

Mass mortality of the vermetid gastropod *Ceraesignum maximum*

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Abstract *Ceraesignum maximum* (G.B. Sowerby I, 1825), formerly *Dendropoma maximum*, was subject to a sudden, massive die-off in the Society Islands, French Polynesia, in 2015. On Mo'orea, where we have detailed documentation of the die-off, these gastropods were previously found in densities up to 165 m⁻². In July 2015, we surveyed shallow back reefs of Mo'orea before, during and after the die-off, documenting their swift decline. All censused populations incurred 100% mortality. Additional surveys and observations from Mo'orea, Tahiti, Bora Bora, and Huahine (but not Taha'a) suggested a similar, and approximately simultaneous, die-off. The cause(s) of this cataclysmic mass mortality are currently unknown. Given the previously documented negative effects of *C. maximum* on corals, we expect the die-off will have cascading effects on the reef community.

Keywords Die-off · *Dendropoma maximum* · Mo'orea · Society Islands

Introduction

Dramatic mass mortality events of marine species, especially invertebrates, are occurring at an increasing rate (Fey et al. 2015). Well-documented examples of precipitous declines include corals (*Acropora palmata*) and sea urchins (*Diadema antillarum*) in the Caribbean (Lessios et al. 1984; Muller et al. 2007), and abalone (*Haliotis cracherodii*) and seastars (*Pisaster ochraceus*) in the eastern Pacific (Hewson et al. 2014). These die-offs often occur rapidly and over large spatial scales, notably in organisms that previously achieved high local densities. For example, *D. antillarum* was once an abundant member of coral reef communities throughout most of the Caribbean. However, in a single year a putative pathogen swept through the Caribbean killing most of the *Diadema* (Lessios et al. 1984). On some islands (Jamaica), it spread at a rate of approximately 29 km week⁻¹ (Hughes et al. 1985).

The sessile vermetid gastropod, *Ceraesignum maximum* (G.B. Sowerby I, 1825), is a member of shallow coral reef communities in the Pacific Ocean and Red Sea. These snails cast mucus nets that cover benthic surfaces. After ~30 min, snails retract their nets, consuming the net and its contents (Kappner et al. 2000). Vermetids, likely through effects of their mucus nets, reduce coral growth and survival (Shima et al. 2010, 2013), alter coral morphology (Colgan 1985; Zvuloni et al. 2008; Shima et al. 2010, 2015), and deter herbivorous fish grazing (Tootell and Steele 2014). Given their ecological importance, it is particularly important to document and understand dramatic shifts in the spatiotemporal distributions of *C. maximum*.

Here we report a recent, massive die-off of *C. maximum* in the Society Islands, French Polynesia. Fortunately, we were conducting fieldwork (in Mo'orea) at the time of this

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event and were able to document its occurrence. Below we provide data collected before, during, and after the die-off to help quantify the duration and extent of the event.

Methods

The Society Islands are an archipelago in the South Pacific and are comprised of both windward islands (including Mo'orea and Tahiti) and leeward islands (e.g., Bora Bora, Huahine and Taha'a; Fig. 1a). Mo'orea and Tahiti are within 20 km of each other. Huahine is ~135 km NW of Mo'orea. 40 km to the west of Huahine is Taha'a, which shares its lagoon with its neighboring island, Raiatea. Approximately 20 km NW of Taha'a is Bora Bora. All of these islands harbor populations of the vermetid snail *C. maximum* (hereafter synonymous with snails) in shallow back reefs.

Beginning in mid-July 2015, we observed that *C. maximum* on Mo'orea had stopped deploying nets. To assess whether snails were under energetic stress, we collected 37 snails to compare their masses with snails previously collected in 2008 ($n = 110$ snails; Phillips and Shima 2010). We collected *C. maximum* from the north shore of Mo'orea using similar methods as in 2008. For each snail, we measured shell aperture diameter to the nearest 0.1 mm, and removed the animal (whole) from its shell, blotted it dry, and measured its wet mass. We compared the log (wet mass) of snails from the two years, with log (aperture diameter) as a covariate, using ANCOVA.

