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Managing an invasive corallimorph at Palmyra Atoll National Wildlife Refuge, Line Islands, Central Pacific

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Abstract In 2007, a phase shift from corals to corallimorpharians (CM) centered around a shipwreck was documented at Palmyra Atoll, Line Islands. Subsequent surveys revealed CM to be overgrowing the reef benthos, including corals and coralline algae, potentially placing coral ecosystems in the atoll at risk. This prompted the U.S. Fish and Wildlife Service, the lead management agency of the atoll, to remove the shipwreck. Subsequent surveys showed reductions in CM around the ship impact site. We explain patterns of spread of the CM in terms of both life history and local currents and show with a pilot study that

pulverized bleach may be an effective tool to eradicate CM on a local scale. If applied strategically, particularly in heavily infested (> 66% cover) areas, active intervention such as this could be an effective management tool to reduce CM impact on localized areas and decrease colonization rate of remaining reefs. This is the first documentation of the response of an invasive cnidarian to shipwreck removal. While this was a singular event in Palmyra, the spatial and temporal patterns of this invasion and the eradications lessons described herein, are useful for anticipating and controlling similar situations elsewhere.

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Introduction

Coral reefs are subject to damage from both natural and anthropogenic causes, including large scale storm events, temperature anomalies and subsequent bleaching events, disease outbreaks on foundational species, overfishing, and ship groundings. The resultant disruption from these events can facilitate colonization or expansion by invasive organisms that can result in phase shifts (Chadwick and Morrow 2011; Hughes et al. 2010). Phase shifts are defined here as “extensive decreases in coral cover coinciding with substantial

increases in some alternative benthic organism, due to a pulse or press disturbance, that have persisted > 5 year” (Norström et al. 2009). For example, mass mortality of the sea urchin, *Diadema antillarum*, throughout the Caribbean from an apparent disease outbreak contributed to a phase-shift from coral- to algal-dominated communities (Lessios 2016). In the Indo-Pacific, similar phase-shifts have occurred in response to shipwrecks where coral dominated communities change to those dominated by opportunist benthic organisms. On Rose Atoll in American Samoa where a fishing vessel wrecked on the reef, the percent cover of turf/cyanobacteria was an order of magnitude higher (40%) in areas surrounding the wreck as compared with reference sites on the same island (Schroeder et al. 2008). In the Line Islands, iron enrichment from shipwrecks fueled growth of invasive cyanobacteria and turf algae (Kelly et al. 2012). Once established, invasive organisms are difficult to control, with failures mostly due to late detection resulting in sufficient time elapsing for invasives to occupy areas too large for eradication to be practical (Hewitt and Campbell 2007). However, in the rare attempts that have been made to manage marine invasives, successes do exist; for instance the complete elimination of the invasive algae, *Caulerpa racemosa* near San Diego, California. This effort was successful because the algae were detected early, were within a well-defined area, and were eradicated before they spread over a large scale (Anderson 2005).

In 2007, a corallimorpharian (CM), *Rhodactis howesii*, was discovered smothering coral reefs at Palmyra Atoll National Wildlife Refuge (Palmyra), a remote atoll within the Line Islands ca. 5° north of the Equator (Work et al. 2008). The CM invasion encompassed a well-defined 1 km² area with a predominant NW to SE orientation surrounding a longline vessel that had wrecked on the atoll in 1991. The distribution of the CM around the shipwreck and around mooring buoys fastened by iron chains suggested that substances leaching from metals, possibly iron, might in part be driving the spread of the infestation on the reef (Work et al. 2008). In response, the US Fish and Wildlife Service (FWS) in collaboration with The Nature Conservancy switched out existing iron mooring chains with stainless steel in 2010. Another conjecture to explain the spread is that CM are an opportunistic, weedy species, competitively superior to other cnidarians such as corals, and

capable of year-round reproduction via sexual (pelagic spawning) or asexual clonal replication (Chadwick-Furman and Spiegel 2000; Chen et al. 1995). Some species of CM can rapidly replicate with a polyp doubling time in as little as 2 months (Chadwick and Adams 1991). *R. howesii* is considered native to Palmyra based on observations of its presence around the atoll prior to the outbreak (Work et al. 2008). Perhaps life history characteristics of the CM population around the shipwreck contributed to the observed rapid spread on the atoll. The increased presence of CM around the ship would be analogous to an outbreaks of other native species such as the crown of thorns seastars on coral reefs (Pratchett et al. 2014).

