Journal of Coastal Life Medicine

journal homepage: www.jclmm.com

Size−related variation in arm damage frequency in the crown−of−thorns sea star, *Acanthaster planci*

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PEER REVIEW

ABSTRACT

Objective: To examine variation in the frequency of arm damage in different sizes of *Acanthaster planci* (*A. planci*), assess how this damage is inflicted by fish predators, and infer the potential role of predation in population regulation.

Methods: Diameters of *A. planci* collected from three sites in the Philippines were measured and arm damage frequency and severity was assessed. Frequency of arm damage was compared between sizes. Feeding behavior of fish predators was also observed in the laboratory.

Results: This study demonstrates that sublethal predation by triggerfishes on *A. planci* result in extensive arm damage. Overall, 60% of *A. planci* sampled across all sites had sublethal injuries. The frequency of individuals with missing or regenerating arms was highest in medium−sized young adults (11–20 cm), which coincides with the phase where *A. planci* shift from cryptic to exposed daytime feeding.

Conclusions: The high incidence of arm damage within intermediate−sized sea stars indicates that predators exercise some level of regulation on *A. planci* populations at a local scale. Identification and protection of putative predators that target the most vulnerable life history stages of *A. planci* are essential in developing population control strategies and reverse sustained declines in coral cover.

1. Introduction

Outbreaks of the crown−of−thorns sea star *Acanthaster planci* (*A. planci*), represent one of the most significant biological disturbances on coral reefs and remain one of the principal causes of wide spread decline in live coral cover in Indo−Pacific reefs[1,2]. Increasing frequency and intensity of outbreak episodes have resulted in progressively slower recovery, which consequently degrades the integrity of reef ecosystems[3–5]. Several hypotheses have been proposed to explain the genesis of these outbreaks events and this issue continues to be debated.

One of the earliest hypotheses is the predator removal hypothesis, which is based on the assumption that *A. planci* populations are normally regulated by high rates of predation and that outbreaks arise as a consequence of the release from predation pressure due to overharvesting of predators[6,7]. Initially, this hypothesis implicated the triton

snail, *Charonia tritonis*, as the major predator of *A. planci*[8]. Since then, it has been expanded to include teleost fish predators, gastropods, crustaceans, and other benthic species (Table 1).

Table 1

Putative predators of live *A. planci* and scavengers* of injured *A. planci* based on direct field and laboratory observations or implied from gut contents.

Predator/scavenger		Reference
Fish	*Epinephelus lanceolatus*	Endean 1977[48]
	Lethrinus atkinsoni	Sweatman 1995[12]
	Lethrinus miniatus	Sweatman 1995[12]
	Lethrinus nebulosus	Birdsey 1988[49]
	Balistoides viridescens	Ormond *et al*. 1973[50]
	Pseudobalistes flavimarginatus	Ormond & Campbell 1974[11]
	Arothron hispidus	Ormond *et al*. 1973[50]
	*Arothron nigropunctatus**	Moran 1992[51]
	Arothron stellatus	Keesing&Halford 1992[27]
	*Chaetodon auriga**	Moran 1992[51]
	*Chaetodon citrinellus**	Glynn 1984[40]
	*Holacanthus passer**	Glynn 1984[40]
	*Pomacanthus semicirculatus**	Moran 1992[51]
	*Cheilinus diagrammus**	Moran 1992[51]
	*Cheilinus fasciatus**	Moran 1992[51]
	Cheilinus undulatus	Ormond & Campbell 1974
	*Thalosomma lucasanum**	Glynn 1984[40]
	*Thalasomma hardwicki**	Moran 1992[51]
	*Chromis caerulea**	Moran 1992[51]
	*Euxiphipops sexstriatus**	Moran 1992[51]
	*Pomacentrus moluccensis**	Moran 1992[51]
Gastropod	*Bursa rubeta*	Alcala 1974[52]
	Cassis cornutus	Birkeland & Lucas 1990[17]
	Charonia tritonis	Endean 1973[8]
	Cymatorium lotorium	Ormond & Campbell 1974[11]
	Murex sp.	Birkeland & Lucas 1990[17]
Crustacean	*Hymenocera picta*	Wickler 1973[53] Glynn 1984[40]
	Neaxius glyptocercus	Birkeland & Lucas 1990[17]
	Panulirus pencillatus	Zann *et al*. 1987[23]
	Promidiopsis dormia	Alcala 1974[52]
	Xanthid crabs	Lucas 1975[54]
Others	*Pherecardiastriata* (worm)	Glynn 1982[10], 1984[40]
	Pseudocorynactis sp. (Corallimorpharia)	Bos *et al*. 2008[55]
	Stoichactissp (anemone)	Chesher 1969[56]
	Acanthaster planci (cannibalistic behavior)	Moran 1986[57]