Following the 2015 snail collection, we suspected that a major die-off had commenced, so we began to assemble three datasets: (1) a time series of *C. maximum* counts on

marked patch reefs at one back reef site on the north shore of Mo'orea ($17^{\circ}28.723'S$, $149^{\circ}50.436'W$, Fig. 2b), (2) one-time surveys of *C. maximum* at sites on Mo'orea and Tahiti (Fig. 2b), and (3) analysis of photographs that were taken by colleagues in the shallow reefs surrounding Mo'orea, Bora Bora, Taha'a, and Huahine.

Time series

As part of another study, we had previously counted *C. maximum* on 11 marked patch reefs on 2 July 2015. These patch reefs were 65.8 ± 4.7 cm in height, 77.9 ± 4.6 cm in diameter (mean \pm SE), and originally occupied by, on average, 34 living *C. maximum*. We did not observe any dead *C. maximum* at this time. Once we suspected a die-off had started, we recounted *C. maximum* three additional times (16 July, 24–25 July and 4 October 2015). On all dates except 2 July, we categorized snails (and shells) based on their physical appearance (Fig. 2c–g).

One-time quadrat surveys

We surveyed seven sites around Mo'orea and two sites on Tahiti from 20 to 27 July 2015. At each site, we haphazardly positioned 0.5-m^2 quadrats around a focal *C. maximum* (living or recently dead), counted all of the living and dead snails, and categorized their state (Fig. 2c–g).

Photographs

To augment our other data, we analyzed photographs taken by colleagues in Taha'a, Bora Bora, Huahine, and from different sites and times in Mo'orea. From each photograph,

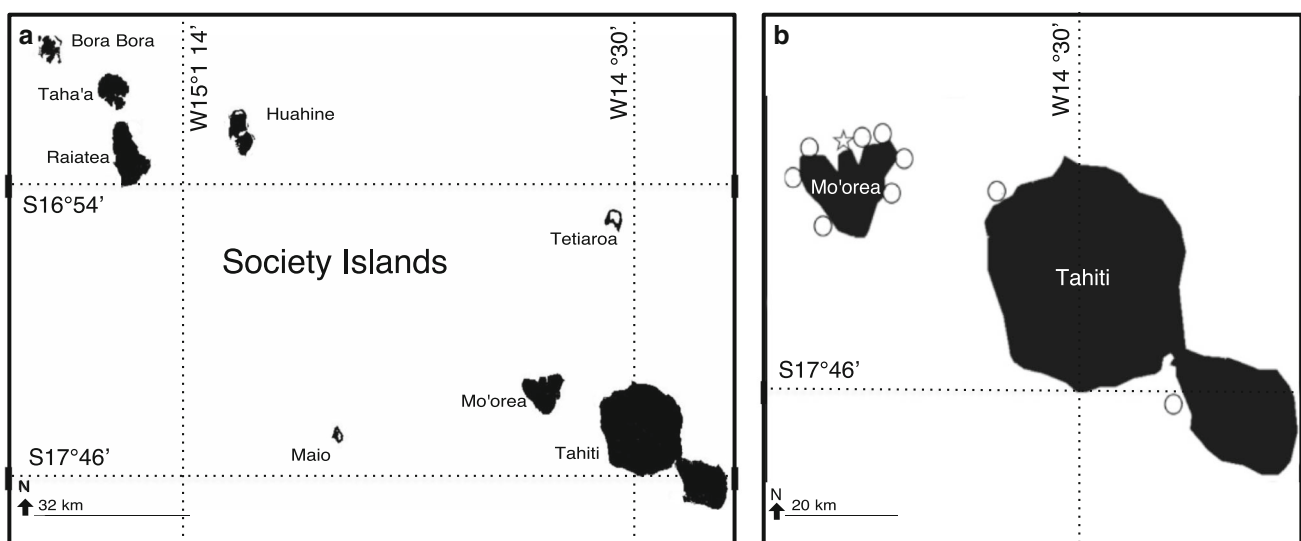


Fig. 1 **a** Map of the Society Islands and **b** enlarged map of Mo'orea and Tahiti; open circles indicate the locations of one-time surveys and the star represents the site where 11 patch reefs were sampled multiple times

