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Benthic Predators Influence Microhabitat Preferences and Settlement Success of Crown-of-Thorns Starfish (*Acanthaster* cf. *solaris*)

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Academic Editors: Sven Uthicke and Michael Wink
Received: 28 October 2016; Accepted: 6 December 2016; Published: 9 December 2016

Abstract: Like most coral reef organisms, crown-of-thorns starfish (*Acanthaster* spp.) are expected to be highly vulnerable to predation as they transition from a planktonic larval phase to settling among reef habitats. Accordingly, crown-of-thorns starfish might be expected to exhibit behavioural adaptations which moderate exposure to predation at this critical stage in their life history. Using pairwise choice experiments and settlement assays, we explored the ability of competent larvae of *Acanthaster* cf. *solaris* to first detect and then actively avoid benthic predators during settlement. Pairwise choice experiments revealed that late stage brachiolaria larvae are able to detect predators in the substrate and where possible, will preferentially settle in microhabitats without predators. Settlement assays (without choices) revealed that larvae do not necessarily delay settlement in the presence of predators, but high levels of predation on settling larvae by benthic predators significantly reduce the number of larvae that settle successfully. Taken together, these results show that crown-of-thorns starfish are highly vulnerable to benthic predators during settlement, and that variation in the abundance of benthic predators may exert a significant influence on patterns of settlement for crown-of-thorns starfish.

Keywords: behaviour; coral reefs; predation; resilience

1. Introduction

As for many benthic reef organisms, settlement is expected to represent one of the major bottlenecks in the life history of crown-of-thorns starfish (*Acanthaster* spp.), whereby relatively naïve planktonic larvae will be exposed to an entirely new suite of potential predators as they transition to living in benthic reef habitats [1]. Reef-based predators include both planktivorous fishes and sessile invertebrates (e.g., corals) that intercept larvae as they swim towards benthic habitats [2,3], as well as infaunal invertebrate predators that will feed on starfish that settle to specific microhabitats [4]. Both pre- and post-settlement mortality play important roles in structuring populations of marine organisms (e.g., [5]), but predation rates are generally highest ($\geq$30% day^{-1}) immediately after settlement (reviewed by Gosselin and Qian [6]). Importantly, high rates of early post-settlement mortality can significantly augment patterns of larval supply, having a major bearing on the distribution and abundance of benthic marine organisms (e.g., [7,8]). Moreover, there will be strong selection for settling larvae to choose microhabitats that minimise predation risk [9], either by avoiding habitats with high abundance of potential predators or preferentially settling in complex microhabitats that provide greater refuge from predators.

Predation on crown-of-thorns starfish may be moderated by high concentrations of saponins and other toxins that are presumed to deter potential predators (e.g., [10]). Notably, three-day-old larval crown-of-thorns starfish have more than two times higher concentrations of saponins than adult starfish [11], which may reflect their increased vulnerability to predation due to limited physical predator defences (e.g., spines). Even so, larval crown-of-thorns starfish are readily consumed by a range of planktivorous reef fishes (e.g., [2]), as well as corals, such as *Pocillopora damicornis* [3]. Accordingly, in laboratory-based experiments, >50% of larvae are lost during settlement, and this may be a result of predation by benthic animals which could not be removed from the settlement substrates [3]. Even after settlement, juvenile crown-of-thorns starfish experience significant rates of mortality (up to 6.49% day^{-1} for one-month-old starfish), which decreases with size and age, and is largely attributed to predation (e.g., [4]).

