of-thorns starfish do deter potential predators. Interestingly, palatability thresholds varied greatly among the nine species of planktivorous fish tested. Most notably, *Amblyglyphidodon curacao* consumed food pellets comprising 100% starfish eggs 1.5 times more than any other fish species, and appeared largely insensitive to increases in the concentration of starfish eggs. After standardising for size, smaller fish species consumed a disproportionate amount of pellets comprising high proportions of starfish eggs, indicating that abundant small-bodied fishes could be particularly important in regulating larval abundance and settlement success of crown-of-thorns starfish. Collectively, this study shows that reef fishes vary in their tolerance to anti-predator chemicals in crown-of-thorns starfish and may represent important predators on early life-history stages.

Keywords *Acanthaster* · Chemical defence · Coral reefs · Predation · Saponins

Introduction

Predation, especially predation on eggs and larvae, is considered among the most important factors that regulate the abundance of marine organisms (Bailey and Houde 1989; Hixon et al. 2002). This is because predation is often the major cause of pre-settlement mortality (e.g. Babcock et al. 1986; Bachiller et al. 2015) and may also be density dependent (Hixon et al. 2012). However, there are few studies that have attempted to quantify predation rates, let alone mortality rates, during pre-settlement life stages of marine organisms (Leis 1991). Moreover, high rates of predation on eggs and pre-settlement larvae are routinely inferred based on the sheer abundance of planktivorous organisms (e.g. Hamner et al. 1988) and the readiness with which such planktivores consume eggs and larvae during experimental feeding studies (e.g. Baird et al. 2001).

The role of predation in regulating populations of crown-of-thorns starfish (*Acanthaster* sp.) is highly controversial. On one hand, over-exploitation of key predators (e.g. giant triton, *Charonia tritonis*) is one of the primary mechanisms put forward to account for the seemingly recent occurrence of outbreaks of crown-of-thorns starfish (Endean 1969). The "predator-removal hypothesis" infers that populations of crown-of-thorns starfish are normally

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regulated by high rates of predation and that outbreaks are due (or partly due) to overharvesting of predators (Endean 1977) and/or resulting trophic cascades (Dulvy et al. 2004). Conversely, crown-of-thorns starfish have well-developed physical and chemical predatory defences and are considered to be largely immune from predation (Lucas et al. 1979; Gladstone 1992). Eggs and larvae of crown-of-thorns starfish have particularly high concentrations of saponins (Barnett et al. 1988), which have been directly implicated in defence against predators (Yamaguchi 1974, 1975; Voogt and Van Rheenen 1979).

The high incidence of injuries among adult *Acanthaster* sp. (e.g. Branham 1973; McCallum et al. 1989; Rivera-Posada et al. 2014) is attributed to sub-lethal predation and suggests that despite their spines and potentially toxic chemicals, adult crown-of-thorns starfish are vulnerable to predation. Accordingly, there are an increasing number of reef fishes and macro-invertebrates that are known to feed on crown-of-thorns starfish (Rivera-Posada et al. 2014). However, it is unclear to what extent these predators kill adult starfish and effectively reduce local densities of crown-of-thorns starfish (Pratchett et al. 2014). Intuitively, predation on smaller starfish is more likely to be lethal, and population modelling suggests that predation during early life-history stages (e.g. eggs and larvae) is likely to be much more important in regulating abundance of crown-of-thorns starfish than adult predation (McCallum 1990, 1992; Morello et al. 2014). There are several (mostly anecdotal) reports of small-bodied reef fishes, predominantly damselfishes, feeding on the eggs and/or larvae of crown-of-thorns starfish (e.g. Pearson and Endean 1969; Keesing and Halford 1992; Ciarapica and Passeri 1993). However, it does seem that there are marked interspecific differences among fishes in their readiness to eat early life-history stages of crown-of-thorns starfish, and apparent differences in the palatability of eggs versus larvae (Lucas et al. 1979; Cowan et al. 2016).

Reef-based planktivores may exert a significant toll on the reproductive output and settlement success of coral reef organisms, both during spawning, when planktivores can take advantage of high concentrations of gametes and zygotes (e.g. Pratchett et al. 2001) and during settlement, when competent larvae must run the gauntlet of potential predators in moving from offshore waters to reef environments (Hamner et al. 1988). While a range of different fishes appear to readily consume larvae of crown-of-thorns starfish (Cowan et al. 2016), relatively few fishes have been seen to consume gametes released when starfish are actively spawning in the field (Gladstone 1992; Pearson and Endean 1969). Pearson and Endean (1969) reported that only one species of damselfish (*Amblyglyphidodon curacao*) consumed eggs released by spawning crown-of-thorns starfish, though there were many different damselfishes and other planktivorous fishes in the vicinity when these observations were made.