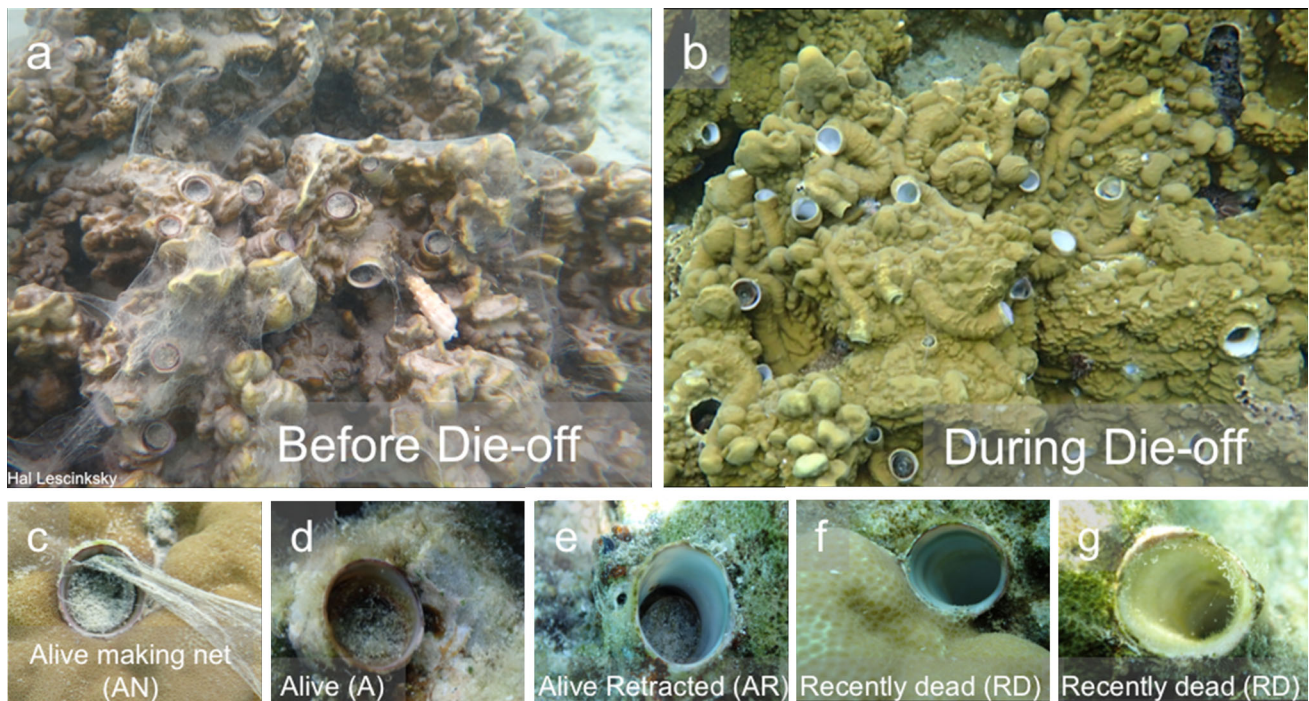


Fig. 2 Photographs of vermetids **a** before the die-off (with nets deployed), and **b** during the die-off (note the absence of nets and retracted snails). The *bottom row* of pictures shows categories of snails that denote the progression of the die-off. **c** Alive and casting nets, AN (“healthy” vermetids); **d** alive, but not casting nets, A

(snails were not healthy); **e** alive but retracted, AR (rapidly declining health); and **f, g** recently dead snails, RD. **f** Tubes in which the snail has recently died are clean and white within the first week of death, but quickly become colonized by algal turf (**g**) within 2 weeks

we determined the status (Fig. 2) of all identifiable *C. maximum*. Photographs were taken between 5 June and 27 August 2015.

