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RESEARCH NOTE

Multi-species consumer jams and the fall of guarded corals to crown-of-thorns seastar outbreaks [version 1; referees: 2 approved]

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Abstract

Outbreaks of predatory crown-of-thorns seastars (COTS) can devastate coral reef ecosystems, yet some corals possess mutualistic guardian crabs that defend against COTS attacks. However, guarded corals do not always survive COTS outbreaks, with the ecological mechanisms sealing the fate of these corals during COTS infestations remaining unknown. In August 2008 in Moorea (17.539° S, 149.830° W), French Polynesia, an unusually dense multi-species aggregation of predators was observed feeding upon guarded corals following widespread coral decline due to COTS predation. Concurrent assaults from these amplified, mixed-species predator guilds likely overwhelm mutualistic crab defense, ultimately leading to the fall of guarded corals. Our observations indicate that guarded corals can sustain devastating COTS attacks for an extended duration, but eventually concede to intensifying assaults from diverse predators that aggregate in high numbers as alternative prey decays. The fall of guarded corals is therefore suggested to be ultimately driven by an indirect trophic cascade that leads to amplified attacks from diverse starving predators following prey decline, rather than COTS assaults alone.

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Referee Status:

	Invited Referees	
	1	2
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1 **Peter W. Glynn**, University of Miami, USA

2 **Ciemon Frank Caballes** , James Cook University, Australia

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Corresponding author: Mohsen Kayal (mohsen.kayal@gmail.com)

Author roles: **Kayal M:** Conceptualization, Investigation, Visualization, Writing – Original Draft Preparation; **Ballard J:** Writing – Original Draft Preparation, Writing – Review & Editing; **Adjeroud M:** Funding Acquisition, Project Administration, Resources, Supervision, Writing – Review & Editing

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Introduction

Identifying ecological processes that drive species trajectories is a prerequisite for ecosystem management. However, community dynamics are sometimes governed by unexpected, indirect interactions and complex emergent properties that can cause runaway responses and abrupt ecological shifts (Silliman *et al.*, 2013; Terborgh & Estes, 2010). Outbreaks of the coral predator crown-of-thorns seastar (COTS) cause widespread coral mortality across the Indo-Pacific Ocean (Pratchett *et al.*, 2014) with often drastic impacts on diverse reef communities (Kayal *et al.*, 2012). However, some coral species possess mutualistic allies that can deter COTS predation. In particular, trapeziid crabs inhabiting large pocilloporids are known for their ability to effectively defend their host corals from COTS assaults (Glynn, 2013; McKeon & Moore, 2014), although guarded pocilloporids do not always survive COTS outbreaks (Leray *et al.*, 2012; see Figure 1). Despite increasing understanding of factors determining coral susceptibility to COTS predation (Glynn, 1976; Kayal *et al.*, 2011; Kayal & Kayal, 2017; Pratchett, 2001; Rouzé *et al.*, 2014), the processes sealing the fate of guarded corals during outbreaks have remained unknown. Here we provide insights into the ecological mechanisms underlying the fall of guarded corals during predatory COTS outbreaks.

Methods

Our observations were performed at the peak of an intense crown-of-thorns seastar (COTS) outbreak that decimated

coral communities around the island of Moorea (17.539° S, 149.830° W), French Polynesia, between 2003 and 2010. General patterns in propagation of COTS swarms around the island, and impacts on corals and other reef communities were described by Kayal *et al.* (2012); Kayal *et al.* (2017). Here, we provide complementary observations that unveil processes leading to the fall of large pocilloporid assemblages that benefit from “anti-COTS” mutualistic defense, the so-called guarded corals. In Moorea, these assemblages are dominated by *Pocilloporida eydouxi*, a species that hosts trapeziid crabs able to deter COTS predation (Leray *et al.*, 2012; McKeon & Moore, 2014; Figure 1). Our observations were performed using SCUBA on the outer reef slope at Tiahura where the COTS outbreaks in Moorea were initiated and had particularly detrimental impacts (Kayal *et al.*, 2012).