Predation has been shown to regulate populations in coral reef communities; in fact, *A. planci* is well known for its ability to alter coral community structure by preferentially feeding on certain species of corals[9]. However, the question of how predation regulates populations of a keystone corallivore like *A. planci* remains poorly understood. Several species have been implicated in population regulation of *A. planci* but mechanisms have not been conclusively demonstrated. Glynn showed that the harlequin shrimp, *Hymenocera picta*, and the polychaete worm, *Pherecardiastriata* were capable of limiting populations of *A. planci* in the eastern Pacific[10]. In contrast, Ormond and Campbell observed that in the Red Sea *H. picta* fed mostly on smaller and less mobile species of sea stars and preferred shallow lagoons on reefs where *A. planci* were uncommon[11]. Attention has also been focused on fish that are generalist benthic carnivores, although observations

of actual predation on *A. planci* are rare and there is little direct and quantitative data to determine predation rates. When juvenile *A. planci* were presented to large fishes in a semi–natural setting, the maximum estimate of predatory mortality was only 0.13% of sea star per day, suggesting that the role of fishes in regulating population dynamics may not be significant at those specific sites[12]. Extensive gut analysis on benthic carnivorous fishes often failed to find remains of *A. planci* and identification has been challenging because it can be confused with other food sources[13,14]. Nevertheless, recent studies report increased incidence of *A. planci* outbreaks in areas subject to fisheries exploitation, suggesting that predation by heavily harvested fish may be a regulatory mechanism that prevents extreme population fluctuations[15].

While large individuals appear to escape predation due to their long poisonous spines and large size, predation pressure on smaller size classes could be high, as supported by the cryptic behavior of small individuals during the day[16], which indicates avoidance of visually orienting generalist fish predators that are active during the day[17]. A high percentage of *A. planci* with missing or regenerating arms suggests that a proportion of predatory encounters are not fatal, although this can be used as an index of relative predation intensity[18]. Several studies have shown that *A. planci* sustain significant, but variable, levels of sublethal predation, in the form of arm damage (Table 2). The most prevalent trend in most sea star species is for the amount of damage to be inversely proportional with size[19,20].

Table 2

Proportion of *A. planci* with arm damage from different locations (arranged from highest to lowest proportion of *A. planci* with missing or regenerating arms).

Location	Year	% Injured	Reference
Philippines	2012	67%	this study
Western Australia	1985	64%	Simpson & Grey 1988[58]
Philippines	2012	62%	this study
Hawaii	1972	60%	Branham 1973[59]
Guam	1991	59%	Lawrence 1991[19]
Philippines	2012	53%	this study
Papua New Guinea	1970	50%	Pyne 1970[60]
GBR	1994	50%	Stump 1996[61]
Western Australia	1985	47%	Simpson & Grey 1988[58]
Ryukyu Islands	1984	46%	Nakamura 1986[62]
Guam	1981	43%	Glynn 1982[10]
GBR	1987	40%	McCallum et al. 1989[18]
Ryukyu Islands	1985	35%	Nakamura 1986[62]
Ryukyu Islands	1986	33%	Nakamura 1986[62]
GBR	1967−1968	33%	Pearson & Endean 1969[63]
Ryukyu Islands	1985	32%	Nakamura 1986[62]
Sudan	1984	30%	Moore 1985[65]
Sudan	1969	29%	Ormond and Campbell 1971[64]
Western Australia	1985	25%	Simpson & Grey 1988[58]
Ryukyu Islands	1984	20%	Nakamura 1986[62]
Sudan	1970	20%	Ormond and Campbell 1971[64]
Panama	1980−1981	17%	Glynn 1982[10]
Fiji	1984−1985	13%	Zann et al. 1987[23]
Sudan	1970	4%	Ormond and Campbell 1971[64]
Sudan	1984	2%	Moore 1985[65]

In this study, we compared the frequency and intensity of arm damage, presumably caused by sublethal predation, on different sizes *A. planci* to determine if there was a size-related trend in the incidence of arm damage and to identify which stages were most vulnerable to attacks by predators. We also describe herein the feeding behavior of fish predators in captivity and characterize the damage caused by their predation activities. Overall, we will discuss the role of predation in regulating populations at different stages of growth.