To reconstruct the spatiotemporal dynamics of the die-off, we examined (1) the time series of live snails at the 11 marked patch reefs and (2) the frequency of snails in each category (Fig. 2) for each day and island after aggregating observations from all three data sources.

Results and discussion

During the first half of July, we observed that vermetids had stopped casting nets (Fig. 2d). Otherwise, snails appeared “normal” (e.g., the body of the snail was located near the aperture of the shell; cf Fig. 2e), although the snail’s body diameter, in many cases, appeared smaller than the diameter of the shell. The “sicker” the snail, the more retracted into the shell it became (alive retracted, AR, Fig. 2e). Snails that were retracted far back into their shells (>30 mm) were typically emaciated, if not in an advanced state of decay. Although tissues of dead snails were found in tubes (e.g., with detached opercula), more frequently the snail was absent. All that remained was the tube, with a clean white interior or with a light film of algal turf

(recently dead, Fig. 2f, g). Our previous observations showed that tubes of snails that had been dead for longer periods of time were heavily encrusted by crustose coral-line algae.

Snails collected in 2015 had only ~70% the body mass of snails that were collected in 2008 ($F_{1,142} = 12.062$, $p < 0.001$; Fig. 3). A freshwater gastropod, *Biomphalaria glabrata*, was reported to lose up to 12.5% of their body mass before dying (Von Brand et al. 1957). *Ceraesignum maximum* lost a considerably greater percentage of their mass during this mortality event. Whatever the cause of mortality, the mass loss was likely intensified by starvation because *C. maximum* had stopped making and casting mucus nets. Additionally, we did not observe egg capsules in affected snails (unlike in previous years, e.g., Phillips and Shima 2010).

Our time series data from 11 patch reefs in Mo’orea showed that 100% of the snails on these reefs died between 2 July and 24–25 July 2015 (Fig. 4). Forty-eight percent perished by 16 July (within two weeks of appearing healthy), and the remaining individuals died within another 9 d, with no recovery noted by October 2015.

By combining our observations on these 11 patch reefs with the quadrats and photographic samples, we pieced together a more complete picture of the spatial and

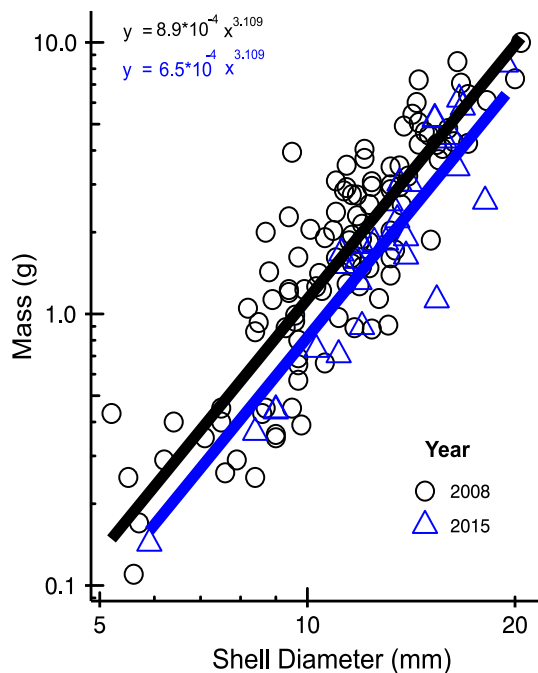


Fig. 3 Relationship between shell aperture diameter and wet mass of snails collected in 2008 (black circles) and 2015 (blue triangles); note that both axes are on log scales. Fitted lines are based on log-transformed data, with the results back-transformed to power functions. Equal slopes (i.e., exponents in the power function) were assumed by ANCOVA and supported by a preliminary test of slope heterogeneity ($F_{1,141} = 2.08$, $p = 0.15$)

