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REPORT

Predation on crown-of-thorns starfish larvae by damselfishes

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Abstract Examining the functional response of predators can provide insight into the role of predation in structuring prey populations and ecological communities. This study explored feeding behaviour and functional responses of planktivorous damselfishes when offered captive reared larvae of crown-of-thorns starfish, *Acanthaster* sp., with the aim of determining whether these predators could ever play a role in moderating outbreaks of *Acanthaster* sp. We examined predatory behaviour of 11 species of planktivorous damselfish, testing: (1) the relationship between predator size and predation rate, both within and among fish species; (2) consumption rates on larvae of *Acanthaster* sp. versus larvae of a common, co-occurring coral reef asteroid *Linckia laevigata*; (3) maximal feeding rates upon both *Acanthaster* sp. and *L. laevigata*; and (4) functional responses of planktivorous fishes to increasing densities of *Acanthaster* sp. Consumption rates of crown-of-thorns larvae by damselfishes were independent of predator size; however, there was a significant negative relationship between predator size and consumption rate of *L. laevigata*, when pooling across all predatory species. Some damselfishes, including *Acanthochromis polyacanthus* and *Amblyglyphidodon curacao*, consumed larval *Acanthaster* sp. at a greater rate than for *L. laevigata.* Most predatory species (all except *A. curacao* and *Pomacentrus amboinensis*) exhibited a Type II functional response whereby the increasing feeding rate decelerated with increasing prey density. In addition to revealing that a wide range of planktivorous fishes can prey upon larvae of *Acanthaster* sp., these data suggest that planktivorous damselfishes may have the capacity to buffer against population fluctuations of *Acanthaster* sp. Importantly, predators with Type II functional responses often contribute to stability of prey populations, though planktivorous fishes may be swamped by an abnormally high influx of larvae, potentially contributing to the characteristic population fluctuations of *Acanthaster* sp.

Keywords Predation · Functional response · Chemical defence · *Acanthaster* · Larvae · Damselfish

Introduction

Predatory release has long been considered a potential cause of outbreaks of the crown-of-thorns starfish, *Acanthaster* sp. (e.g., Endean 1969). Essentially, key predators of adult starfishes (such as the giant triton and/or predatory reef fishes) have been subjected to extensive or sustained harvesting pressure, and it is thought that this may have drastically reduced rates of predation and adult mortality, leading to outbreaks of *Acanthaster* sp. (e.g., Endean 1969; Campbell and Ormond 1970; Owens 1971; Dulvy et al. 2004). While scientific interest in predators of *Acanthaster* sp. has traditionally focussed on predators of adult (or at least post-settlement) stages (e.g., Endean 1969; Campbell and Ormond 1970; Owens 1971; Dulvy et al. 2004), predatory regulation might equally occur during spawning and at pre-settlement and settlement stages (e.g., Babcock

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et al. 1986; Westneat and Resing 1988; Bachiller et al. 2015).

Acanthaster sp. must run the gauntlet of the plankton feeders throughout their planktonic development (Lucas 1975). However, few studies have attempted to identify potential predators on the eggs or larvae of *Acanthaster* sp.; in part, logistic challenges to sampling the early life stages of *Acanthaster* sp. in the field make it difficult to quantify natural rates of predation. Further, high levels of toxicity (saponins) were once thought to effectively protect early life history stages from predation (e.g., Lucas et al. 1979). However, these may be consumed in large numbers by reef fishes, including some Pomacentridae and Chaetodontidae (e.g., Pearson and Endean 1969; Keesing and Halford 1992; Ciarapica and Passeri 1993). On coral reefs, planktivorous pomacentrid fishes are highly efficient predators, capable of removing a large proportion of the zooplankton in near reef waters (Hamner et al. 1988). If planktivorous fishes readily consume eggs and larvae of *Acanthaster* sp., their high densities and high feeding rates may significantly influence reproductive and settlement success (Kingsford and MacDiarmid 1988). Moreover, small changes in rates of predation and survivorship at the pre-settlement life stages of *Acanthaster* sp. could have significant effects on adult abundance (McCallum 1988, 1990).

The potential ecological importance of planktivorous fish predation as a regulatory factor upon populations of *Acanthaster* sp. depends largely upon the ability of the predators to find and consume prey (Hassell 1978). A common method that provides insight into the dynamics of predator–prey systems is the quantification of the functional response (Abrams 1990; Buckel and Stoner 2000; Nilsson and Ruxton 2004), described by the intake rate of prey as a function of prey density (Holling 1959b). Functional responses are categorised as Type I, II, or III (e.g., Galarowicz and Wahl 2005; Gustafsson et al. 2010). Type I functional response describes a linear increase in feeding rate with increasing prey density, until reaching a saturation point (Holling 1959a). This is most commonly observed in filter-feeding species (e.g., Jeschke et al. 2004) and is assumed to result when handling time is negligible, so that consumption increases in direct proportion to the densities of prey (Jeschke et al. 2002). The Type II functional response is defined by a feeding rate that increases at a decelerating rate towards a satiation point (Holling 1959a) and assumes that handling time and searching time are mutually exclusive (Kaspari 1990; Baker et al. 2010). It typically describes the foraging behaviour of species capable of handling only one prey item at a time, and where there are no increases in capture success with increases in the rate of encounter for given prey items (Real 1977; Abrams 1990). The Type III functional response describes a feeding rate that initially increases with increasing prey densities and then decelerates towards a maximum value, producing a characteristic sigmoidal curve (Holling 1959a; Nachman 2006). This pattern is produced by factors that affect the probability of detection or attack of prey items, including learned behaviour, prey switching, capture success, or aggregation of prey (Murdoch 1973; Morgan and Brown 1996).