Results and discussion

In August 2008 at 12 m depth on Tiahura reef, we observed an unusually dense aggregation of coral-eating butterflyfishes jamming around guarded pocilloporids, the last coral bastions that had yet resisted swarms of the predatory seastar (Figure 2, Supplementary Image 1). Widespread coral decline had previously wiped out much of resident populations of coral-feeding butterflyfishes (Kayal *et al.*, 2012), pushing starving survivors to aggregate around the guarded corals. The aggregation of 9 butterflyfishes within a single square-meter (9 fish.m⁻²), as captured in Figure 2, was particularly surprising, as density of the coral-feeding butterflyfish assemblage on this reef location

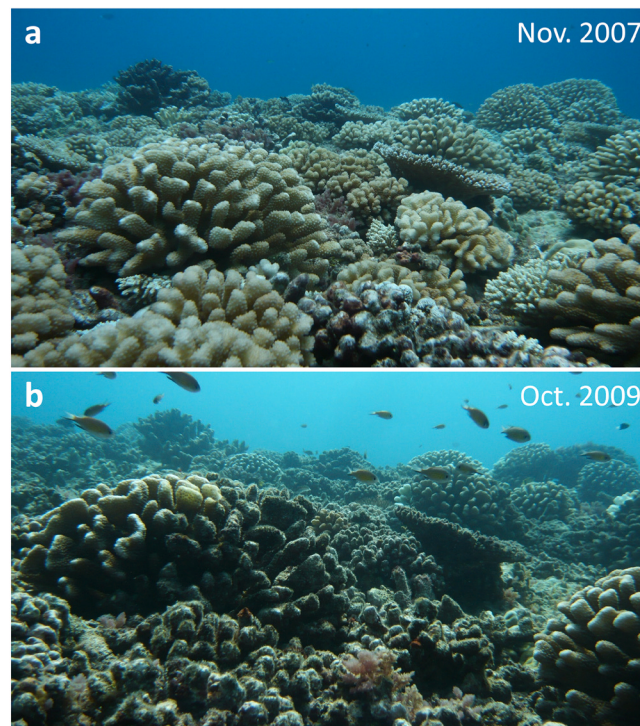


Figure 1. Widespread coral decline and survival of guarded corals that partially or fully resisted seastar predation. Pictures were taken at 6 m depth on Tiahura reef in Moorea, French Polynesia, before (a) and after (b) this location was invaded by crown-of-thorns seastar (COTS) swarms. White feeding scars characteristic of recent COTS predation can be seen on several of the guarded coral colonies (*Pocillopora eydouxi*) in b.



Figure 2. Aggregation of a diversified guild of 10 macro-predators simultaneously feeding upon a guarded coral. This aggregation was observed following widespread coral decline (note the absence of live coral in the background) in August 2008 at 12 m depth on Tiahura reef in Moorea, French Polynesia. The predator guild was composed of a crown-of-thorns seastar (COTS) and nine butterflyfishes from species *Chaetodon ornatissimus*, *C. pelewensis*, *C. quadrimaculatus*, *C. reticulatus*. White feeding scars characteristic of recent COTS predation can be seen on the guarded coral (*Pocillopora eydouxi*).

had dropped to the much lower average value of 4.3 ± 0.9 SE fish.200m⁻² (surveyed in June 2008, equivalent to 0.02 fish.m⁻²). The observed aggregation thus represented a more than 400-times concentration of the predation pressure exerted by the butterflyfishes, and was targeting a guarded pocilloporid that was already under attack by COTS (Figure 2, Supplementary Image 1).