temporal progression of the die-off. On Mo'orea, snails appeared healthy until early July. Between 4 and 18 July, snails stopped casting mucus nets. The die-off in Mo'orea appeared to be complete by 22 July (Fig. 5a). Results from the quadrat sampling in the waters around the island of Tahiti showed that the die-off had already occurred by 27 July (Fig. 5b). Photographic evidence from Bora Bora indicated that the die-off occurred between 5 June and 26 August, while the die-off on Huahine likely occurred in mid-August (Fig. 5b). The data from Huahine, however, are limited. Taha'a was the only island with evidence of healthy snails in July and August (Fig. 5c).

We hypothesize that the die-off of *C. maximum* was the result of a pathogen. The widespread nature of the die-off is similar to that experienced by *D. antillarum* in the Caribbean in the 1980s (Lessios et al. 1984). Mortality of *D. antillarum* was attributed to an unidentified, waterborne pathogen. However, if the putative pathogen affecting *C. maximum* was dispersed via currents, it is difficult to explain why those individuals from waters surrounding Taha'a, which lies near affected islands, were spared. The hydrography around the Society Islands is not well described and provides little insight in this regard. It is also possible that a disease could be spread as a consequence of human activity; all of these islands are tourist destinations

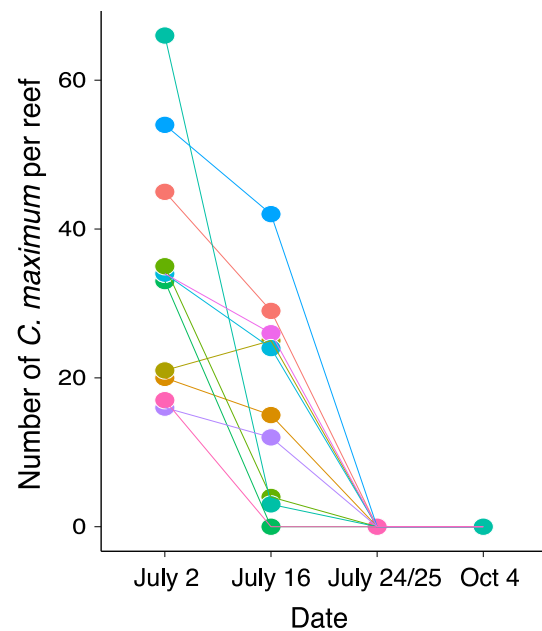


Fig. 4 Number of live vermetids (*C. maximum*) on 11 patch reefs censused just prior to (2 July 2015), during (16 July) and after (24–25 July and 4 October) the die-off in Mo'orea. On 2 July, all snails we observed were alive, but by 24–25 July there were no living *C. maximum*. Each line indicates a different reef. Reefs were 65.8 ± 4.7 cm in height, 77.9 ± 4.6 cm in diameter (mean \pm SE). Note that the y axis is ordinal

with cruise ships and ferries moving between them. We are presently working with invertebrate pathologists to investigate potential pathogens.

Notably, the die-off was highly specific; only *C. maximum* appeared affected. Through October 2015, other benthic invertebrates (e.g., corals, clams, and other vermetids) were alive and behaving normally. Indeed, other vermetid species (*Dendropoma platypus*, *Petalochonchus keenae*, and *Serpulorbis variabilis*) were casting nets during and after the die-off. The highly specific nature of this event suggests that an environmental anomaly was unlikely the underlying cause. Environmental anomalies (e.g., increased temperature) can lead to widespread effects, but other organisms that are sensitive to environmental fluctuations, e.g., corals, would also be expected to be affected. The *C. maximum* die-off occurred in the austral winter (average temperature ~ 26 °C; Washburn 2015), and thus temperatures were likely not as high as those reached during the austral summer (average temperature ~ 28 °C; Washburn 2015). Coral bleaching events have repeatedly occurred in French Polynesia and have sometimes lasted until late July (Penin et al. 2007). However, we did not observe a concurrent bleaching event in Mo'orea in 2015. Although it is unlikely that an abrupt change in the physical environment was the primary driver of *C. maximum* mortality, disease-mediated mortality can be exacerbated by