2. Materials and methods

2.1. Specimen collection

A total of 310 *A. planci* specimens were collected from three sites in central Philippines: 100 from within the Tandayag Marine Sanctuary (9.452 812° N, 123.237 449° E), 132 from Tandayag Reef (9.458701° N, 123.233460° E) in Amlan, Negros Oriental, on September, 2012; and 78 from Mactan, Cebu on October 2012 (10.249 711° N, 123.977143° E). Local fishermen free dove between 5 m to 15 m depth and collected all sizes of cryptic and exposed *A. planci* that they could find using improvised bamboo tongs. Specimens were immediately transported to the laboratory and kept in holding tanks were at a depth of 0.5 m with flow-through ambient seawater (temperature 28 °C, pH 8.4, salinity 33 ppt). All sea stars were measured and assessed for arm damage within three days of collection.

2.2. Morphometric analysis and arm damage assessment

Maximum whole body diameter was measured to the nearest cm from the tip of the longest arm to the tip of the arm opposite to this, following Pratchett *et al*[21]. Specimens were photographed once they settled flat on the white slate with a ruler for reference. Measurements were verified by image analysis of referenced photographs using Image J[22]. Size structure between the three populations sampled was compared using Kruskal–Wallis Test in lieu of One-way ANOVA because normality and homogeneity of variance did not improve after transformations. Sea stars were turned over on their ventral side and the number of arms was counted based on the ambulacral grooves that have tube feet. Arm damage was recorded by counting the number of arms with fresh injuries, missing arms, or regenerating arms (Figure 1). Body size (diameter) was plotted against proportional incidence of arm damage (proportion of individuals with damaged arms over total number of individuals per size class) and a curve was fitted to this data using the peak three-parameter lognormal function under the dynamic curve-fitting tool in SigmaPlot 12.0 (Systat Software Inc., USA).
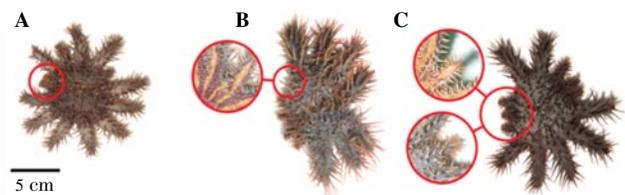

Figure 1. Characteristics of arm damage in *A. planci*.
A: Freshly damaged arm; B: Missing arm; C: Regenerating arm.

Size class data was pooled across all sites and classified into three categories: ⩽10 cm, 11–20 cm, and ⩾21 cm, which correspond with changes in foraging and emergence behavior[16,23]. Variation in arm damage incidence between size class categories was analyzed using One-way ANOVA, followed by Tukey's *post hoc* comparisons. Severity index was calculated by dividing the number of injured or damaged arms with the total number of arms for each sea star. Differences in arm damage severity between size class categories were analyzed using Kruskal–Wallis Test, as transformations did not improve normality and homogeneity of variance.

2.3. Laboratory testing of putative predators

The following potential fish predators and scavengers, with corresponding total lengths of each specimen, were collected from the reef across the IEMS Marine Laboratory: titan triggerfish [*Balistoides viridescens*, Bloch & Schneider 1801 (*B. viridescens*); 18 cm, 15 cm], yellow-margin triggerfish [*Pseudobalistes flavimarginatus*, Rüppell 1829 (*P. flavimarginatus*); 16 cm], white-spotted pufferfish [*Arothron hispidus*, Linnaeus 1758 (*A. hispidus*); 21 cm], threadfin butterflyfish (*Chaetodon auriga*, Forsskål 1775 (*C. auriga*); 13 cm), green damselfish [*Chromis caerulea*, Cuvier 1830 (*C. caerulea*); 4 individuals at 6 cm), and lemon damselfish (*Pomacentrus moluccensis*, Bleeker 1853 (*P. moluccensis*); 4 individuals at 6 cm). Four each of *C. caerulea* and *P. moluccensis* and one each of *B. viridescens*, *A. hispidus*, and *C. auriga* were placed together inside a 0.2 m³ glass aquarium with flow-through ambient seawater to observe predation on live *A. planci*. Four intact (8–15 cm diameter) sea stars were placed with above mentioned potential fish predators. A GoPro Hero HD video camera was used to record activity for two straight days divided in four 4-hour intervals (08:00–11:00, 12:00–15:00, 17:00–20:00, and 21:00–24:00). Videos were immediately reviewed after being downloaded into the computer hard drive. In another experiment, one *B. viridescens* and one *P. flavimarginatus* were placed together in the glass aquarium with three live, intact *A. planci* (7 cm, 14 cm, 21 cm diameter). The choice of these fish predators was based on previously recorded encounters with *A. planci*. Activity was also recorded for two straight days at the same intervals and predation behavior and resulting damage were documented upon review of the videos (see supplemental material).