The purpose of this study was to test whether crown-of-thorns starfish can detect the presence of benthic predators within potential settlement substrates (largely based on chemoreception, *sensu* [12]), and thereafter, explore the extent to which larval crown-of-thorns starfish preferentially settle in microhabitats with and without predators present. There has been much work on the role of chemoreception in the selection of settlement substrates by marine larvae (reviewed by Pawlik [13]). For example, larval fishes and corals use chemical cues to discriminate between settlement substrates [14] and degraded and healthy reefs [15], as well as respond to the presence of conspecifics [16]. Similarly, brachiolaria larvae of crown-of-thorns starfish respond to chemical cues associated with specific bacterial films, causing them to discriminate between different substrates during settlement (e.g., [12,17,18]). Moreover, adult crown-of-thorns starfish have been shown to use chemoreception both to locate and orientate towards potential prey [19] and feeding conspecifics [20]. Given the inherent ability of crown-of-thorns starfish to respond to chemical stimuli, combined with potentially intense predation pressure at settlement, we expect that larval crown-of-thorns starfish are able to both detect and actively avoid predators during settlement.

2. Materials and Methods

2.1. Collection and Maintenance of Study Species

Adult *Acanthaster* cf. *solaris* [21] were collected from reefs around Lizard Island (14°40′ S; 145°27′ E) in the northern Great Barrier Reef between October and November 2015. All experiments were conducted at the Lizard Island Research Station. Spawning was induced following Cowan et al. [2]. One mL 10^{-4} M 1-methyladenine (1-MA) was injected into the gonads in each arm, through the aboral side of each starfish, which immediately induced spawning in males. Females, meanwhile, spawned within 20–30 min of administering 1-MA. To ensure that a mix of genotypes was used, gametes were collected using glass pipettes from at least 3 individuals of each sex. 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. Fertilization 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 rearing chambers was changed daily. Larval development was monitored daily, and late brachiolaria stage larvae were placed in separate rearing containers prior to use in experiments.

2.2. Preparation of Cues

Settlement experiments were conducted using coral rubble encrusted with crustose coralline algae (CCA), which was collected from shallow reef environments (<3 m depth) on the sheltered (north-west) side of Lizard Island. Rubble was broken into 1–2 cm pieces. Prior to experiments, all motile fauna were removed from coral rubble by manually removing fauna and repeatedly rinsing small fragments in saltwater. To ensure that rubble fragments were free of any potential infaunal predators, we also immersed fragments in freshwater for 30 s prior to using them in experiments. Although potential epibenthic predators were physically removed from the rubble, CCA and other encrustations were left intact. The predominant motile invertebrates removed from freshly collected rubble were polychaetes (mainly Nereididae and Amphinomidae). Amphinomidae polychaetes, *Pherecardia striata*, are known to prey upon newly settled *Acanthaster* cf. *planci* [22,23], and thus extracted polychaetes were retained for predation experiments. Trapeziid crabs (*Trapezia flavopunctata*, *Trapezia bidentata*, and *Trapezia cymodoce*) were collected by manually removing crabs with plastic forceps from *Pocillopora* corals collected from lagoonal reefs at Lizard Island. Corals were then maintained in a separate aquarium with flow-through seawater, for a minimum period of one week, prior to use in experiments. We did not distinguish between specific crab species or polychaete species in any of the experiments.

2.3. Predation Rates by Benthic Predators

To quantify predation rates by polychaetes and trapeziid crabs on brachiolaria larvae of crown-of-thorns starfish, individual predatory organisms (n = 16 for polychaetes; n = 8 for crabs) were placed in 70 mL specimen containers with 0.2 µm FSW and 10 brachiolaria larvae. No habitat was added in order to minimise the possibility of larval mortality occurring due to factors other than predation by the study organism. Predators were allowed to feed for 12 h through the night (18:30–06:30), and the number of starfish larvae that remained after this period was recorded. Controls were also conducted in which 10 brachiolaria larvae were added to 70 mL specimen containers with no predators.