In 2013, the FWS secured funding to disassemble and remove the shipwreck at Palmyra Atoll NWR with all the metal shipped back to the mainland U.S. for scrap. Our objectives were to (1) document the distribution of CM at Palmyra before and after shipwreck removal, (2) examine the life history of CM and the oceanographic conditions that could help explain the observed patterns of spread, and (3) test methods for control CM.

Methods

Surveys

In 2011 and 2016, surveys of CM infestation were conducted following protocols described previously (Work et al. 2008). Briefly, a snorkeler was towed at an approximate speed of ca. 50 m/min over benthic transects that originated from the shipwreck site towards the 8 major points of the compass (N, NE, E, SE, S, SW, W, NW). Every minute (ca. 50 m), the towboat stopped, and the snorkeler subjectively integrated benthic cover during the tow scoring the level of CM infestation based on percent cover using the following 0–3 scale: 0 = no CM; 1 = ca. 1–33%; 2 = 34–66%; and 3 = > 67% CM cover. Visual area covered by each 1 min tow was ca 500 m². Tows continued until at least three consecutive stops scored at 0 were obtained or until it became too deep (20–25 m) to see the benthos from the surface or too shallow (< 1 m) for effective vessel operation. To quantify the directional spread of CM, we tested whether the pattern of CM invasion deviated significantly from a uniform circle surrounding the ship by

plotting and testing for circular uniformity and reflective symmetry (Rao Jammalamadaka and Sen Gupta 2001). Areal coverage of CM was calculated by plotting the infestation and measuring the area of splined polygons surrounding the limits of mild (Score 1), moderate (Score 2), or severe (Score 3) infestation.

The original spread of the CM around the wreck was on the western reef shelf of Palmyra Atoll. However, evidence of CM on reef slopes to the north and south of the atoll prompted us to record depth distribution of CM on the forereef at five sites surrounding the atoll (Fig. 1a). These sites were chosen because they are historically established benthic survey stations for researchers at Palmyra Atoll. At each site, transect lines were initiated at a depth of 27.4 m and deployed perpendicular to shore up the reef slope and onto the reef flat to a depth of ca. 0.1 m. This configuration required four 30 m transects to be laid end-to-end and separated by 1 m. Depth was

recorded every 10 m moving along each transect line, and the average depth recorded per transect line. This strategy gave four depth categories from deep to shallow (e.g. tape 1 deployed at 27.4 m = deep reef and tape 4 deployed onto the reef flat = shallow). The presence/absence of CM was recorded every m (point intercept) along each 30 transect giving a total of 124 points at each site. CM cover for each depth category (n = 4) was pooled for the 5 sites. Average percent CM cover for the four depth categories was compared using Kruskal–Wallis analysis of variance, because data did not fit assumptions of normality by the Shapiro–Wilks test ($W = 0.68365, p = 2.48e-05$).

Oceanography

Once established, it was expected that CM spread from the shipwreck site would occur via the dispersal of larvae and clonal fragments directed by ocean