3. Results

3.1. Morphometrics and arm damage

The diameter of all specimens collected ranged from 4.4 cm to 29.7 cm [mean=(17.0±5.9) cm]. There was no significant difference in the size frequency distribution between sampling sites (H=1.472, *df*=2, *P*=0.479). Sample sizes for the three size class categories, pooled across all sites, were as follows: ≤10 cm (*n*=47, 15%), 11–20 cm (*n*=176, 57%), and ≥21 cm (*n*=87, 28%).

Incidence of arm damage was 67%, 53%, and 62% in Site 1 (Tandayag Marine Sanctuary), Site 2 (Tandayag Reef), and Site 3 (Mactan), respectively. Altogether, 60% (185 of 310) of sea stars sampled had arm damage (Table 2). The relationship between sea star size (diameter) and the proportional incidence of arm damage was non–linear (Figure 2), which is in contrast with the inverse size–damage relationship shown in most asteroids[19,20]. There was a significant relationship between sea star size and proportional incidence of arm damage best described by the peak three–parameter lognormal distribution (R^2= 0.776, $F_{2,24}$=41.608, *P*<0.000 1), where rates of injury were much less in the smallest and largest samples, and highest in intermediate sizes.
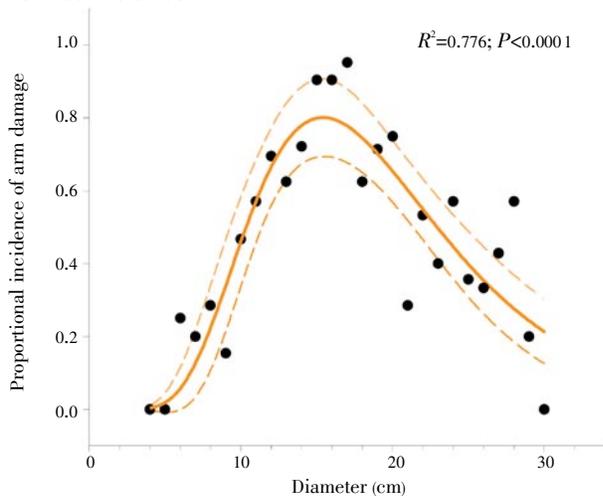

Figure 2. Relationship between sea star diameter and frequency of individuals with damaged arms.

Bold line represents best fit curve based on peak three–parameter lognormal equation: Predicted incidence of arm damage=13.429^{−0.5[ln(diameter/18.224)/0.410]^2}/diameter. Dashed lines are 95% confidence intervals.

Similarly, when pooled across all sites and grouped by size class, there was a significant difference in the incidence of arm damage between categories ($F_{2,6}$=19.523, *P*=0.002) (Figure 3A). Pairwise comparisons using Tukey's *post hoc* test show that the incidence of arm damage in the 11–20 cm size class category [mean=(77±7)%] was significantly higher than the ≤10 cm [mean=(27±11)%] and ≥21 cm [mean=(45±11)%] categories. Individual levels of severity ranged from 6% to 67% (mean= (24±14)%] injured arms per total number of arms. There was no significant difference in the levels of arm damage severity between