The specific functional responses of predators are important because they determine the extent to which predators potentially regulate prey abundance or respond to changes in prey abundance (Eggleston 1990; Eggleston et al. 1992; Taylor and Collie 2003; Ward et al. 2008). Importantly, when predators exhibit a Type II response, prey species occurring at low densities within a closed system suffer an increased risk of mortality and may be driven to extinction (Murdoch and Oaten 1975; Hassell 1978; McCallum et al. 1989). When predators exhibit a Type III response however, prey in low-density populations experience a reduced risk of mortality (Hassell 1978). Thus, on a single patch, a Type III response can be stabilising, whilst a Type II response can be destabilising. If, however, there is sufficient larval mixing between patches, predators exhibiting a Type II functional response may be capable of stably maintaining prey populations at low levels across most of a metapopulation (McCallum 1988). In such situations, two stable equilibria may exist across patches, where most patches have very low prey densities, though a small number of patches have very high prey densities. Whilst the low-density equilibrium is locally stable, sufficiently high larval influx from other patches may lead to a switch in states (McCallum 1988). Larval mixing between starfish populations on the Great Barrier Reef (GBR) is known to occur at very large scales, exceeding that of individual reefs (e.g., Hock et al. 2014). Therefore, sufficiently large numbers of predators exhibiting Type II functional responses could contribute to generally low densities of *Acanthaster* sp. at most reefs and most of the time.

We examined feeding behaviour of planktivorous damselfishes in a series of laboratory assays where fish were provided with varying densities of captive reared larvae of *Acanthaster* sp. This study aims to establish whether planktivorous reef fishes could be important in regulating abundance and/or contribute to extreme fluctuations in abundance of *Acanthaster* sp. Specifically, we tested (1) the relationship between predator size and predation rate, both within predator species and across the planktivorous fish community; (2) consumption rate of larvae of *Acanthaster* sp. versus larvae of a common, co-occurring coral reef asteroid *Linckia laevigata*; (3) maximal feeding rates upon both *Acanthaster* sp. and *L. laevigata*; and (4) functional response of fishes feeding upon *Acanthaster* sp. The blue starfish, *L. laevigata*, was selected as a comparative species as it co-occurs with *Acanthaster* sp. and has a similar larval development pattern (Yamaguchi 1973). While *L. laevigata* is generally very common (e.g., Williams 2000), it does not exhibit extreme fluctuations in abundance as seen in populations of *Acanthaster* sp. If predation activity upon the early life stages of *Acanthaster* sp. is much reduced compared to predation upon other starfish, this might explain why *Acanthaster* sp. exhibit population outbreaks while most other starfishes have generally much more stable population sizes.

Materials and methods

Collection and maintenance of study species

This study was conducted at Lizard Island Research Station. Adult *Acanthaster* sp. and *L. laevigata* were collected from reefs at Lizard Island (14°40′S; 145°27′E) in the northern GBR during October–November 2015. Spawning was induced by injecting 1 mL of 10^{-4} M 1-methyladenine into the gonads in each arm, through the aboral side for *Acanthaster* sp. and through the tube feet for *L. laevigata*. Gametes were collected from three to four individuals of each sex to ensure that a mix of genotypes was used. Spawning commenced immediately for males, and within 30 min for females. Sperm was rinsed in 0.2 µm filtered seawater (FSW) and refrigerated at 4 °C prior to use. Eggs were collected from around the arms of females following their release from gonopores and rinsed with 0.2 µm FSW. Fertilisation was achieved by adding sperm to reach a final sperm–egg ratio of approximately 100:1. Fertilised eggs were transferred to 16-L larval rearing chambers at a density of approximately 1–2 larvae mL^{-1}. Chambers were maintained at 28.4 ± 1.1 °C (mean ± SD). Larvae were fed twice daily on a mixture of cultured algal species (*Dunaliella tertiolecta* and *Chaetoceros muelleri* at a concentration of 5000 cells mL^{-1} of each species). Water in the chambers was changed daily. Bipinnaria stage larvae were used in experiments. At this stage, the two larval species exhibited minor differences in colour, opacity, shape, and size (Fig. 1).