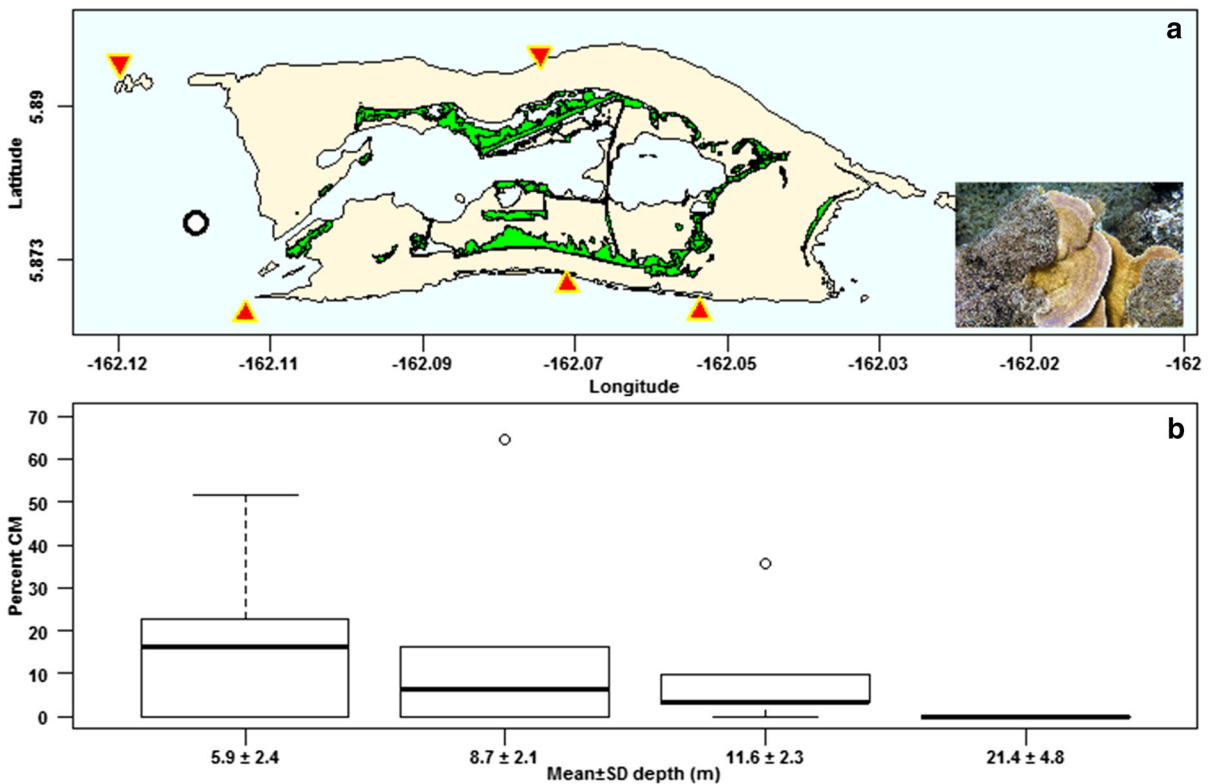


Fig. 1 a Map of Palmyra showing the shipwreck site (circle) and locations of depth transects (red triangles). Also shown are shallow reef flats (beige) and emergent land (green). Inset photo shows *Montipora patula* overgrown by corallimorpharians (CM). b Box plots displaying percent cover of CM in 5 transects

at 4 depth intervals: median percent corallimorph cover (line), first and third quartile (boxes), whiskers (1.5 times the interquartile range from the top (bottom) of the box), and outliers (dots). Depths are mean \pm SD of 20 points (4 points per transect in 5 transects total)

currents, followed by competitive monopolization of the benthos by the dispersed propagules (Chadwick-Furman and Spiegel 2000; Chen et al. 1995). To examine the relationship between sea surface height or currents and CM distribution, we used satellite data collected between 1993 and 2015. For sea surface height, we downloaded AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data) weekly surface height data from NOAA ocean watch (<http://oceanwatch.pifsc.noaa.gov/>). For geostrophic ocean currents, we used OSCAR (Observing Systems Capability Analysis and Review) $1/3^\circ$ weekly data from NASA Jet Propulsion Lab (https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg). We obtained sea surface height and calculated current speed and direction from zonal and meridional vectors in an area immediately around Palmyra encompassing -162.3 W, 5.6 N to -162 W to 6 N. Sea surface height, current speed, and direction were averaged for 1993–2015. All analyses were done using R packages *ncdf4*, *circular*, *rgdal*, *geosphere*, and *GISTools* (R Development Core Team 2011) and data were interpreted in light of existing literature on finer spatiotemporal current patterns around Palmyra to see how they might inform future management of the infestation.

Test method of CM control

Because chlorine was successfully used to eradicate invasive *Caulerpa* on a local scale in California (Anderson 2005), we chose this chemical to evaluate its suitability for CM control. We did this using 3×3 m tarps and sandbags to contain solid-phase chlorine pool sanitizer pucks (Trichlor or trichloroisocyanuric acid). The concept was to place intact or pulverized chlorine pucks directly on CM, cover them with tarps sealed by sandbags at the edges, and leave the tarps overnight. This would allow dissolution of chlorine leading to sufficiently elevated chlorine levels to kill all CM underneath the tarps. In May and June 2011, empirical trials were first done to assess the amount of chlorine necessary to kill 100% of CM in controlled settings at Palmyra. Ten to twenty *R. howesii* collected from reef flats were placed in four 5 L buckets of aerated seawater, varying amounts of crushed chlorine tablets added, and mortality assessed the next morning along with total dissolved chlorine (mg/L) using a commercially available colorimetric

chlorine analysis kit (Hach, Loveland, CO). These trials showed that a minimum of 0.4 g/L of crushed chlorine was needed to kill 100% CM overnight with total concentration of chlorine in seawater ranging from 3 to 11 mg/L the morning following application.