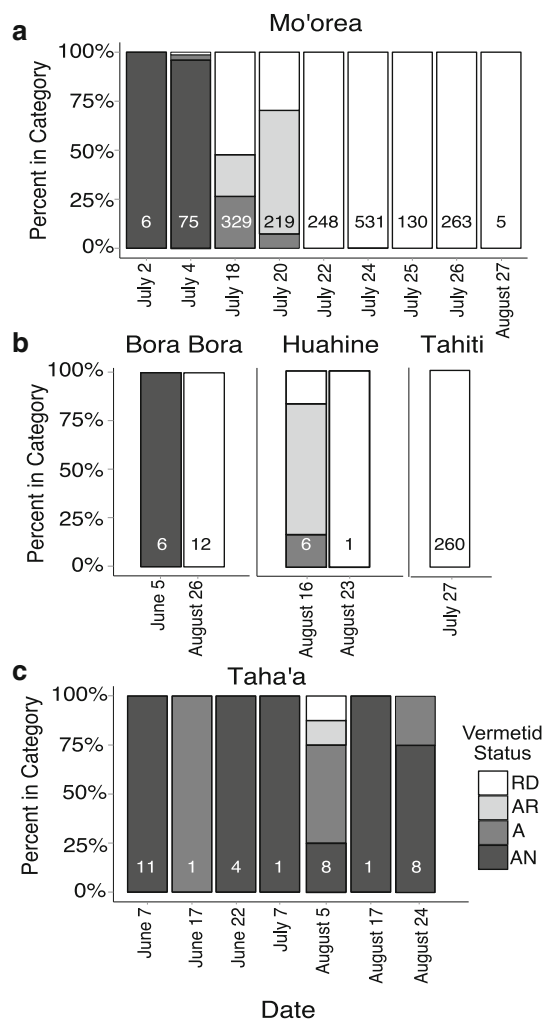


Fig. 5 Relative abundance of snails that were alive with a net (AN, dark gray), alive without a net (A, mid-gray), alive but retracted (AR, light gray) or recently dead (RD, white; see Fig. 2) in **a** Mo'orea, **b** Bora Bora, Huahine, and Tahiti, **c** Taha'a. The numbers inside the bars are the total number of vermetids recorded that day. Bora Bora, Huahine, and Taha'a data are from photographs provided by colleagues, as are the data from Mo'orea on 2 and 4 July and 27 August

environmental triggers (Harvell et al. 2002). The role of the physical environment and pathogens therefore remains unknown.

Precipitous declines in *C. maximum* may have occurred previously. Discussion with local Polynesians (who consume *C. maximum*: Shima et al. 2010) indicated that the population of *C. maximum* declined in the early 1980s. The cause of that decline is unknown and was undocumented. The two declines may indicate that populations of *C. maximum* exhibit boom and bust cycles, potentially triggered by disease and/or environmental phenomena.

In summary, we documented rapid, mass mortality of *C. maximum* around the islands of Mo'orea, Tahiti, Huahine,

and Bora Bora. Taha'a was the only island investigated where we observed living snails. On Mo'orea, the loss occurred swiftly, resulting in the death of millions of snails. Snail mortality is generally low (~10% annually; Shima et al. 2016), which further highlights this cataclysmic decline in which 100% mortality occurred in less than one month. To date, we do not know the cause(s) of this mass mortality event, but we are investigating environmental anomalies and signatures of disease. As snails are known to have negative effects on corals (Shima et al. 2010), this radical change in *C. maximum* abundance may alleviate one of the stressors on reefs and aid in reef recovery.

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