size class categories across all sites (H=0.927, *df*=2, *P*=0.629) although there were several individuals within the 11–20 cm size class category that had high levels of severity (Figures 3B). There was no significant difference in the proportion of regenerating arms per total number of injured arms (H=2.771, *df*=2, *P*=0.250), however, the proportion of regenerating arms decreases in larger sizes [*i.e.* (83±29)% in ≤10 cm, (71±34)% in 11–20 cm, and (65 ± 36)% in ≥21 cm size class category].
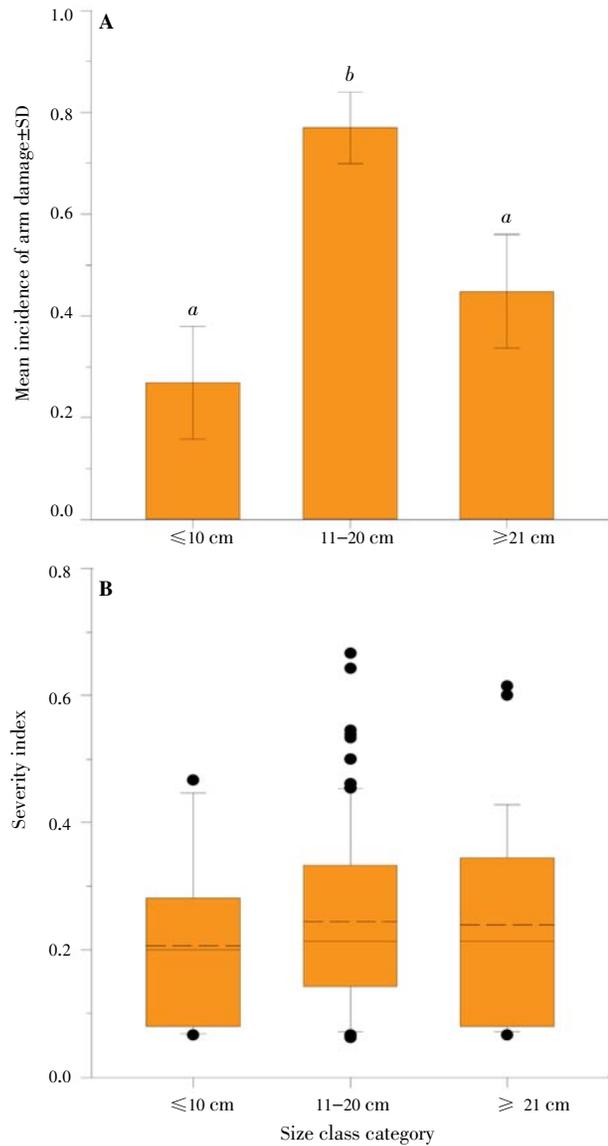

Figure 3. Incidence and severity of arm damage.

A: Proportion of individuals with arm damage for each size class category– similar letters above error bars indicate no significant difference based on Tukey's *post hoc* comparisons; B: Index of arm damage severity per size class–dashed lines are means.

3.2. Predation behavior and resulting damage

Videos of predation activity showed that the triggerfishes, *B. viridescens* and *P. flavimarginatus*, were aggressively attacking *A. planci*. In most encounters, triggerfish initially bit off and spit out spines which resulted in the shortening and blunting of spines; before proceeding to take the skin off and ingest internal organs (see supplemental video).

The other mechanism used is by directly biting the tip of the arm and eventually consume the entire arm including digestive glands and gonads. Other fish were not observed attacking live and intact *A. planci*, instead, *A. hispidus* fed on a large amount of *A. planci* remains on the bottom of the aquarium. Smaller fish (*C. auriga*, *C. caerulea*, *P. moluccensis*) picked on exposed internal organs of injured sea stars and also fed on suspended particles when the bottom was disturbed as a result of the feeding activity of *A. hispidus*. When *B. viridescens* and *P. flavimarginatus* were placed with *A. planci* representing size class categories described in this study, without the other fish, similar predation behavior was observed. In addition, attacks were observed in all size classes. Both triggerfish were observed biting the arms of *A. planci* but in a few occasions did not result in arm damage when the sea star was not properly anchored on the surface of the tank; instead, they ended up dragging the sea star and turning it with the ventral side facing up. The smallest *A. planci* (7 cm) in the aquarium had short spines and was bitten directly on the central disk by *B. viridescens*, subsequently killing the sea star (see supplemental video).

4. Discussion

Several attempts to locate aggregations of juvenile *A. planci* have been unsuccessful and they continue to elude researchers[24,25]. This partly explains the smaller sample size for the ≤10 cm size class category in this study. Surveys and large–scale collection efforts usually encounter larger specimens (>30 cm). However, none of the specimens collected in this study were larger than 30 cm. The maximum body size (29.7 cm) of all specimens sampled in this study indicates that recruitment is fairly recent (<2 years). The presence of different size classes signifies that there might have been a progressive accumulation of different cohorts or multiple recruitment events in these reefs, although persistent populations have remained at low levels and have not progressed into massive outbreaks.