We then did field eradication trials in the vicinity of the shipwreck in areas where CM infestation was essentially 100% to minimize adverse effects on other reef organism. Intact or pulverized chlorine tablets were placed in sealed plastic containers and wrapped in a folded tarp that was secured with bungee cords to form a tarp package. Lead weights were fastened to the package and the whole thing deployed to the bottom (ca. 8–9 m deep) along with sandbags. A diver salted out chlorine onto CM on site underwater whilst two divers followed and unrolled the tarp over the chlorine. The edges of the tarp were then sealed with sandbags (Fig. 2a). Tarps were left overnight (minimum of 12 h) and removed the following morning. Four 3×3 m plots, each separated from each other by ca. 3 m, were assayed. In one, intact chlorine pucks were placed under the tarp. For three other trials, chlorine pucks were pulverized with a hammer prior to use. To assess efficacy of eradication, five random 1 m^2 quadrats were photographed within each of four 3×3 m treatment plots at day 1 and 7 post-treatment and approximately 15 months later. Based on a rarefaction curve, 70 random points were generated for each photo using ImageJ and percent substrate quantified as bare, crustose coralline algae (CCA), macroalgae, and CM. We focused on macroalgae and CCA because of their negative (Done 1992) and positive (Harrington et al. 2004; Price 2010) effects on coral recruitment, respectively. The presence of newly recruited benthic organisms such as corals was also recorded.

Results

Surveys

In 2007, the infestation covered ca. 1 km^2 (Work et al. 2008). In 2011, the infestation covered a 3.3 km^2 area adopting a pronounced NW to SE orientation with the region of heavy infestation ($> 66\%$) expanding to ca. 0.7 km^2 or 21% of the total CM area (Figs. 3, 4). After removal of the ship in 2013, the 2016 survey showed that the CM infestation appeared to split into separate

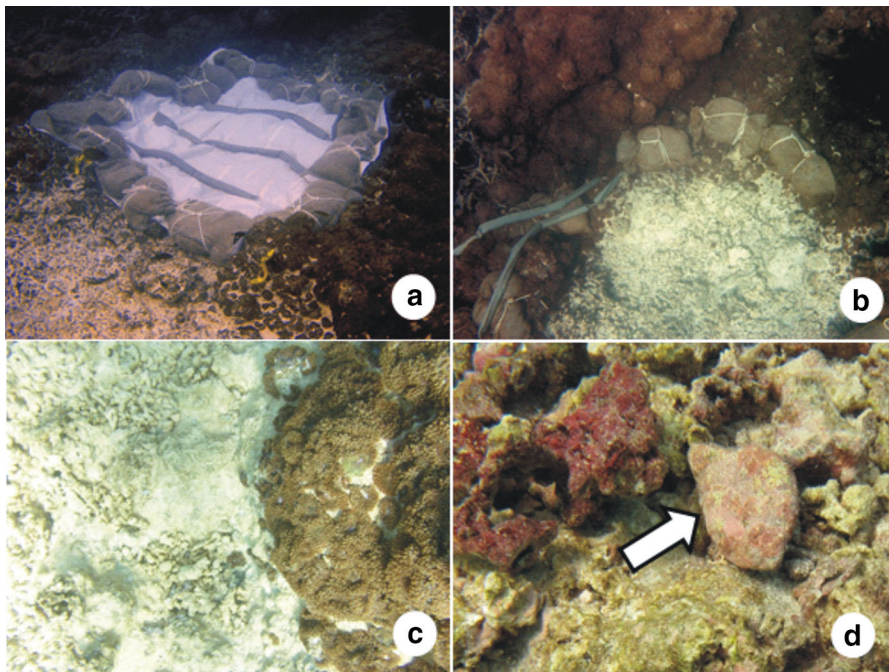
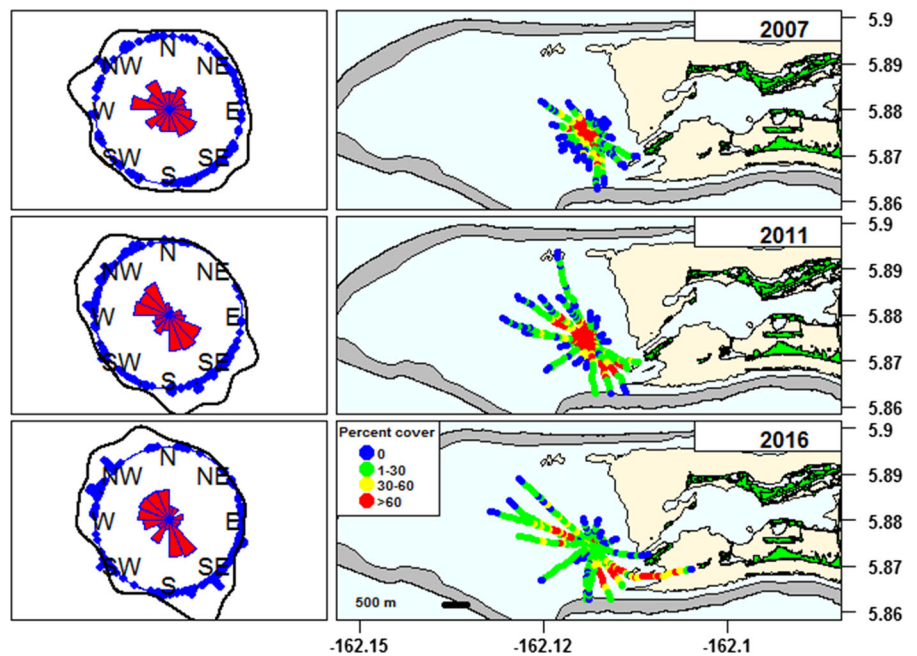