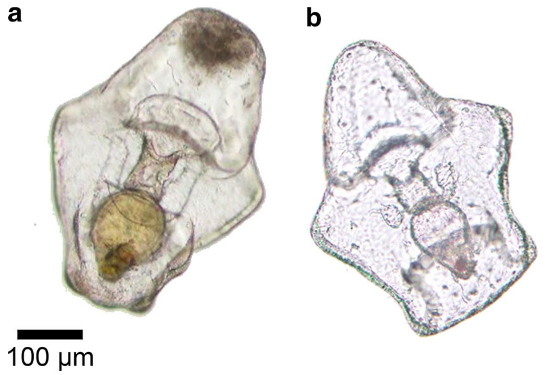


Fig. 1 Bipinnaria larvae of **a** *Acanthaster* sp. and **b** *Linckia laevigata*

Eleven species of damselfish (*A. sexfasciatus*, *A. polyacanthus*, *A. curacao*, *C. atripectoralis*, *C. viridis*, *C. rollandi*, *D. aruanus*, *D. reticulatus*, *N. azysron*, *P. amboinensis* and *P. moluccensis*), which are among the most common planktivorous fishes on the northern GBR, and commonly occur within habitats occupied by adult *Acanthaster* sp. (e.g., Pearson and Endean 1969), were collected using fence nets or clove oil from reefs at Lizard Island. All fishes were maintained with conspecifics in 32-L flow-through aquaria with PVC pipes for shelter until they were acclimatised to tank conditions. Fish were fed a commercial dried fish food and were considered acclimatised when they readily fed on food provided. This took 1–9 d depending on the species.

Experimental design

To test predatory behaviour on larval starfish, 2 h prior to the experiment individual fish were transferred to 10-L plastic aquaria containing 0.2 µm FSW and 5-cm-long open-ended PVC tubing for shelter. Throughout the course of the experiment, water temperature ranged between 26.4 and 27.8 °C. Fish were starved for 24 h prior to the start of feeding experiments, in an attempt to standardise for hunger within and among species.

During the experimental trials, individual fish were provided with specified densities of *Acanthaster* sp. or *L. laevigata*. Fish were allowed to feed for 1 h before being removed, and aquaria water was then sieved through a 70-µm mesh to capture and count the number of uneaten larvae. Individual fish were used only once in each experiment. During control trials in which the predator was absent, 100% of larvae were recovered from aquaria.

Consumption rate

To examine the effect of predator size on predation rate, individual fish of various size (Table 1) were provided with 100 larvae of either *Acanthaster* sp. or *L. laevigata* for 1 h. Fish were weighed in a 400-mL beaker filled with seawater immediately after the experiment. Linear regression was then used to test whether the number of larvae consumed over the test period varied with the size (specifically weight) of fish, both within and among predator species. Consumption rates on larvae of *Acanthaster* sp. versus larvae of *L. laevigata* were then compared using *t* tests for each of the eleven damselfish species separately.

Functional response and satiation limits

Functional responses were explored by providing individual fish with larvae of *Acanthaster* sp. at one of seven

Table 1 Weight range in g of planktivorous pomacentrid fish predators, provided with 100 larvae of either *Acanthaster* spp. or *Linckia laevigata*

Predator species	Range (*Acanthaster*)	Range (*Linckia*)
Abudefduf sexfasciatus	11.56–59.67	23.85–60.18
Acanthochromis polyacanthus	7.00–31.28	15.06–46.75
Amblyglyphidodon curacao	5.75–31.83	5.81–41.55
Chromis atripectoralis	2.65–8.60	2.35–11.35
Chromis viridis	2.10–6.97	1.67–4.35
Chrysiptera rollandi	0.50–1.86	0.58–2.34
Dascyllus aruanus	1.22–5.88	1.59–4.20
Dascyllus reticulatus	2.06–7.51	1.35–4.42
Neopomacentrus azysron	1.85–5.77	1.33–4.69
Pomacentrus amboinensis	0.51–16.05	0.38–7.73
Pomacentrus moluccensis	0.50–6.80	0.65–3.10

different densities: 2, 5, 10, 25, 50, 75 and 100 larvae 10 L^{-1} seawater. *D. aruanus* and *P. amboinensis* were not satiated when provided with 100 larvae, so additional trials were conducted with up to 300 larvae 10 L^{-1}. Functional responses for each fish species were modelled in the statistical program R (R Core Team 2015). When the response is suspected to be independent of handling time, the Type I response can be modelled (Eq. 1), where N is the number of prey eaten, α is the attack rate, N_0 is the number of prey available, and T is the total time available.

$$N = \alpha N_0 T \tag{1}$$

The Type II functional response is most typically represented by the Holling's (1959b) 'disc equation' (Eq. 2), where h is handling time.