2.4. Static Choice Chambers

To test the ability of settling *Acanthaster* sp. larvae to detect and respond to olfactory cues associated with potential settlement substrates and/or potential predators, we used static choice chambers consisting of two 10 L aquaria (chambers) connected by 150-mm diameter clear acrylic pipe. Substrates, with and without potential predators, were added to 0.2 µm FSW 24 h prior to the onset of experiments. Cues offered were: (i) the coral, *Pocillopora damicornis* without any infaunal organisms; (ii) *P. damicornis* with commensal trapeziid crabs; (iii) cleaned rubble; (iv) rubble with predators (polychaetes); and (v) adult *A.* cf. *solaris.* These cues were added to one or both chambers, in the combinations: (a) Cleaned rubble vs. FSW; (b) Rubble with polychaete predators vs. FSW; (c) Cleaned rubble vs. rubble with polychaete predators; (d) Cleaned rubble vs. coral; (e) Coral vs. FSW; (f) Coral with commensal crabs vs. FSW; (g) Coral vs. coral with commensal crabs; (h) Adult *A.* cf. *solaris* vs. FSW, offering larvae a pairwise choice of water sources. Larvae (n = 10) were individually placed in the centre of the pipe connecting both chambers, allowing horizontal movement towards one or the other aquaria. During trials, both aquaria were covered to minimise wind-driven water movement. Trials were conducted on a single larva, and larvae were not re-used. A choice was scored when the larvae moved well outside of the connecting tube and into one or the other of the two aquaria; there were no instances of larvae swimming back into the tube after entering an aquarium. If no choice was made after one hour, the larva was removed and "no choice" was recorded. After five replicates the chamber was cleaned and the water sources were switched to the opposite side to ensure that preferences were not biased for one side of the chamber. The response of larvae to each pairwise choice of cues was analysed using a Chi-square goodness of fit test against equal expected proportions, using Yates's correction, as expected counts were ≤ 5.

2.5. Settlement Assays

Settlement assays were conducted to determine whether the presence of benthic predators causes differences in rates of larval settlement. Ten larvae were introduced into 250 mL beakers filled with 0.2 µm FSW and containing one of two treatments: cleaned rubble (n = 7); or rubble with predators (polychaetes) (n = 7). Polychaetes were used as the predators in these experiments (cf. trapeziid crabs), because they naturally associate with rubble (cf. trapeziid crabs that generally associate with live coral). Controls were conducted in which larvae were introduced to 250 mL beakers ($n = 7$) containing only 0.2 µm FSW. Beakers were visually examined for indication of settlement/predation at 1, 2 and 6 h: when larvae were no longer swimming in the water column, they were assumed to have settled, or been consumed by predators. At 12, 24, 36 and 48 h, the number of larvae still swimming and the number that had settled out of the water column were counted. Larvae detected on the bottom of the beaker were counted as settled and checked under a microscope at the end of the experiment for evidence of metamorphosis. At 48 h, all substrates were also examined under a microscope for evidence of settled and metamorphosed individuals.

A repeated measures permutational analysis of variance (PERMANOVA) with "Treatment" (3 levels, fixed) and "Time" (4 levels, random) was run to test whether the biological habitat and presence or absence of predators had an effect on settlement success of larvae. PERMANOVA is a non-parametric technique that can be used in analysing univariate data [24]. Analyses were conducted using the PERMANOVA+ add-on for PRIMER v.6 (Primer-E Ltd., Plymouth, UK), using the Euclidian distance measure and 9999 permutations of the residuals under a reduced model, to calculate the significance of the pseudo-F statistic. Post-hoc pair-wise comparisons used Monte-Carlo asymptotic *p*-values (p_{MC}), as the number of unique permutations was low.

3. Results

3.1. Potential Predators

All three categories of potential benthic predators tested in this study (polychaetes, trapeziid crabs and scleractinian corals) caused elevated rates of mortality among late stage (competent) brachiolaria larvae of crown-of-thorns starfish (Figure 1). Mortality rates for starfish larvae exposed to individual polychaete worms averaged 1.9 larvae (out of 10) ± 0.6 (SE). For starfish larvae exposed to individual trapeziid crabs (ca. 10 mm carapace diameter), mortality rates were 4.5 larvae (out of 10) ± 0.9 (SE). By comparison, 100% of larvae survived across all controls. Mortality rates for starfish larvae exposed to the scleractinian corals, *Pocillopora damicornis*, were not explicitly measured, but all larvae that came into contact with the polyps were immediately consumed.