The purpose of this study was to test for interspecific differences among planktivorous damselfishes in their feeding response to increasing proportions of eggs from crown-of-thorns starfish contained within standardised food pellets. If chemicals (e.g. saponins) contained in the eggs of *Acanthaster* sp. are an effective deterrent of planktivores, we would expect to see fish reduce consumption of pellets as the proportion of starfish eggs they contain increases (sensu Lucas et al. 1979). However, response to chemical defences is likely to vary among predators; those that exhibit only weak responses to increases in the proportion of starfish eggs (and therefore concentrations of anti-predation chemicals) in standardised food pellets, indicate fishes that might be more important as predators of *Acanthaster* sp. eggs. We tested nine species of planktivorous damselfish (*Amblyglyphidodon curacao*, *Chromis atripectoralis*, *C. viridis*, *Chrysiptera cyanea*, *C. rollandi*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis* and *P. moluccensis*), selected based on their numerical abundance on mid-shelf reefs in the northern Great Barrier Reef, Australia (Sweatman et al. 2000; Pratchett et al. 2012; Komyakova et al. 2013).

Materials and methods

Egg collection

Adult *Acanthaster* sp. were collected from Arlington Reef (16°43′S; 146°03′E) in the northern Great Barrier Reef (GBR) during September 2014. Gonads were dissected from two female *Acanthaster* sp. to ensure that a mix of genotypes was used. Gametes were collected following methods described by Kamya et al. (2014): ovaries were rinsed in 1-µm filtered seawater to remove immature eggs and then placed in 10^{-5} M 1-methyl-adenine solution to induce ovulation. Spawned eggs were collected after approximately 1 h, rinsed in fresh seawater, checked microscopically for quality (i.e. shape, integrity, germinal vesicle breakdown), then mixed in approximately equal proportions. Eggs were centrifuged on the lowest setting (200 rpm) to remove excess seawater, frozen at −80 °C and freeze-dried for transport.

Fish collection

The nine species of damselfish (*A. curacao*, *Chromis atripectoralis*, *C. viridis*, *Chrysiptera cyanea*, *C. rollandi*, *D. aruanus*, *D. reticulatus*, *P. amboinensis* and *P. moluccensis*) were collected using a combination of fence nets and clove oil on reefs at Lizard Island (14°40′S; 145°27′E)

in the northern GBR in June 2015. Fish were maintained with conspecifics in 32-L flow-through aquaria at the Lizard Island Research Station (LIRS) for a minimum of 48 h to acclimatise to laboratory conditions before being used in feeding trials. Fish were offered commercial dried fish food (New Life Spectrum) and fed to satiation each morning; they were considered acclimatised when they readily fed on the food pellets.

Palatability trials

Experimental feeding trials were conducted using standardised food pellets made by pureeing squid-mantle flesh, an equal volume of distilled water and sodium alginate at 2% of total wet mass (after Lindquist 1996; Lindquist and Hay 1996; Baird et al. 2001). The mixture was spread into a thin layer and a 0.25 M solution of calcium chloride was poured over it to set the gel. The gel was then rinsed in distilled water and cut into pellets of 0.5 mm diameter, each weighing 600 µg. Five food treatments were produced by substituting unfertilised eggs of *Acanthaster* sp. for 20, 40, 60, 80 and 100% of the squid-mantle flesh. The actual proportional content of *Acanthaster* sp. eggs in food pellets in each treatment was 11, 24, 41, 62 and 89% respectively, after accounting for the volume of distilled water and binding agent.

Feeding trials were conducted in the flow-through (open) aquarium system at LIRS. Fish were placed individually in 32-L flow-through aquaria and starved for 24 h prior to feeding trials. Fish ($n = 6$–9 per species and treatment level) were randomly assigned to one of the six feeding treatments using varying proportions (0, 20, 40, 60, 80 and 100%) of eggs of *Acanthaster* sp. versus squid-mantle flesh. Each fish was used only once, and trials were run over 16 consecutive days. Aquaria were emptied, cleaned and re-filled between consecutive feeding trials. A control pellet was introduced at the start of every trial to ensure that the fish was ready to eat. If the control pellet was consumed, five pellets from one of the six treatments were introduced in turn into the aquarium. Successive pellets were introduced once the previous pellet had been consumed, or after 2 min if the pellet was rejected. The fate of each pellet of each treatment was recorded as: (1) accepted—the fish immediately retained the pellet; (2) mouthed and accepted—the fish retained the pellet after spitting it out one or more times; (3) mouthed and rejected—the fish rejected the pellet after capturing and spitting it out several times; (4) rejected—the fish rejected the pellet after capturing and spitting it out only once; or (5) untouched—the fish visually inspected the pellet and rejected it without mouthing. At the end of each trial, a control pellet was added to ensure that any rejection responses were not due to satiation.