$$N = \frac{\alpha N_0 T}{1 + \alpha h N_0} \tag{2}$$

Prey replacement could not be achieved in our experiments without disruption to the study species; therefore, it was more appropriate to use the 'random predator equation' (Rogers 1972), which describes a Type II functional response but additionally accounts for prey depletion (Eq. 3). As N appears on both sides of the equation, this was modified using the *Lambert W* function (W in Eq. 3; Bolker 2008) from the emdbook package in R (Bolker 2010), where T is the total time available.

$$N = N_0 - \frac{W\left(\alpha h N_0 e^{-\alpha(T - hN_0)}\right)}{\alpha h} \tag{3}$$

When the attack rate is considered as a function of prey density, rather than remaining constant across prey densities, as in a Type II response, the Type III response can be modelled. In the most general form, α is a hyperbolic function of N_0 (Juliano 2001):

$$\alpha = \frac{(d + bN_0)}{(1 + cN_0)} \tag{4}$$

where b, c, and d are constants. The Type III functional response, incorporating prey depletion, can be written as per Hassell et al. (1977):

$$N = N_0\left(1 - e^{\frac{(d + bN_0)(hN - T)}{(1 + cN_0)}}\right) \tag{5}$$

Logistic regression analyses of the proportional mortality of prey as a function of prey density, within the frair package in R (Pritchard 2014), enabled discrimination between Type II or Type III responses. Type II response was indicated by a significantly negative first-order term, and Type III response was indicated by a significantly positive first-order term, followed by a significantly negative second-order term (Juliano 2001). The suggested Type II or Type III model, along with a Type I model, was then fit to data, and AIC values were compared to determine the model of best fit, indicated by lowest AIC value.

Functional response curves were fit to the data using maximum likelihood estimation from the bblme package in R. Parameters of interest relating to a predator's foraging behaviour can be extracted from the fitted functional response models (Jeschke et al. 2002). As the scaling coefficient, the attack rate is one such parameter that describes the initial slope of the curve (Hassell and May 1973; Jeschke et al. 2002). Differences in the extracted attack rate parameters were compared using ANOVA and post hoc Tukey test, providing an indication of the most important predators at low larval densities.

Results

Consumption rate

There was no significant effect of fish size (specifically, weight) on consumption rates of larvae of *Acanthaster* sp. either among ($F_{(1,90)} = 3.79$, $p > 0.05$) or within fish species ($F_{(10,90)} = 1.52$, $p > 0.05$). For *L. laevigata*, increasing weight of the fish predator had a significantly negative effect on consumption rate of larvae when pooling for all fish species ($F_{(1,97)} = 4.02$, $p = 0.05$); however, this was attributable to the low levels of consumption by some larger species (e.g., *A. sexfasciatus*) and there was no significant effect of weight of the predator on consumption rate within fish species ($F_{(10,97)} = 1.34$, $p > 0.05$).

Consumption rate of *Acanthaster* sp. differed significantly from consumption rate of *L. laevigata* for three of the eleven predatory fish species (Fig. 2). *N. azysron* consumed significantly more larvae of *L. laevigata* than that of *Acanthaster* sp. ($t_{(16.75)} = -3.58, p < 0.01$), whilst consumption rate of larvae of *Acanthaster* sp. was significantly greater than that of larvae of *L. laevigata* for *A. curacao* ($t_{(18.68)} = 2.25, p = 0.04$) and *A. polyacanthus* ($t_{(11.79)} = 2.58, p = 0.02$). Consumption rate of the two larval species was not significantly different for eight of the eleven predatory species ($p > 0.05$).

Functional response

Logistic regression suggested that changes in the feeding rates of most predatory species (*A. polyacanthus, A. sexfasciatus*, *C. atripectoralis*, *C. rollandi*, *C. viridis*, *D. aruanus*, *D. reticulatus*, *N. azysron* and *P. moluccensis*) with increasing densities of *Acanthaster* sp. larvae was best represented by a Type II functional response whereby the increasing feeding rate decelerated with increasing food density (Fig. 3). A Type III functional response, described by a significantly positive first-order term followed by a significantly negative second-order term, was exhibited for *A. curacao* and *P. amboinensis* (Fig. 4). However, visual comparisons of fitted models suggested the range of prey densities offered to *P. amboinensis* was not sufficiently high to effectively capture satiation; additional replicates, including at higher initial prey density, would reveal a satiation point and better capture the full shape of the curve (Fig. 4c).

Predicted satiation points, based on the asymptote of the fitted model (Figs. 3, 4), were highly variable between species, ranging from consumption of approximately 14 *Acanthaster* sp. larvae h^{-1} (*C. viridis*) to a consumption rate of approximately 158 *Acanthaster* sp. larvae h^{-1} for *D. aruanus* (Fig. 3).

Parameter estimates of each functional response model with the appropriate data set revealed variable attack rates between predatory species ($F_{10,118} = 13.45$, $p < 0.01$). Attack rates of *D. aruanus* and *A. curacao* were found to be the highest and were significantly greater than the attack rates of *C. viridis* ($p = 0.03$), *A. sexfasciatus* ($p < 0.01$), *N. azysron* ($p < 0.01$), *A. polyacanthus* ($p < 0.01$), *C. atripectoralis* ($p < 0.01$), and *P. amboinensis* ($p < 0.01$, $p < 0.01$) (Fig. 5).