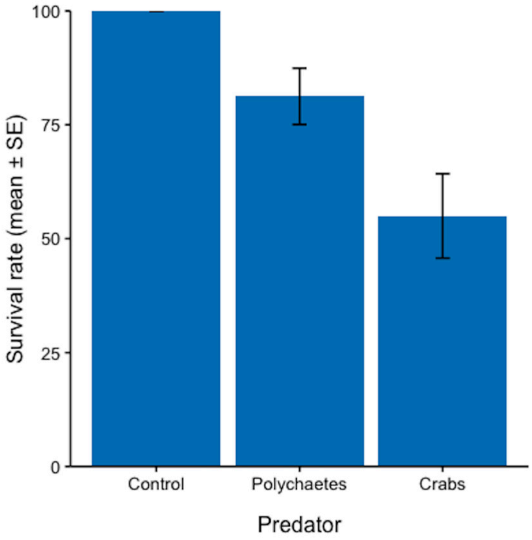

Figure 1. Mean survival (± SE) of brachiolaria larvae during a nocturnal, 12-h period, in the absence of predators versus when exposed to polychaetes and trapeziid crabs.

3.2. Static Choice Chambers

A total of 80 brachiolaria larvae were used in static choice experiments, across 8 different treatments (Figure 3). Of these 80 larvae, a total of 55 larvae moved outside of the connecting tube, actively swimming towards one or other of the adjoining aquaria containing alternative settlement substrates or cues. Starfish larvae did exhibit significant avoidance of predators (both trapeziid crabs associated with *Pocillopora* coral ($\chi^2 = 6.2$, df = 2, $p = 0.05$), and polychaete predators naturally associated with freshly collected pieces of rubble ($\chi^2 = 7.4$, df = 2, $p = 0.02$) relative to FSW (Figure 2). However, starfish larvae did not discriminate when comparing settlement substrates (rubble with conspicuous CCA and the scleractinian coral, *P. damicornis*) with and without predators (polychaetes: $\chi^2 = 0.2$, df = 2, $p = 0.90$, crabs: $\chi^2 = 3.8$, df = 2, $p = 0.15$; Figure 2). When comparing corals with and without trapeziid crabs, 6 (out of 10) of the starfish larvae remained within the connecting tube (and did not venture into either of the adjoining aquaria) for the entire period of observation (60-min).