The incidence of arm damage in *A. planci* across all sites (60%) is among the highest in reported proportions of *A. planci* with missing and regenerating arms from different locations. McCallum *et al*. showed that sublethal arm damage on *A. planci* could be used as an index of predation intensity on a given population[18]. Using sublethal damage as a metric, this indicates that predation intensity is high among sampled populations. Predation by generalist fish predators may play a direct[7] and/or indirect[15] role in regulating *A. planci* populations sampled in this study. McCallum proposed that a predation rate of 1.5% per sea star per day is sufficient to prevent an outbreak[7]. Several species have been directly implicated in population regulation of *A. planci*. Significant levels of predation by triggerfishes and pufferfishes were observed in the Red Sea and feeding rate calculations demonstrated that this could account for reductions in *A. planci* numbers from outbreak densities of approximately 2000 adults down to around 5–20

sea stars per kilometre reef face[11]. The pufferfish, *Arothron stellatus*, had been observed to consume entire small adults (20 cm) in less than 10 min[26]. Indirectly, large piscivorous fishes reduce the densities of benthic carnivorous fishes and relieve predation pressure on invertebrates that feed on small *A. planci*[15]. Benthic epifauna have been found to be important predators of small *A. planci* that are very cryptic and are often inaccessible to fish predators[26,27].

In this study, triggerfishes (*B. viridescens* and *P. flavimarginatus*) were observed, in captivity, to directly attack and feed on live *A. planci* of all sizes. The abundance and biomass of triggerfishes in our study sites were not directly quantified. Nevertheless, modeling studies have demonstrated that hypothetical rates of predation by generalist predators, such as triggerfishes, are capable of regulating populations of sub–adult *A. planci*[28–30]. Triggerfishes have also been identified as keystone predators of sea urchins[30,31]. On the coral reefs of East Africa, for example, the orange–lined triggerfish (*Balistapus undulatus*) is a keystone predator that regularly consumes up to 75% of the burrowing sea urchin, *Echinometra mathaei*, which is the most dominant sea urchin in Kenyan reefs[30,32]. The careful removal of spines exhibited by *B. viridescens* prior to ingestion of arms and internal organs, despite its powerful jaw morphology equipped for predation on sea urchins and other hard–shelled animals[33], supports the defensive role of spines in *A. planci*. Remains of *A. planci* have been found in the stomachs of 30 *P. flavimarginatus* in Fiji but this was not directly witnessed or documented by video or photograph[34]. Endean also recorded remains of juvenile *A. planci* in the gut of a Queensland grouper, *Epinephelus lanceolatus*[35]. However, these studies were not able to make a distinction whether these fish fed on live sea stars or only fed on remains, as is the case of *A. hispidus* which was observed to consume large quantities of *A. planci* remains but was never observed directly attacking intact sea stars.

Triggerfishes exposed to different sizes of *A. planci* in the aquarium did not show a strong preference for specific size classes in terms of the frequency of attacks, although more injuries were inflicted on smaller specimens. Hiding places for the sea stars were not provided in the aquarium, thus each sea star was equally exposed to the predators. The variability of frequency in arm damage between size classes in the field could be a function of physical and behavioral changes that occur during these stages in natural conditions. Small juveniles that feed on crustose coralline algae on the underside of the reef framework are cryptic and are mostly active at night[23,36]. Field mortality rates during this algae–feeding stage can be as high as 6.49%, mostly due to predation by benthic epifauna[27]. This cryptic behavior continues during the early coral–feeding stage around 13–18 months with an estimated diameter of less than 10 cm[16,23]. Foraging activity of *A. planci* at this stage is heavily influenced by predator avoidance and implicates generalist fish predators that are active during the day as important predators of small *A. planci*[26]. This also explains the small number of sea stars belonging to the 1–10 cm size class as

well as the low frequency of arm damage on these smaller *A. planci*. After 20 months (diameter >10 cm), *A. planci* shift from cryptic to daytime feeding and at 24 months (~15 cm), sexual maturation and active migration will commence[23]. This exposes the sea star to visually searching predators and with developed gonads, *A. planci* at this stage could be more energetically rewarding as prey[37]. Although large adult *A. planci* are also equally exposed and may even be more nutritionally rewarding with its maximally developed gonads rich in proteins and lipids and it is still a very large prey for all but the largest predators are heavily reinforced by its long poisonous spines. Reduced predation or incidences of arm damage on large individuals have been reported in other echinoderms[38,39].