Discussion

This study shows that at least 11 different species of planktivorous damselfish will readily prey upon larvae of *Acanthaster* sp., clearly refuting the idea that these larvae

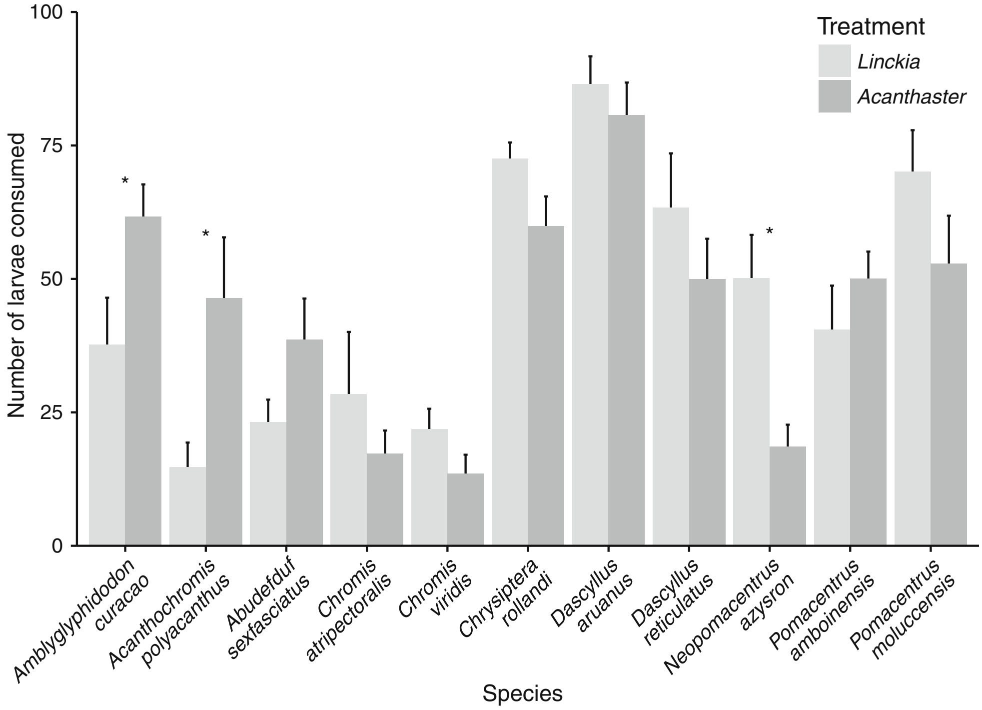


Fig. 2 Mean number of prey consumed (±SE) by planktivorous fish predators in 1 h when larvae of *Acanthaster* sp. or *Linckia laevigata* were provided at a density of 10 L^{-1}. Asterisks denote a significant difference in consumption rate of *Acanthaster* sp. and *L. laevigata*