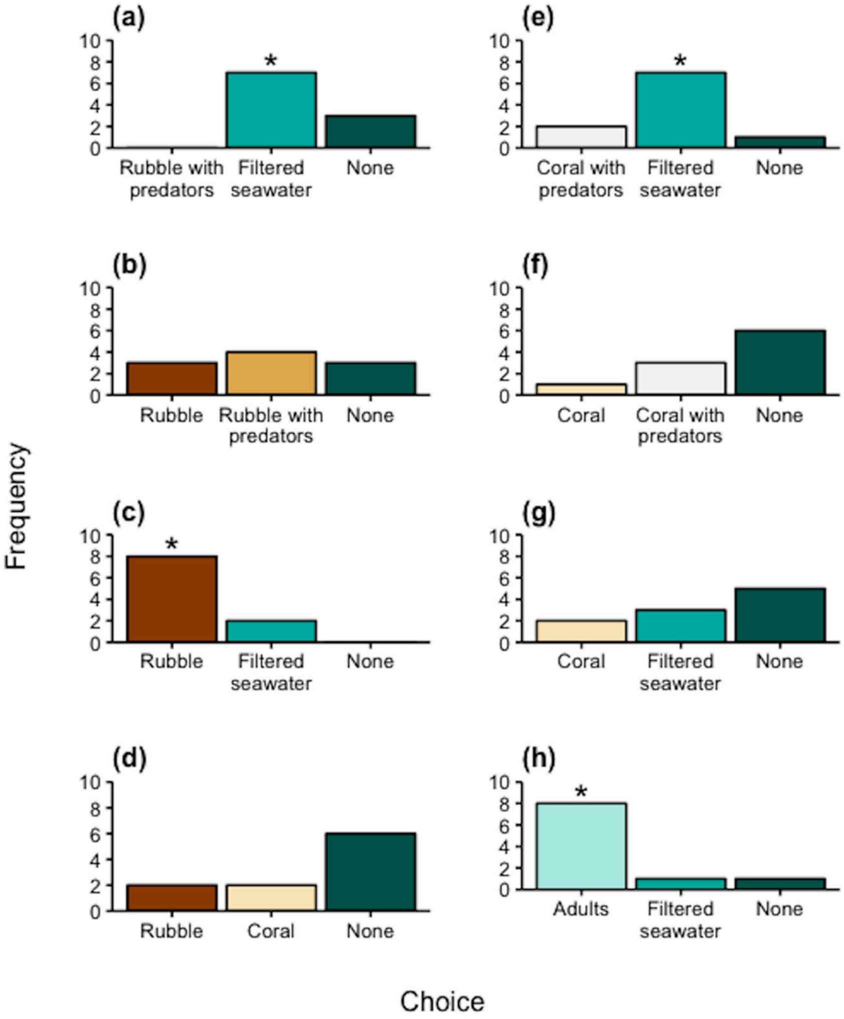

Figure 2. Behavioural response of brachiolaria larvae when offered a pairwise choice of cues: (**a**) Cleaned rubble vs. rubble with polychaete predators; (**b**) Rubble with polychaete predators vs. filtered seawater; (**c**) Cleaned rubble vs. filtered seawater; (**d**) Cleaned rubble vs. coral; (**e**) Coral vs. coral with commensal crabs; (**f**) Coral with commensal crabs vs. filtered seawater; (**g**) Coral vs. filtered seawater; (**h**) Adult crown-of-thorns starfish vs. filtered seawater. * Indicates a significant difference in larval choice frequency indicated by Chi-square goodness of fit test.

In the absence of predators (i.e., using rubble and live coral from which all predators had been removed), brachiolaria larvae of crown-of-thorns starfish exhibited strong and significant preference for cleaned rubble with conspicuous CCA over FSW ($\chi^2 = 10.4$, df = 2, $p < 0.01$). However, there was no significant difference in response when larvae were offered coral versus FSW ($\chi^2 = 1.4$, df = 2, $p = 0.50$; Figure 2e). Starfish larvae also did not significantly discriminate when offered a choice of cleaned rubble (with CCA) versus coral ($\chi^2 = 3.2$, df = 2, $p = 0.20$; Figure 2c). Larvae exhibited the strongest preference when comparing adult *Acanthaster* cf. *solaris* with FSW ($\chi^2 = 9.8$, df = 2, $p < 0.01$), with 8 (out of 10) larvae swimming towards adult conspecifics (Figure 2h).

3.3. Settlement Assays

A total of 210 larvae were used in the settlement assay, across three treatments (Figure 3). Of these 210 larvae, a total of 126 larvae were recovered after 48 h, either still swimming, or in contact with the substrate. There was a significant effect of treatment on the number of larvae still swimming in the settlement assay (Pseudo-$F_{(2,54)} = 13.27$, $p_{perm} < 0.01$). However, there was no significant effect of time (Pseudo-$F_{(3,54)} = 2.17$, $p_{\mathrm{perm}} > 0.05$) and no significant interaction between treatment and time (Pseudo-$F_{(6,54)} = 1.26$, $p_{perm} > 0.05$). In the presence of a settlement substrate, significantly fewer larvae were recorded as swimming, compared to the control ($t = 4.88$, $\mathrm{p_{MC}} < 0.01$), and this was regardless of the presence of polychaete predators ($t = 5.28$, $\mathrm{p_{MC}} < 0.01$). However, there was no significant difference in the number of larvae still swimming in the presence of a substrate with, versus without, polychaete predators ($t = 0.69$, $\mathrm{p_{MC}} > 0.05$; Figure 3a).