To analyse variation in palatability of food pellets across the six treatments with increasing concentrations of eggs

from *Acanthaster* sp., we initially compared the proportion of pellets that were consumed (regardless of whether they were mouthed). Transformations did not improve the normality of data; therefore, these data were analysed using a permutational analysis of variance (PERMANOVA), using the PERMANOVA + add-on for PRIMER v.6 with treatment and species as fixed factors, using the Euclidian distance measure, and 9999 permutations of the residuals under a reduced model to calculate the significance of the pseudo-F statistic. In cases where there were not enough unique permutations (<100) to determine permutational p-values (p_{perm}), Monte Carlo asymptotic p-values (p_{MC}) were used (Anderson et al. 2008). Data on the proportion of pellets consumed were square-root transformed prior to analysis. Pairwise comparisons were done using Benjamini–Hochberg-adjusted p-values to control false discovery rate. We also tested for changes in responses of fishes to successive food pellets (conditioning), using a Kruskal–Wallis test to assess whether there were significant differences in ingestion of pellets across all replicate fish used in each treatment ($n = 6$), based on the order of pellet.

Size-based dosage responses

To standardise for variation in the size of fish (both within and among species), length of all individuals was recorded (Table 1). Weight was estimated using length–weight ratio estimates for each species, obtained from fishbase (www.fishbase.org). The absolute quantity (mg) of eggs in each food pellet was then divided by the weight (g) of each fish to provide a dosage. Standardised response (accounting for the weight of individual fish) was analysed with logistic regression using the binomial GLM routine in R (RStudio Version 0.99.903) and checked for overdispersion. To compare palatability responses among fishes, a median rejection dose (RD_{50}) (cf. median lethal dose) was calculated for each species. This analysis assumes that variation in the sensitivity of putative predatory fishes to anti-predation chemicals in eggs of crown-of-thorns starfish is size based. However, larger fishes are likely to consume more eggs than smaller individuals or species, and so accounting for size is also necessary in establishing the importance of different planktivorous damselfishes as predators on eggs of crown-of-thorns starfish.

Results

Palatability of Acanthaster *sp. eggs*

There was a significant effect of both predator species (Pseudo-$F_{8,283} = 3.34$, $p_{perm} < 0.01$) and treatment (Pseudo-$F_{5,283} = 128.44$, $p_{perm} < 0.01$), and a significant

Table 1 Size range (total length (TL) in mm) and relative abundance of planktivorous pomacentrid fish predators used in this study

| Predator species	Size range TL (mm)	Relative abundance
Amblyglyphidodon curacao	47–90	0.9
Chromis atripectoralis	38–90	1.0
Chromis viridis	41–80	2.5
Chrysiptera cyanea	37–60	–
Chrysiptera rollandi	25–50	–
Dascyllus aruanus	33–63	0.4
Dascyllus reticulatus	36–75	0.4
Pomacentrus amboinensis	31–70	1.0
Pomacentrus moluccensis	25–55	7.3

Data on relative abundance come from Pratchett et al. (2012) and Komyakova et al. (2013), which measured abundances of damselfishes at multiple locations and habitat around Lizard Island. Relative abundance is expressed relative to the abundance of *Pomacentrus amboinensis*, which was surveyed in both studies. Neither study presented data on abundance of *Chrysiptera* spp.