Fig. 2 **a** Sand bag and tarp deployment to kill CM, 2011; note bare substrate lower left of plot that was treated the previous day. **b** Plot after removal of tarp. **c** Close up of **b** taken at the

same time. **d** Close up of **c** 15 mo. after treatment showing substrate covered with live CCA (arrow) and other biota such as the brown encrusting sponges to the left and above the arrow

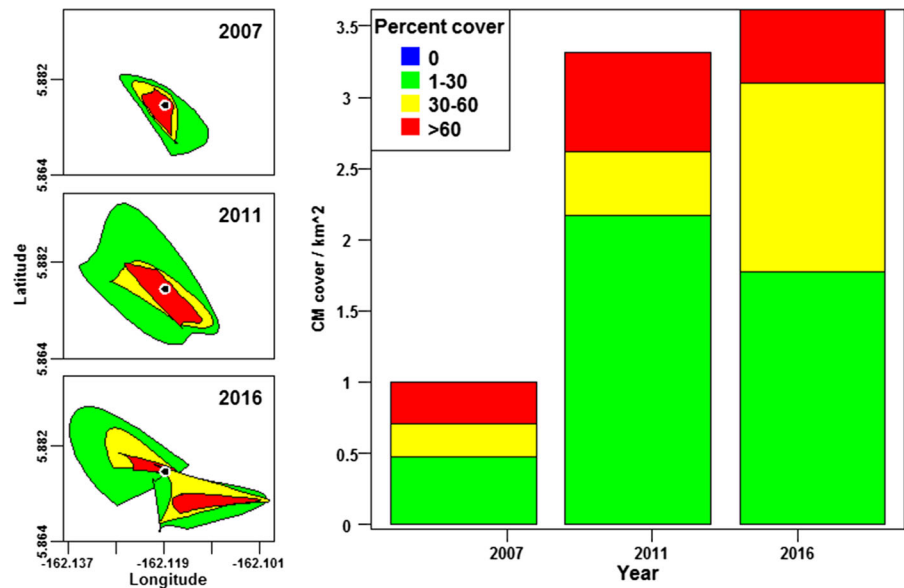
Fig. 3 Extent of corallimorph (CM) invasion from 2007 (top) to 2016 (bottom). Left panels are (from center), rose petal plots (red), circular histograms (blue) and kernel density (black line) of CM infestation, Right panels are survey transects with points graded as percent cover of CM with longitude (x-axis) and latitude (y-axis). The shipwreck was removed in 2013. Beige and green in maps are reef flat and emergent land, respectively whilst grey is reef crest