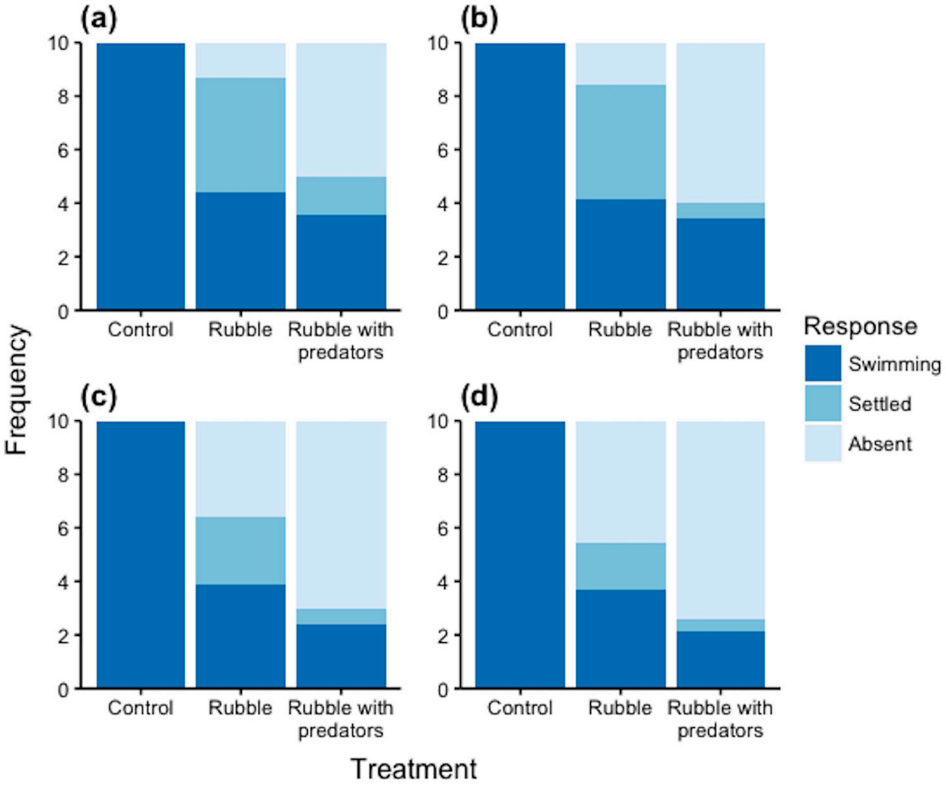

Figure 3. Mean number of larvae still swimming, settled and absent in each treatment after (**a**) 12, (**b**) 24, (**c**) 36, and (**d**) 48-h.

A total of 12 larvae were recorded as settled after 48 h, across the three treatments. In the absence of a substrate, 0% of larvae were induced to settle. There was a significant effect of treatment (Pseudo-$F_{(2,54)} = 13.60$, $p_{perm} < 0.01$) and time (Pseudo-$F_{(3,54)} = 3.80$, $p_{perm} = 0.01$), and a significant interaction between treatment and time (Pseudo-$F_{(6,54)} = 2.29$, $p_{perm} = 0.05$) on the number of larvae that were recorded as settled in the settlement assay (Figure 3b). The number of settled larvae that were recovered from the cleaned rubble treatment was significantly greater than for the control at 12 ($t = 3.67$, $p_{MC} < 0.01$), 24 ($t = 3.43$, $p_{MC} < 0.01$), 36 ($t = 3.58$, $p_{MC} < 0.01$), and 48 ($t = 2.46$, $p_{MC} = 0.03$) hours. There was no significant difference in the number of settled larvae in the cleaned rubble treatment, compared to the rubble with predators treatment after 12 h ($t = 2.01$, $p_{MC} > 0.05$); however, a significant decrease in the number of settled larvae recorded in the predator treatment from 12 to 24 h ($t = 2.52$, $p < 0.05$) meant that the number of settled larvae in the cleaned rubble treatment was significantly greater than for the rubble with predators treatment at 24 h ($t = 2.71$, $p_{MC} = 0.02$) and 36 h ($t = 2.57$, $p_{MC} = 0.03$) (Figure 3b). Although not significant, the number of settled larvae in the cleaned rubble treatment decreased from 12 to 48 h ($t = 2.26$, $p_{MC} > 0.05$), so the number of settled larvae in the cleaned rubble treatment, versus rubble with predators, was not significantly different after 48 h ($t = 1.53$, $p_{MC} > 0.05$). Notably however, 55% of larvae that settled in the absence of predators had undergone metamorphosis at 48 h, compared to 0% when predators were present.