interaction between predator species and treatment (Pseudo-$F_{40,283} = 2.45$, $p_{perm} < 0.01$) on the proportion of pellets consumed by fish. All fishes in this study readily consumed food pellets containing up to 80% of eggs from crown-of-thorns. However, the nine species of planktivorous damselfish varied in the extent to which they would consume food pellets containing 100% eggs from crown-of-thorns starfish (Fig. 1). Pairwise comparisons indicated that five of the predator species (*Chrysiptera rollandi*, *D. reticulatus*, *P. amboinensis*, *Chromis viridis* and *P. moluccensis*) consumed significantly fewer of the pellets containing 100% eggs, compared to all other treatments, and two species (*Chrysiptera cyanea* and *Chromis atripectoralis*) consumed significantly fewer pellets containing the highest concentration of eggs, however, the proportion of pellets consumed that contained 100% eggs was not significantly different from the proportion consumed that contained 80% eggs (Fig. 1c,g). *Dascyllus aruanus* exhibited significant declines in the consumption of food pellets with increasing concentrations of starfish eggs (Pseudo-$F_{5,43} = 6.32$, $p_{perm} < 0.01$; Fig. 1b); however, pairwise comparisons did not meet Benjamini–Hochberg criteria. While *A. curacao* also consumed fewer food pellets with increasing concentrations of starfish eggs, rates of ingestion did not differ across the six treatments (Pseudo-$F_{5,30} = 1.43$, $p_{MC} > 0.05$; Fig. 1a). *Amblyglyphidodon curacao* consumed the highest proportion of food pellets of the nine species of fish tested and consumed 1.5 times more of the pellets containing 100% starfish eggs than any other fish species.

Chrysiptera rollandi was the only species that exhibited significant changes in responses to food pellets (conditioning) depending on order (Kruskal–Wallis, χ^2 (4, $N = 30$) = 11.71, $p = 0.02$); fish that were offered pellets containing 100% eggs of crown-of-thorns starfish tended to reject (after mouthing) pellets one and two, but pellet five tended to be rejected (without mouthing) or left untouched. When considering only the fate of individual pellets (retained vs. rejected), there was no significant difference in response to pellets through time. Results were therefore pooled, disregarding the order in which pellets were offered, to compare the overall proportion of pellets that were consumed.

