



RESEARCH NOTE

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

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v2 First published: 13 Nov 2017, 6:1991 (doi: [10.12688/f1000research.13118.1](https://doi.org/10.12688/f1000research.13118.1))
 Latest published: 02 Mar 2018, 6:1991 (doi: [10.12688/f1000research.13118.2](https://doi.org/10.12688/f1000research.13118.2))

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.

Open Peer Review

Referee Status:

Invited Referees

1 2

REVISED

version 2

published
02 Mar 2018

version 1

published
13 Nov 2017



report



report

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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

Competing interests: No competing interests were disclosed.

How to cite this article: Kayal M, Ballard J and Adjeroud M. **Multi-species consumer jams and the fall of guarded corals to crown-of-thorns seastar outbreaks [version 2; referees: 2 approved]** *F1000Research* 2018, **6**:1991 (doi: [10.12688/f1000research.13118.2](https://doi.org/10.12688/f1000research.13118.2))

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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.*

First published: 13 Nov 2017, **6**:1991 (doi: [10.12688/f1000research.13118.1](https://doi.org/10.12688/f1000research.13118.1))

REVISED Amendments from Version 1

We have updated our manuscript following judicious comments provided by the referees. The new version notably includes further information, as well as an extended discussion, on the reported ecological process and its prevalence in our study system. The new version also provides more details on coral mutualist crustaceans and clearer [Figure 1](#), [Figure 2](#), and [Supplementary Image 1](#). Following comments from the referees, we have added arrows to the figures, in order to clarify which parts we are referring to. We are thankful to the referees for their constructive remarks.

See referee reports

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 and alpheid shrimps 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 (typically above 60 cm diameter) pocilloporid assemblages that benefit from “anti-COTS” mutualistic defense, the so-called guarded corals. In Moorea, these assemblages are dominated by *Pocillopora eydouxi*, a species that hosts trapeziid crabs and alpheid shrimps able to deter COTS predation ([Glynn, 2013](#); [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](#)).

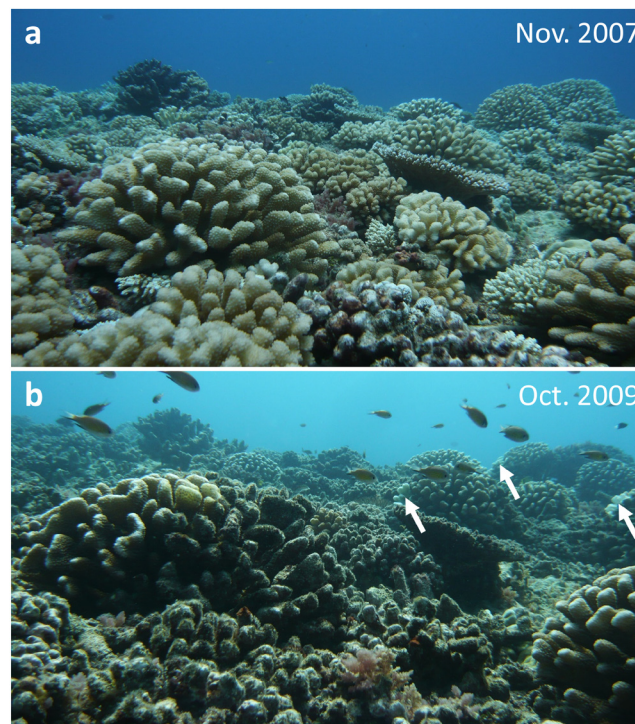


Figure 1. Widespread coral decline and survival of guarded corals that partially or fully resisted seastar predation. Pictures were taken at 6 m depth on Tiahura reef in Moorea, French Polynesia, before (a) and after (b) this location was invaded by crown-of-thorns seastar (COTS) swarms. Surviving guarded corals typically measured above 60 cm in diameter. Arrows in b indicate white feeding scars characteristic of recent COTS predation on several of the guarded coral colonies (*Pocillopora eydouxi*).



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 guarded coral measured approximately 70 cm in diameter. 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*. Arrows indicate white feeding scars characteristic of recent COTS predation on the guarded coral (*Pocillopora eydouxi*).

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. While butterflyfishes were increasingly observed to gather around guarded corals as the COTS outbreak progressed around the island, the aggregation of 9 butterflyfishes within a single square-meter (9 fish.m²), as captured in Figure 2, was particularly surprising. Density of the coral-feeding butterflyfish assemblage on this reef location had dropped to the much lower average value of 4.3 ± 0.9 SE fish.200m² following the COTS outbreak (surveyed in June 2008, equivalent to 0.02 fish.m²). 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 trapezoid 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. The relative contribution of the

butterflyfishes, as compared to COTS, to the death of guarded corals at this stage remains unclear. Further research is needed to quantitatively evaluate the aptitude of coral mutualists to withstand attacks from mono- versus multi-specific predators at different abundances. This particularly applies when the predator guilds involve specialized coral-feeding species from distant phyla with different feeding modes, such as fishes that sample polyps through repeated rapid bites and seastars that consume large portions of coral tissue over extended amount of time. 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.

Data availability

All data underlying the results are available as part of the article and no additional source data are required.

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). Arrows indicate white feeding scars characteristic of recent COTS predation on the guarded coral (*Pocillopora eydouxi*).

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

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Current Referee Status:  

Version 1

Referee Report 07 February 2018

doi:10.5256/f1000research.14230.r30512



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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 eydouxii* to *Pocillopora eydouxii*.

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

Are all the source data underlying the results available to ensure full reproducibility?

Yes

Are the conclusions drawn adequately supported by the results?

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?

No

Are all the source data underlying the results available to ensure full reproducibility?

Yes

Are the conclusions drawn adequately supported by the results?

Yes

Competing Interests: No competing interests were disclosed.

Referee Expertise: Reef coral biology and ecology.

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