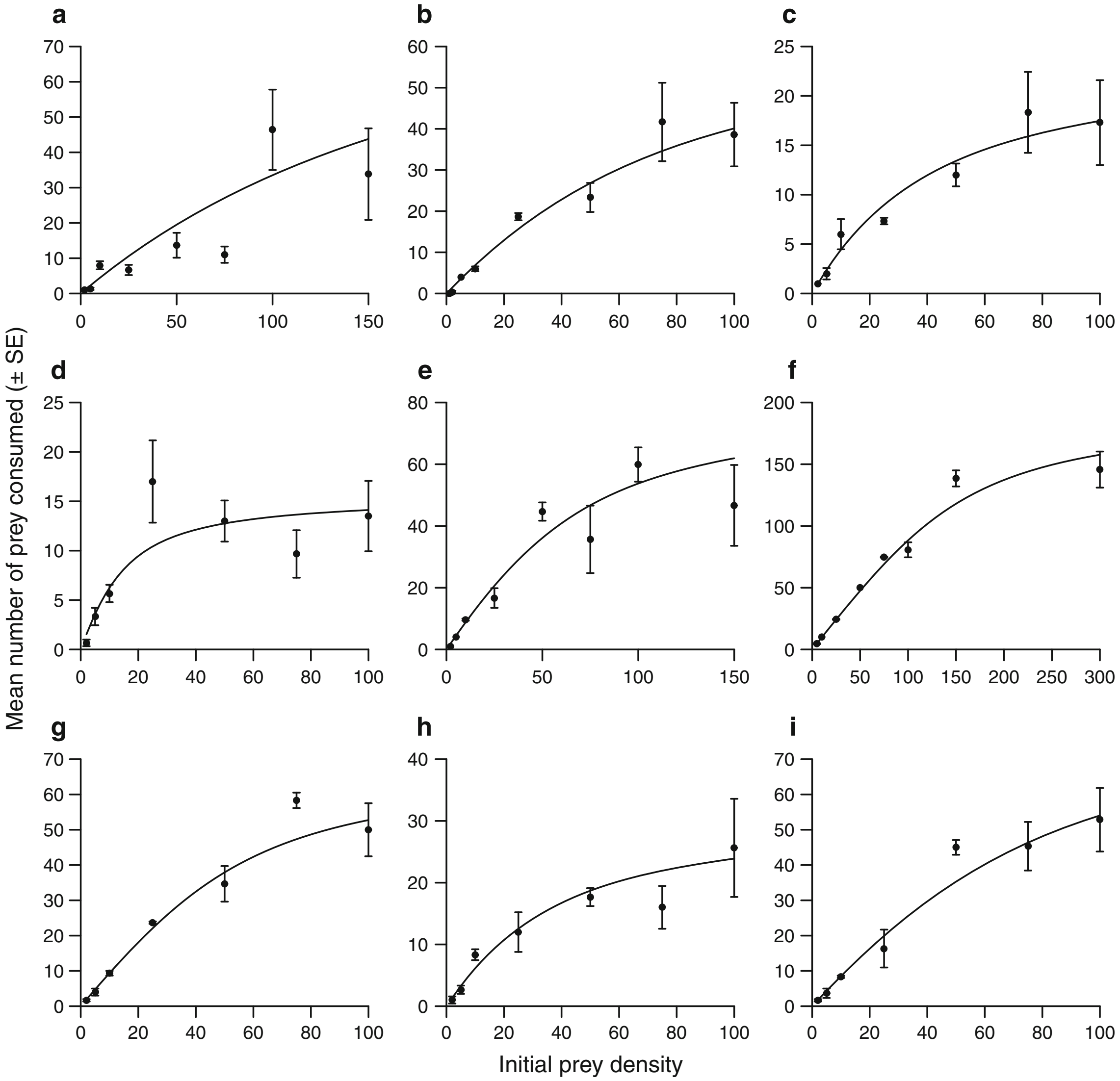


Fig. 3 Type II functional response curves for planktivorous pomacentrid fishes **a** *Acanthochromis polyacanthus*, **b** *Abudefduf sexfasciatus*, **c** *Chromis atripectoralis*, **d** *Chromis viridis*, **e** *Chrysiptera rollandi*, **f** *Dascyllus aruanus*, **g** *Dascyllus reticulatus*, **h** *Neopomacentrus azysron* and **i** *Pomacentrus moluccensis* preying on larvae of *Acanthaster* sp., modelled by Rogers' random predator equation (Rogers 1972)

are effectively (chemically) protected from predators (e.g., Lucas et al. 1979), and supporting previous studies (e.g., Pearson and Endean 1969; Keesing and Halford 1992; Ciarapica and Passeri 1993) that suggest larval crown-of-thorns starfish are highly vulnerable to predation. Importantly, most of the fish species tested (all but *N. azysron*) fed upon larvae of *Acanthaster* sp. at equal or greater rates than larvae of a comparable starfish, *L. laevigata*. These results suggest that toxins present in larval crown-of-thorns starfish (saponins) are largely ineffective in reducing predation, at least by common and widespread damselfishes. This directly contradicts the work by Lucas et al. (1979), who showed that all four of the damselfishes tested (*Chromis caerulea*, *A. polyacanthus*, *D. aruanus*, and *N. azysron*) significantly avoided artificial food pellets containing saponins extracted from eggs of *Acanthaster* sp., relative to equivalent food pellets without saponins added. Taken together, these studies suggest that fishes are able to detect saponins and find them generally distasteful or unpalatable compared to a palatable control, but this is not sufficient to deter fishes from actually feeding on whole larvae of crown-of-thorns starfish.

Rates of predation upon larvae of *Acanthaster* sp. varied among planktivorous damselfishes, but were independent of predator size. This pattern may be due to prey size relative to predator size, which can influence prey preference in generalist predators (Lafferty and Kuris 2002). For most fishes, both the size and range of sizes of prey