After standardising for size (weight) among fishes, the median rejection doses (RD$_{50}$) to pellets containing starfish eggs ranged from 0.10 ± 0.02 (SE) for *Chromis atripectoralis* to 0.53 ± 0.13 for *Chrysiptera rollandi* (Fig. 3a). Increasing the absolute amount of *Acanthaster* sp. eggs relative to the size of fishes significantly increased the probability of rejecting food pellets in seven fish species: *Chromis atripectoralis* (GLM, $\chi^2 = 2.75$, $p < 0.01$), *C. viridis* (GLM, $\chi^2 = 2.61$, $p < 0.01$), *P. amboinensis* (GLM, $\chi^2 = 2.31$, $p = 0.02$), *D. aruanus* (GLM, $\chi^2 = 2.60$, $p < 0.01$), *Chrysiptera cyanea* (GLM, $\chi^2 = 2.12$, $p = 0.03$), *P. moluccensis* (GLM, $\chi^2 = 2.59$, $p < 0.01$) and *C. rollandi* (GLM, $\chi^2 = 2.37$, $p = 0.02$) (Fig. 2). An increase in dosage of 0.011 mg *Acanthaster* sp. eggs g^{-1} fish (equivalent to a single additional egg g^{-1} fish) increased the odds of rejection by these seven species by a factor of 1.39 (*Chromis atripectoralis*, 95% CI = 1.14, 1.86), 1.57 (*C. viridis*, 95% CI = 1.20, 2.43), 1.39 (*P. amboinensis*, 95% CI = 1.10, 2.00), 1.19 (*D. aruanus*, 95% CI = 1.06, 1.39), 1.20 (*Chrysiptera cyanea*, 95% CI = 1.06, 1.51), 1.08 (*P. moluccensis*, 95% CI = 1.03, 1.17) and 1.07 (*C. rollandi*, 95% CI = 1.02, 1.14). Increasing the absolute amount of *Acanthaster* sp. eggs relative to the size of fishes did not increase the probability of rejecting food pellets for *A. curacao* (GLM, $\chi^2 = 1.44$, $p = 0.15$) or *D. reticulatus* (GLM, $\chi^2 = 1.92$, $p = 0.05$).
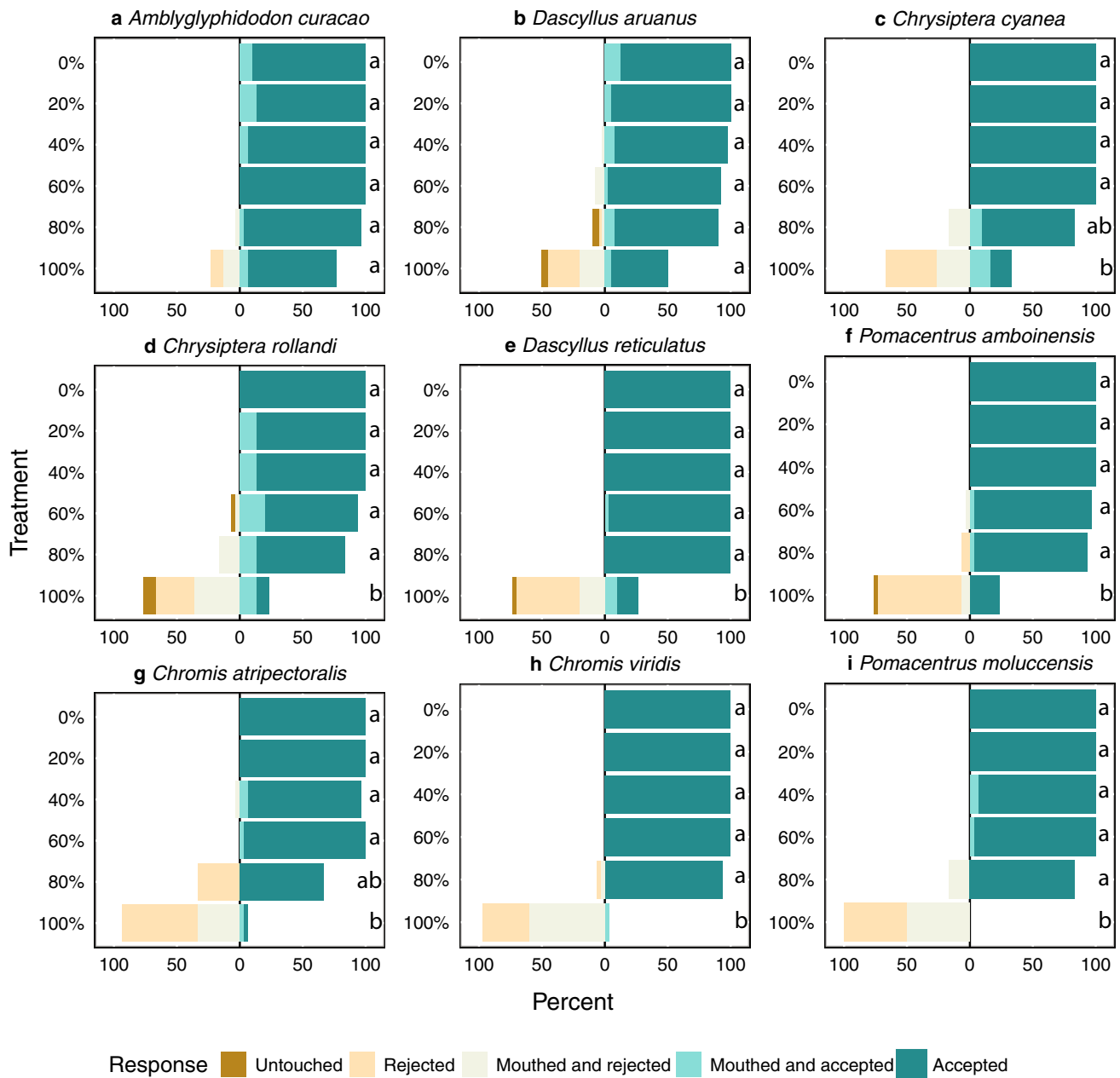
Fig. 1 Graded response to the palatability of *Acanthaster* sp. eggs by nine planktivorous damselfishes based on five pellets offered to 337 feeding individuals across an increasing treatment gradient of 0, 20, 40, 60, 80 and 100% of feed pellets made up of *Acanthaster* sp. eggs. Accepted = the fish immediately retained the treatment pellet; mouthed and accepted = the fish spat out the treatment pellet one or more time, before retaining it; mouthed and rejected = the fish spat out the treatment pellet one or more time, ultimately rejecting it; rejected = the fish mouthed the treatment pellet once and rejected it; untouched = the fish approached the treatment pellet and rejected it, without mouthing