It can also be argued that injuries incurred during earlier stages will be visible as it grows into the adult phase and signs of past regeneration may never be entirely lost; therefore cumulatively, frequency of arm damage will be higher in older and larger classes. This was not the case in this study as there was no significant difference in levels of severity and proportion of regenerating arms between size classes.

Although predation may only be fatal in few instances, sublethal attacks may increase mortality, as it will be detrimental to the general fitness of *A. planci*. Compared to most asteroids, the low skeletal content of *A. planci* makes retention of integrity after damage more difficult. In this study, *B. viridescens* repeatedly attacked *A. planci* that already had injuries from previous encounters. In addition, *C. auriga* was also feeding on exposed organs on the arms of *A. planci* that were attacked by *B. viridescens*. Glynn[40] suggested that exposure of internal organs increase the likelihood of further attacks by a broader array of predators or scavengers and reported that internal tissues of *A. planci* appear acceptable as food to fishes (*i.e.* the Cortez rainbow wrasse *Thalassoma lucasanum*, the king angelfish *Holacanthus passer*, and the speckled butterflyfish (*Chaetodon citrinellus*) even if it is not part of their ordinary diet.

Sublethal predation is a removal of biomass and therefore could result in a loss of production. Arm damage or other injuries results in energetic costs that include decrease in ability to obtain nutrients, and reallocation of nutrients to regeneration instead of reproduction or overall somatic growth[19,20]. Because the vital digestive (*Pyloric caeca*) and reproductive (gonads) glands are located along the arms, damage is very costly among asteroids[41]. The high percentage of injured arms that were regenerating indicates that the healing and regeneration process are often prioritized. Furthermore, reallocation of resources towards regeneration could compromise the defense and immune responses of *A. planci*. Opportunistic pathogens will be better able to infect individuals with open injuries and exposed internal organs and increase the likelihood of disease transmission[42–44].

In addition, *A. planci* has a relatively thin integument in comparison with other asteroids and tissue extracts showed much lower antibiotic properties than other asteroids,

showing a weak activity against gram negative bacteria[45], which are abundant in the marine environment—traits that clearly contribute to increased susceptibility to disease after injury. Moreover, maintaining a high metabolic rate to recover from injuries during times of scarce food supply such as those observed at the end of outbreaks may jeopardize survival by channeling resources away from maintenance needs and could alternatively explain why sea stars with arm damage were relatively smaller in size.

This study shows that the phase where *A. planci* shift from cryptic to exposed daytime feeding[16,23] followed by the onset of sexual maturity (gonad development) and migration is the "window of vulnerability" described by McCallum *et al*[18]. Then again, small juveniles (1–10 cm) are also more likely to be completely consumed rather than escape with sublethal damage, while larger individuals (<20 cm) are relatively prone to infection after damage by partial predation[17]; therefore, medium-sized *A. planci* in this study showed a higher frequency of partial predation. The high frequency and level of arm damage in young adult *A. planci* (11–20 cm) suggests that predators exercise regulation on this size range of *A. planci* populations at a local scale. Models demonstrate that species like *A. planci* have two relatively stable population levels: A lower one where abundance is limited by predation and an upper one where predator pressure is reduced and it becomes limited by its own food supply[29]. Furthermore, Sweatman[15] showed that protection of reefs indirectly mitigate *A. planci* populations by protecting fish species that feed on *A. planci* or allowing large piscivorous fish to flourish thereby reducing the densities of benthic carnivorous fishes and relieve predation pressure on invertebrates that feed on small *A. planci*[15]. It is noteworthy that specimens collected from within a no-take marine reserve (Tandayag Marine Sanctuary) had the highest incidence of arm damage (67%). Based on surveys conducted by Stockwell *et al.*[47] the reef within the protected area has 142 fish species, with mean density of 2 307 reef fishes per 500 m^2, while there were only 77 reef fish species within the control site and less than half the mean density inside the marine reserve at 1 030 fish per 500 m^2. These surveys also indicate an increasing trend in terms of reef fish density and biomass. As a no-take marine reserve for over 15 years, there is a higher probability of encounters between *A. planci* and fish predators within the protected area compared to fished sites. The density and biomass of predatory reef fishes (groupers, jacks, snappers and emperors) within the Tandayag MPA was highest compared to other reefs surveyed around the area[46]. De Dios and Dyalso found that the lowest densities of *A. planci* among areas surveyed around Sogod Bay, Philippines were those from inside protected areas[46], where *Pseudocorynactis* sp., a known *A. planci* predator[55], was abundant.