4. Discussion

Given limited capacity for inter-reef movement of adult crown-of-thorns starfish [22], their abundance on any given reef is fundamentally dependent on rates of successful settlement and recruitment. To maximise settlement success, it would be expected that crown-of-thorns starfish preferentially settle to locations and microhabitats that minimise exposure to potential predators (e.g., [25]), either settling in locations that are naturally depauperate of potential predators or selecting microhabitats that provide refugia from predators. This study shows that settling larvae of *Acanthaster* cf. *solaris* are highly vulnerable to a range of different benthic predators, including scleractinian corals and their commensals (e.g., trapeziid crabs), as well as polychaete worms that were commonly found on freshly collected pieces of coral rubble, adding to the wide range of predators known to feed on early life-stages of *Acanthaster* spp. (e.g., [2–4,26]). Given the vulnerability of crown-of-thorns starfish to predators (reviewed in Cowan et al. this issue), it is likely that there are many more predators within the coral reef benthos capable of feeding on settling or post-metamorphic starfish. Once a more complete range of potential predators is established, or those that have the most significant impact on settlement and recruitment success of crown-of-thorns starfish, it will be important to test for spatial variation in abundance and diversity of these predators. For highly fecund species, such as *Acanthaster* spp., small changes to the rates of mortality at these early life stages are likely to have significant knock-on effects, and may account for spatial and temporal variation in the incidence of outbreaks [27,28].

Larvae of coral reef organisms, including fishes and corals, use chemical cues to distinguish between healthy and degraded reefs [15]. The attraction of brachiolaria larvae of *Acanthaster* cf. *solaris* to cues from cleaned rubble and deterrence from these substrates when polychaete predators were present suggests that larvae are able to detect these predators and may have the capacity to avoid settling to environments with high densities of benthic predators. This indicates a mechanism by which crown-of-thorns larvae can similarly distinguish between healthy and degraded reefs, as degraded reefs can have reduced densities of benthic predators. Polychaetes are amongst the most numerous and abundant component of the macrofauna found within the reef matrix (e.g., [29]) and are indicator species for marine degradation [30]. Both abundance and species richness of polychaetes are reduced in fished sites, compared to marine protected areas, as a result of trophic cascades [31]. Reefs that have been damaged by cyclones also have reduced polychaete abundance [32]. This may be an important factor in shaping recruitment patterns of *Acanthaster* spp. to reefs, with degraded reefs being more attractive to settling larvae.

Settling *Acanthaster* spp. larvae were not attracted to live coral substrates, and given that corals will prey upon settling larvae, this may explain the rejection of these substrates regardless of the presence, or absence, of commensal predators. Rather, settling crown-of-thorns starfish may actually avoid areas with high coral cover [33]. It has been suggested that larvae of crown-of-thorns starfish preferentially settle in areas with high abundance of adult conspecifics because the feeding activities of these adult starfish provide areas of recently dead coral, representing suitable settlement habitats [34] as well as minimizing the risk of predation by live corals [33]. Supporting this, our analyses of settlement preferences based on static choice chambers confirmed that larvae are significantly attracted to adult conspecifics. While other invertebrates including echinoderms settle on, or near to, conspecifics [13,35], this is the first time that it has been demonstrated for *Acanthaster* spp. and work is required to establish the mechanistic basis of this behaviour.