Discussion

As for most marine invertebrates, the eggs and larvae of *Acanthaster* sp. are potentially susceptible to a wide range of planktivorous predators (Lucas 1975; Cowan et al. 2016). Despite this, research on the role of predation in regulating populations of crown-of-thorns starfish has focused almost exclusively on rates of predation on post-settlement life stages, predominantly adult starfish (e.g. Endean 1969; Campbell and Ormond 1970; Dulvy et al. 2004). This is mainly attributable to the widely held assumption that few (if any) potential predators will eat eggs or larvae of crown-of-thorns starfish based on early research that demonstrated the toxicity of saponins (Mackie et al. 1977) and complete avoidance of larvae of crown-of-thorns starfish by planktivorous fishes (Yamaguchi 1974, 1975). However, more

Fig. 2 Probability of acceptance of feed pellets across increasing dose of *Acanthaster* sp. eggs g^{-1} fish by nine planktivorous damselfishes
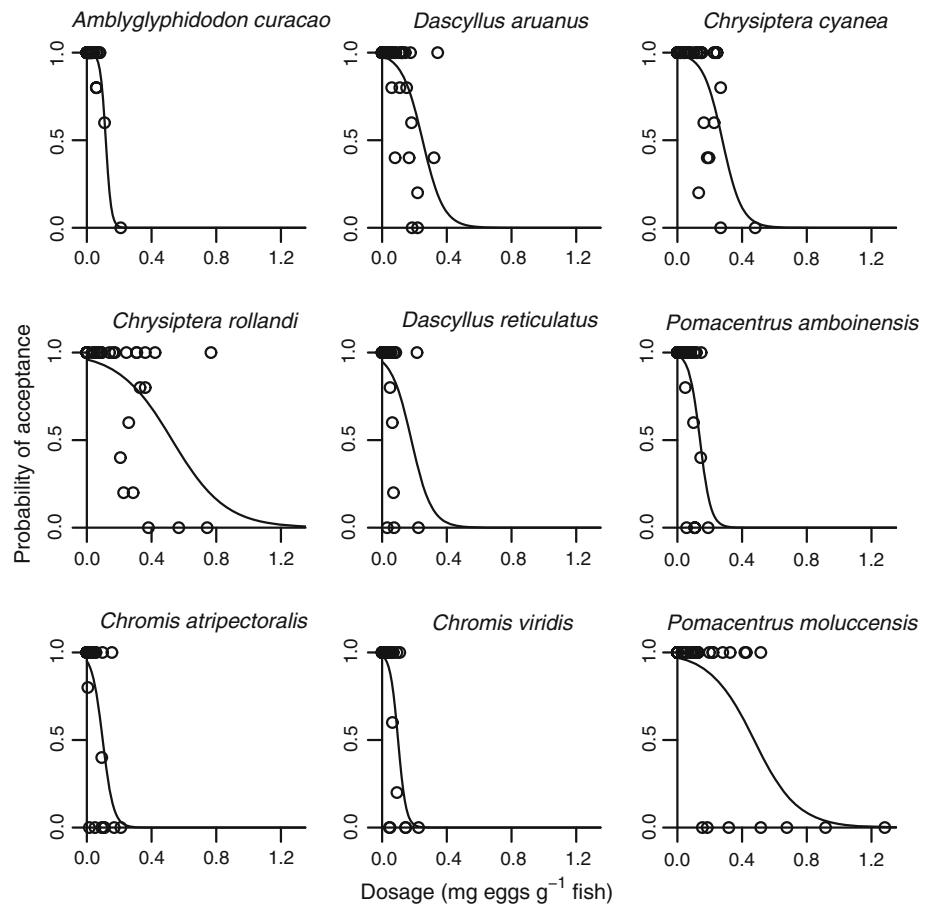
recent experimental studies (e.g. Cowan et al. 2016) indicate that pre-settlement life stages of crown-of-thorns starfish are indeed vulnerable to predation. Importantly, experiments have shown that multiple species of common and widespread damselfish readily consumed larvae of crown-of-thorns starfish and could eat hundreds of larvae before becoming satiated (Cowan et al. 2016). While the effectiveness of saponins was not explicitly tested, the data do not suggest that saponins render larvae sufficiently unpalatable to deter these potentially important predators.