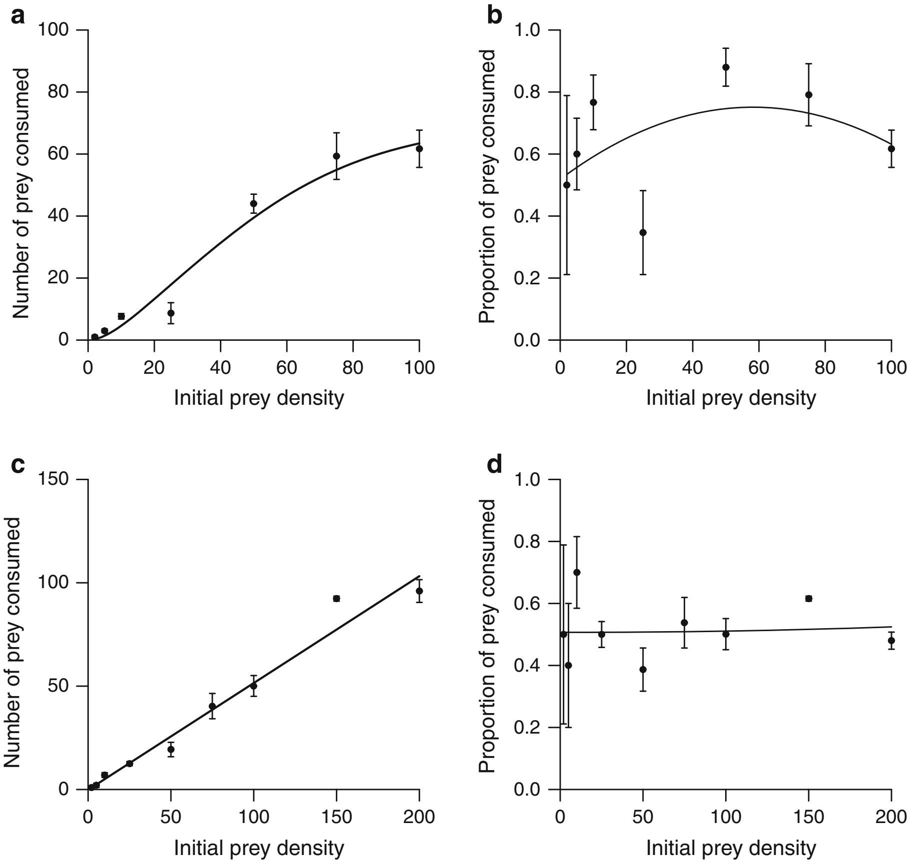


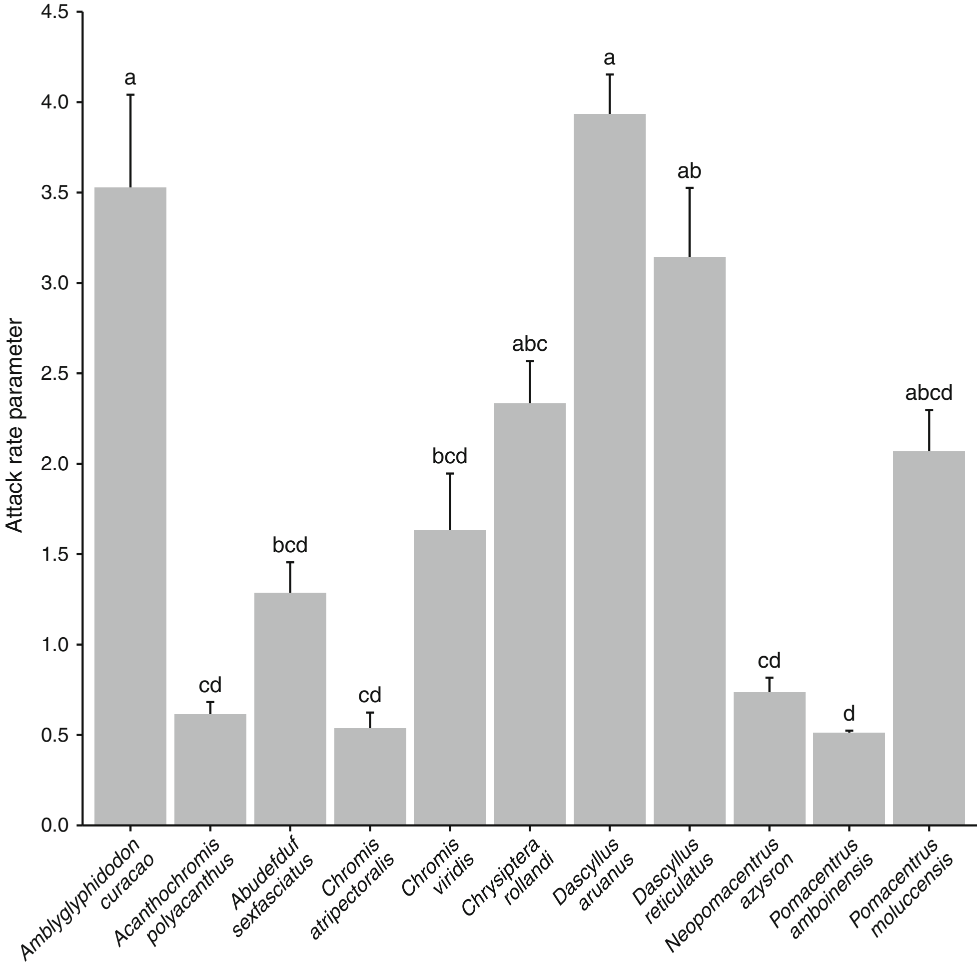
Fig. 4 Predation of *Acanthaster* sp. larvae by *Amblyglyphidodon curacao* (**a**, **b**) and *Pomacentrus amboinensis* (**c**, **d**). **a**, **c** Mean ± SE number of prey consumed at each density; the Type III functional response (Hassell et al. 1977) where attack rate increases with prey density. **b**, **d** Proportional mortality of *Acanthaster* sp. at each density, and curve generated from second-order logistic regression analysis

consumed generally increase with increasing predator size (Keast and Webb 1966; Popova 1967, 1978; Nielsen 1980; Persson 1990; Juanes 1994): larger predators eat larger prey, whilst the minimum prey size may change only slightly over a wide range of predator sizes. Further, as fish typically prefer larger food particles (e.g., Werner and Hall 1974), the comparatively larger larvae of *Acanthaster* sp. may be consumed in preference to species with smaller larvae, including *L. laevigata*, if they co-occur in the plankton.