Whilst *Acanthaster* spp. larvae may preferentially settle in habitats with fine-scale topographic complexity to minimise mortality in the early life stages [9], numerous presumed predators are abundant in the reef matrix (e.g., [23,36,37]) and results of the settlement assay suggest that settlement is induced in the presence of a cue from substrates (cleaned rubble with naturally attached crustose coralline algae), with the presence of benthic predators unlikely to cause larvae to delay settlement (Figure 3a). Lack of difference in the number of settled larvae recovered from the rubble with predators treatment compared to the control, despite significant difference in the numbers of larvae still swimming in the settlement assays, indicates high levels of predation upon settling larvae, and is supported by our measurements of benthic predation rates. Additionally, no fully metamorphosed juveniles were recovered from treatments containing predators, compared to cleaned rubble treatments, in which 55% of settled starfish had metamorphosed. These data suggest that on a local scale, healthy benthic fauna is highly important in reducing successful recruitment of *Acanthaster* spp. through predation on settling larvae. Settlement substrate and predation by benthic predators may explain high variability in recruitment rates of *Acanthaster* sp. observed by Nakamura et al. [38]. Acroporids and *Acanthaster* sp. likely prefer to settle on similar substrate types, but variation in local abundance of benthic predators may have a more significant effect on recruitment of *Acanthaster* sp. compared to corals, for which recruitment was observed approximately 1 month after spawning [38].

In addition to the methods outlined in this study, we tested the ability of *Acanthaster* cf. *solaris* larvae to respond to olfactory cues using two-channel Atema flumes [39]. The flow rate in the flume chamber was set to the lowest possible speed (0.1 $\text{L}\cdot\text{min}^{-1}$), which allowed larvae to maintain their position and move across the current, whilst also ensuring laminar flow. Food dye was used to test for laminar flow and confirm separation of water sources. Individual larvae were placed in the centre of the test chamber, allowing choice between the two streams and movement towards a preferred water source. Whilst larvae were able to maintain position and move across the flow of water in the Atema flume chamber, we could not determine with confidence whether larvae were actively choosing one cue over the other: larvae were observed to move from the central starting position; however, they settled against either the outer edges or inner partition of the flume chamber and appeared to become trapped. Adaptation of the flume chamber to exclude edges in which larvae could become trapped would likely overcome this; thus, this may be an efficient method to test the response of *Acanthaster* spp. larvae to a range of environmental cues. Further, this demonstrates an ability of, at least the late-brachiolaria stage, larvae to move against a light current. This could be important in enabling larvae to manoeuvre across the reef matrix when searching for a suitable settlement habitat.

5. Conclusions

Variation in the abundance of benthic predators is likely to have a significant influence on settlement patterns of the crown-of-thorns starfish, as indicated by the avoidance of late-stage brachiolaria larvae of substrates that contain predators and low rates of settlement and metamorphosis on these substrates. Healthy benthic fauna is therefore likely to be important in regulating abundance and moderating settlement success of *Acanthaster* spp. Any extrinsic threat to benthic communities, including disruptive effects that may lead to trophic cascades, are likely to reduce the buffering capacity of coral reefs, increasing susceptibility to devastating outbreaks of crown-of-thorns starfish. Demographic studies of marine invertebrates often reveal particularly intense mortality in the period immediately following settlement (e.g., [6,40]). Studies described herein may also be extended to newly settled, post-metamorphic juveniles, with the aim of determining predation rates and further examining their behavioural responses to environmental cues.

Acknowledgments: This project was funded by an Ian Potter Foundation 50th Anniversary Commemorative Grant awarded to Z.L.C. by the Australian Museum's Lizard Island Research Station. We would like to thank Alexander Buck, Alexia Graba-Landry, Sam Matthews and Ben Mos for their assistance. Invertebrate collection was permitted under Great Barrier Reef Marine Park Authority permit number G15/38002.1. *Acanthaster* sp. were collected under Great Barrier Reef Marine Park Authority permit number G13/35909.1.

Author Contributions: All authors contributed equally to the concept and layout of this paper. Z.L.C. and S.D. compiled and analysed the data; Z.L.C. and M.P. wrote the paper; S.D. and C.C. edited the paper.

Conflicts of Interest: The authors declare no conflict of interest.

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