Saponin concentrations in crown-of-thorns starfish are reported to vary with ontogeny, being 2.5–5 times greater in larvae than eggs (Barnett et al. 1988). Given that larvae of crown-of-thorns starfish are readily consumed by a range of common damselfishes (Cowan et al. 2016), it seems unlikely that the lower saponin concentrations in eggs of crown-of-thorns starfish would effectively deter potential predators. However, results from the current study suggest that there are effective anti-predation chemicals contained in the eggs of crown-of-thorns starfish. Notably, there was a decline in the consumption of food pellets with increases in the proportion of starfish eggs, especially when the proportion of starfish eggs in food pellets was ≥80% (Fig. 1). Moreover, a very high proportion (96%) of the

food pellets that were ultimately rejected were first mouthed by fishes, suggesting that food pellets with high concentrations of starfish eggs were rejected based largely on taste. In all, only 28% (78/280) of food pellets made using 100% starfish eggs (with water and binding agents) were consumed by fishes, compared to 98% of pellets with ≤60% starfish eggs. It is also noteworthy that no obvious toxic effects were observed in fish that consumed pellets containing eggs of crown-of-thorns starfish.

Despite general declines in acceptance of food pellets with increasing proportions of crown-of-thorns starfish eggs, some fishes appeared much more accepting of anti-predation chemicals, including saponins, contained in the pellets. Importantly, nearly all the food pellets with >80% starfish eggs were consumed by *A. curacao,* and to a lesser extent by *D. aruanus.* Notably, *A. curacao* is the only species of coral reef fish that has been observed feeding directly on eggs newly released by naturally spawning crown-of-thorns starfish (Pearson and Endean 1969). *Amblyglyphidodon curacao* and *D. aruanus* also had the highest attack rates on larvae of crown-of-thorns starfish (Cowan et al. 2016). This suggests that these species may be particularly insensitive to saponins and could have a comparatively greater role in predation on early life-history

stages of crown-of-thorns starfish. It is also likely that consumption capacity of fish will be affected by individual size of the predator, with larger fish expected to be capable of consuming more eggs or larvae before becoming satiated. Thus, in addition to being more accepting of the anti-predation chemicals contained within all life stages of *Acanthaster* sp., the comparatively large size of *A. curacao* (Fig. 3b) further suggests that this species would be more important in consuming eggs and larvae of *Acanthaster* sp. and may therefore help to regulate abundance of crown-of-thorns starfish in some circumstances. However, after standardising for size, the smaller damselfish species tend to consume greater quantities of pellets with higher concentrations of starfish eggs (Fig. 3). Given that smaller fishes can be extremely abundant on coral reefs (the
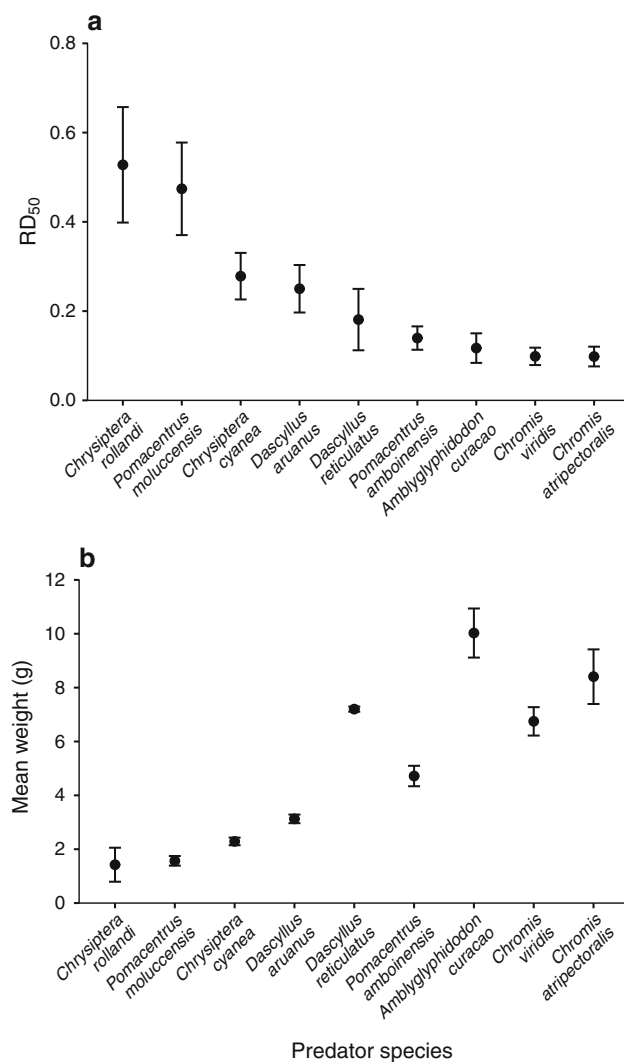
smallest damselfish considered in this study, *P. moluccensis*, is much more abundant than the larger-bodied species such as *A. curacao* and *Chromis atripectoralis*; Table 1), they may have significant capacity to regulate larval abundance and settlement success of crown-of-thorns starfish. However, we should prioritise field-based estimates of survivorship across all life stages of crown-of-thorns starfish, which might be achieved by quantifying declines in the densities of starfish larvae within bodies of water exposed to specific assemblages of planktivorous reef fishes.