Predators consuming more prey at lower densities should have a higher attack rate parameter, owing to the greater initial slope of the line describing their functional response. Predatory species such as *D. aruanus*, *A. curacao*, *D. reticulatus*, and *C. rollandi* which have a higher initial attack rate are likely to be disproportionately important in reducing effective settlement rates when *Acanthaster* sp. populations are at normal, low densities. Of these, *A. curacao* may be particularly important in reducing recruitment of *Acanthaster* sp., as this species was found to consume larvae of *Acanthaster* sp. at a significantly higher rate than it consumed larvae of the comparative species, *L. laevigata*. As densities of larval *Acanthaster* sp. increase on a reef, for example during a mass influx of larvae, those predators with high satiation limits (e.g., *D. aruanus* and *P. amboinensis*) would be most important in potentially reducing the number of larvae and therefore effectively reducing settlement rates. When coupled with field observations that have detected high larval densities of up to 53.3 individuals m^{-3} (Suzuki et al. 2016), our results suggest that planktivores could substantially reduce incoming *Acanthaster* sp. larvae. Regarding both initial attack rates and satiation limits, *D. aruanus* emerges as the most important of the eleven damselfish species tested in this study, representing the most efficient predator of *Acanthaster* sp. larvae across both low and high larval densities. In contrast, *C. atripectoralis* had a low attack rate and a low satiation limit, though we also need to take account of variation in actual abundances of the different predators in different reef environments.

The planktivorous damselfishes considered in this study primarily exhibited Type II functional responses, suggesting that they may be capable of consuming sufficient larvae of crown-of-thorns starfish to effectively suppress settlement rates when larvae are already scarce, thereby contributing to very low natural densities of *Acanthaster* sp. This does not mean, however, that the initiation and spread of outbreaks can be directly attributed to spatial and temporal patterns in the abundance of these damselfishes (and/

Fig. 5 Functional response parameter, attack rate *a*, presented as mean + SE. *Letters* indicate significantly different groupings for attack rate parameters by predatory species, determined by post hoc Tukey test



or other planktivorous organisms), because very high densities of larvae, which are a necessary condition for the rapid and pronounced onset of outbreaks (e.g., secondary outbreaks), are likely to swamp even the combined consumption capacity of all planktivorous reef fishes (McCallum 1988). At best, high densities of planktivorous fishes, especially those species that selectively target larvae of *Acanthaster* sp. and are capable of eating very large numbers of such larvae, may contribute to low densities of *Acanthaster* sp. recorded outside of outbreak conditions, thereby reducing (in part) the incidence of new outbreaks.

If damselfishes, and/or other planktivorous reef fishes, are important in suppressing local densities of *Acanthaster* sp., any extrinsic threats to the abundance or composition of planktivorous fish assemblages may in turn give rise to population outbreaks of crown-of-thorns starfish. Importantly, several of the damselfishes considered in this study are extremely vulnerable to coral depletion (e.g., Pratchett et al. 2012). This means that there is a potentially important feedback loop where high densities of crown-of-thorns starfish, which effectively remove essential habitat for coral-dwelling damselfishes (e.g., *D. aruanus*), may actually contribute to increased survival of larval starfish and therefore promote even higher densities of crown-of-thorns starfish and ever greater coral loss. This may be important in the formation of primary outbreaks, in which the population builds up gradually over successive years (e.g.,, Pratchett 2005).

In conclusion, this study shows that coral reef damselfishes, probably like many other planktivorous reef fishes, will readily consume larvae of crown-of-thorns starfish, and each individual fish can eat hundreds of larvae before becoming satiated. Planktivorous fishes may therefore be important in regulating the abundance of crown-of-thorns starfish by moderating settlement success, and especially when starfish are in low abundance, potentially preventing the onset of outbreaks. It remains to be tested whether large-scale variation in the abundance and diversity of planktivorous fishes may account (in part) for spatial and temporal patterns of outbreaks of crown-of-thorn starfish, but high densities of damselfishes are not necessarily, in themselves, insurance against outbreaks of *Acanthaster* sp. What is needed is much more focussed research on the demographics of both low-density (nonoutbreak) and high-density (outbreak) populations of crown-of-thorns, estimating not only the rates of reproduction, settlement, and mortality, but also considering key biological interactions that moderate these rates.

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