Guarded pocilloporids in Moorea have shown the ability to resist devastating COTS predation for several years (McKeon & Moore, 2014; Figure 1). However, concurrent assaults from such locally amplified, mixed-species predatory guilds likely overwhelm the ability of trapeziid crabs and other exo-symbionts to defend host pocilloporids, ultimately causing the fall of guarded corals. Indeed, coral occupation by mutualist communities is determined by strict rules of territoriality and competition (Glynn, 2013; Leray *et al.*, 2012), which limits the abundance of inhabiting guardians in host colonies, and therefore their ability to sustain predatory assaults. Coral decline has already been identified as an engine of COTS movements and prey selection during

outbreaks (Kayal *et al.*, 2011; Kayal *et al.*, 2012; Silliman *et al.*, 2013). Our observations suggest that further cascading effects include aggregating diverse predators in numbers surpassing mutualistic defenses, eventually leading to the collapse of guarded corals. We therefore advocate the importance of controlling COTS outbreaks at the earliest stages, before trophic cascades could lead to a runaway collapse of coral communities.

Competing interests

No competing interests were disclosed.

Grant information

Mohsen Kayal's Ph.D. studies were supported by grants from Polynésienne des Eaux and Planète Urgence.

The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Supplementary material

Supplementary Image 1. Additional photographs capturing the predatory guild aggregating around a guarded coral following widespread coral decline. Pictures (a, b) were taken in August 2008 at 12 m depth on Tiahura reef in Moorea, French Polynesia, at the peak of an intense outbreak of the coral-eating crown-of-thorns seastar (COTS). The observed macro-predator aggregation was composed of one COTS and nine individuals from resident butterflyfish species *Chaetodon ornatissimus*, *C. pelewensis*, *C. quadrimaculatus*, *C. reticulatus* (see Figure 2). White feeding scars characteristic of recent COTS predation can be seen on the guarded coral (*Pocillopora eydouxi*).

[Click here to access the data.](#)

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Ciemon Frank Caballes 

ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Qld, Australia

This is an interesting observation of a relatively high concentration of a multi-species predator guild on corals that were initially spared from crown-of-thorns seastar (COTS) predation. The ultimate demise of "guarded" Pocilloporids may have been due to a high density of starving COTS (at the peak of an outbreak) feeding on whatever coral was left and overwhelming mutualistic crabs in the process. The overall impact of the butterflyfish, in terms of coral mortality, was most likely lower compared to COTS.

It is unclear whether this was a widespread occurrence or a one-time observation. A brief description of the feeding behaviour of COTS and butterflyfishes (relative contribution to coral mortality), as well as the defensive behaviour of Trapeziid crabs will be useful.

METHODS: Change *Pocilloporida eydouxi* to *Pocillopora eydouxi*.

SUPPLEMENTARY IMAGE 1: Feeding scars are not clear in the pictures.

Is the work clearly and accurately presented and does it cite the current literature?

Yes

Is the study design appropriate and is the work technically sound?

Yes

Are sufficient details of methods and analysis provided to allow replication by others?

Partly

If applicable, is the statistical analysis and its interpretation appropriate?

Not applicable

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Yes

Competing Interests: No competing interests were disclosed.

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Referee Report 12 December 2017

doi:[10.5256/f1000research.14230.r27894](https://doi.org/10.5256/f1000research.14230.r27894)



Peter W. Glynn

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The alpheid shrimp guard, *Alpheus lottini*, also should be noted as defending pocilloporid corals from COTS attacks. This shrimp guard occurs world-wide on pocilloporid corals.

It would also be worth noting the defensive behaviour, if any, of the crustacean guards toward the fish corallivores.

'White feeding scars' are referred to in Fig. 1 and Fig. 2 (supplementary image). These are difficult to make out in the photographs. I suggest adding arrows to make these easier to see. Also, it would be useful to know the approximate diameters of the *P. eydouxi* colonies.

Is the work clearly and accurately presented and does it cite the current literature?

Yes

Is the study design appropriate and is the work technically sound?

Yes

Are sufficient details of methods and analysis provided to allow replication by others?

Yes

If applicable, is the statistical analysis and its interpretation appropriate?

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