A significant issue in testing palatability of food particles, and thereby the effectiveness of potential anti-predation chemicals, is that rates of ingestion will vary with the hunger of the predator tested (Lucas et al. 1979), as well as the size, abundance and nutritional content of different food items. The experimental procedures in this study specifically tested whether fishes detected and responded to changes in the concentration of potential anti-predation chemicals in standardised food particles, but did not necessarily inform whether fishes would or would not eat eggs released by naturally spawning crown-of-thorns starfish. It is clear, however, that some species are much more likely to represent important predators on eggs of crown-of-thorns starfish (Pearson and Endean 1969) and explicit consideration needs to be given to distribution and abundance of these fishes relative to the occurrence of outbreaks of *Acanthaster* sp.

Predation by planktivorous fishes is suggested to be an important source of egg mortality for many marine invertebrates such as corals (Babcock et al. 1986; Baird et al. 2001). However, very high levels of fecundity and simultaneous spawning among aggregations of marine invertebrates are likely to overwhelm the consumption capacity of local assemblages of predators (Westneat and Resing 1988) and therefore ensure survival of at least some gametes and zygotes. Crown-of-thorns starfish are extremely fecund (Conand 1984) and it is possible that the quantity of eggs released, especially when starfish occur in high densities and spawn en masse, will far exceed the consumption capacity of local predators. However, planktivorous fish predators may be important in moderating the reproductive success of crown-of-thorns starfish in non-outbreak populations, thereby preventing concentrations of propagules sufficient to cause outbreaks.

While we used unfertilised eggs in our experiment, it is unlikely that the results would change if eggs were fertilised, as the damselfish species tested have been shown to readily consume *Acanthaster* sp. larvae (Cowan et al. 2016). Methods similar to those used by Cowan et al. (2016) could potentially be used to test consumption of *Acanthaster* sp. eggs against eggs of another species or an alternate food source. However, this would be more

Fig. 3 Consumption capacity of *Acanthaster* sp. eggs by nine putative planktivorous fish predators. **a** Median rejection dose (RD_{50}) ($\pm$SE) of *Acanthaster* sp. eggs. **b** Mean observed weight of planktivorous damselfishes

difficult due to the very small size of the eggs and the rapid degradation of unfertilised eggs, which would limit the number of replicates and predator species that could be tested. Furthermore, it is more difficult to differentiate *Acanthaster* sp. eggs from eggs of other coral reef species, than it is to differentiate between larvae of different species. The diameter of *Acanthaster* sp. eggs is reported to be in the range of 0.22–0.25 mm (Caballes et al. 2016), which is approximately half the size of our pellets. This difference in size would presumably mean that actual eggs are more difficult for fishes to discern, especially in the wild. However, the largest species tested in this study (*A. curacao*) has been observed consuming *Acanthaster* sp. eggs in the field (Pearson and Endean 1969), making it likely that other smaller planktivorous fishes would also be capable of consuming eggs. While it is possible that there might be interspecific differences in the readiness with which different fishes consume particles of a specific size, we believe that the biggest constraint on consumption of *Acanthaster* sp. eggs would be the presence of saponins and other anti-predator chemicals, as examined in our study.

Based on consistent declines in acceptance of food pellets containing increasing proportions of crown-of-thorns starfish eggs, our study reaffirms that deterrents (i.e. saponins and/or other chemicals) in eggs of *Acanthaster* sp. limit consumption by at least some potential predators. However, interspecific differences in the responses of planktivorous fishes to *Acanthaster* sp. eggs suggest that comparisons of egg palatability should be expanded to consider a wider range of taxa. *Acanthaster* sp. eggs are slightly negatively buoyant upon release (Birkeland and Lucas 1990); thus, benthic organisms that have been considered as predators on settling larvae (Yamaguchi 1973) might also be important as predators on the eggs. Further, spatial distribution of predatory species should be considered as a factor in both buffering against population fluctuations of crown-of-thorns starfish and in the propagation of outbreaks. More specifically, reefs with higher abundance of tolerant species, such as *A. curacao* and *D. aruanus*, may have greater capacity to buffer against outbreaks, but this needs to be explicitly examined.

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