A logical next step would be to directly test different size classes in a semi-natural setting in the field[12] to determine what proportion of predatory encounters are lethal and compare the palatability of different sizes of *A. planci*. There have been no studies on the changes in toxicity (*i.e.* saponin concentrations) and mechanical

resistance (*i.e.* spine length and body wall stiffness) during the different stages of growth of *A. planci*. Predation rates on different reefs with variable levels of predatory fish abundance should also be compared. Global degradation of reefs and the threat of climate change impacts provide renewed incentive to manage all sources of coral mortality, particularly *A. planci* outbreaks, regardless of whether or not these are natural or due to anthropogenic disturbances. In the Great Barrier Reef for example, models predict that the absence of *A. planci* predation alone, despite ongoing damage from tropical cyclones and bleaching, can reverse the progressive degradation of reefs and increase coral cover by 0.89% per year[3].

Recent reports of widespread coral damage caused by massive outbreaks in the Philippines, the Great Barrier Reef, Japan, French Polynesia, Samoa and elsewhere in the Indo–Pacific emphasize the urgency of research to develop preventive and responsive mitigation measures. Effective management and control of outbreaks can only be achieved by integrating different approaches: improvement of water quality, protection of predators and their habitats, biological control, and physical removal.

Conflict of interest statement

We declare that we have no conflict of interest.

Acknowledgements

Comments

Background

Outbreaks of the crown of thorns starfish has become a serious threat to socially and economically important coral reefs in the Indo–Pacific in the last several decades. In order to address this danger, scientists have been looking into various aspects of the biology of crown of thorns starfish including predator/prey interactions that may be involved in triggering, worsening and prolonging these events. It is hoped that insight gained from these inquiries will provide or fine tune management tools allowing crown of thorns starfish populations to be adequately controlled.

Research frontiers

The research presented in this manuscript describes studies that aim to tease apart various aspects of crown of thorns starfish as prey items that will give insight into this aspect of crown of thorns starfish outbreaks. They seek to discern if certain life stages may be more susceptible to predation than others. They additionally measure the *in–situ* presence of possible predators and employ captive studies to observe predation tactics by presumed predators.

Related reports

Crown of thorns starfish and their destructive outbreaks have been the focus of high numbers of studies and sometimes heated debates since the late 70s. The present work acknowledges the bulk of this work and add a few more significant pieces of the puzzle of crown of thorns starfish outbreak dynamics and their control. Besides the practical application of the work described, this work adds to the voluminous work on the complex species interactions included in studies of crown of thorns starfish and other species population dynamics.

Innovations and breakthroughs

This work describes a novel way of the determination of several aspects of crown of thorns starfish population dynamics related to the possibility/hypothesis that predation upon them may be one of the more important restraining variables. They also look at the presence and abundance of teleost predators in the wild and make captive observations of the methods these fish use when preying upon crown of thorns starfish, where little has been observed in the wild.

Applications

Results obtained clearly show that medium sized crown of thorns starfish are most vulnerable to predation and a key life history stage that may regulate whether crown of thorns starfish numbers remain at normal levels or increase into destructive outbreaks. Future studies and management efforts would do well to focus on crown of thorns starfish of this key size range. There still remains the complexities of direct (predation) and indirect (predator biology and ecology) causes of crown of thorns starfish outbreaks, and this study clearly indicates that certain fish species are important natural components of crown of thorns starfish population regulation.

Peer review

This is an important line of study that significantly adds to a long line of crown of thorns starfish focused researches. It succeeds in answering several key questions concerning the natural predator control of crown of thorns starfish in the wild. Additionally it provides insight into predatory mechanisms not observed previously. Both lines of inquiry clearly answer previous questions and point to logical next lines of questioning (a hallmark of quality scientific inquiry)

and practical solutions to the bigger questions their work addresses.

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