NW and SE components centered on the former shipwreck site covering a total of 3.6 km² with the region of heavy infestation occupying ca. 0.5 km² or

14% of the total infestation (Figs. 3, 4). The distribution of the CM deviated significantly from circular uniformity (Rao's test statistic = 185; *P* value < 0.001) and

Fig. 4 Left panels are splined convex hull polygons for areas lightly (green), moderately (yellow), and severely (red) infested with CM for 2007–2016. Bar plot is relative amounts of surface area occupied by each CM infestation level by year. Dot indicates location of shipwreck that was removed in 2013



manifested significant NW to SE reflective symmetry (mean angle in radians: 3.12; 95% CI 1.77, 4.47) (Fig. 3). Compared to 2007 and 2011 (Figs. 4, 5a), there was a notable reduction in CM at the shipwreck

site in 2016 (Figs. 4, 5b). However, by 2016 the SE portion of the CM infestation wrapped around the SW side of Palmyra. Reefs that previously had been largely devoid of CM in 2007 and 2011 (Fig. 5c) had become

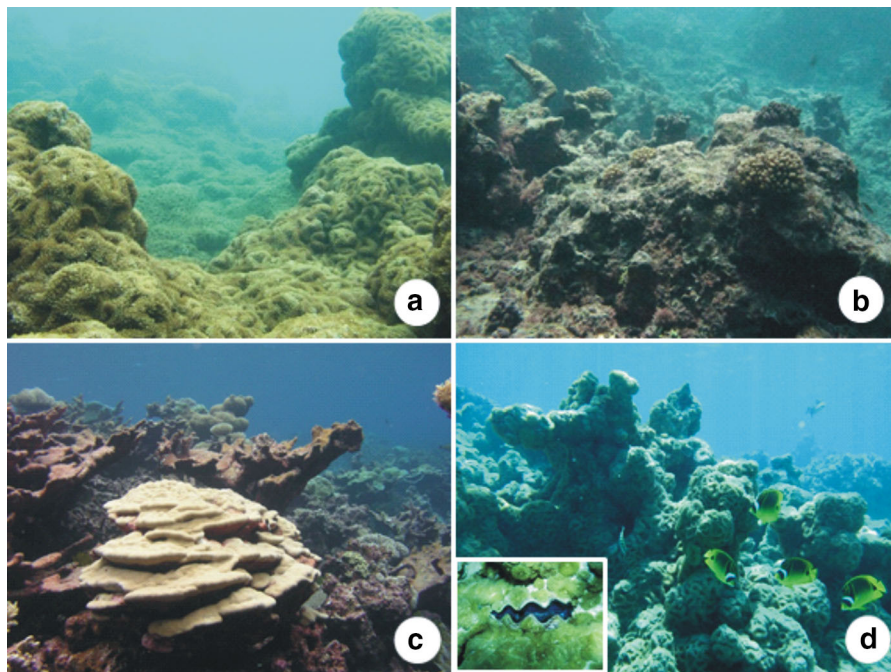


Fig. 5 Time series of benthos. Shipwreck site (a, b) and SE region (c, d). Note almost complete coverage of benthos by CM in 2007 (a) and benthos mostly bereft of CM in 2016 (b). On SW side of atoll, benthos was dominated by corals in 2011 (c), but by

2016 (d) there was complete smothering of corals (d) and Tridacnid clams (inset) by CM. Note similar phenomenon was observed with invasive CM in the red sea (Chadwick-Furman and Spiegel 2000)

completely smothered by CM in 2016 (Fig. 5d). At the five survey sites (Fig. 1a), CM were most abundant at mean depth of 5 m and declined to absence at 21 m (Fig. 1b). No significant difference was found in percent of CM cover at the four depth categories (Kruskal–Wallis Chi-squared = 5.5, df = 3, p = 0.14).

Oceanography

Geostrophic currents at Palmyra have a predominantly E to NE direction with a mean current speed of ca. 0.3 m/s and a range from ca. 0 to 1 m/s (Fig. 6). Current speed (Fig. 7a) and sea surface height (Fig. 7b) were highest in September and lowest in May.

Test method of CM control

Application of chlorine in situ resulted in an overnight reduction in CM cover from 100 to 25% (Fig. 2b, c) killing most of the biota under the tarp including invertebrates (worms, crabs, molluscs) that were in cracks and interstices of the substrate but not visible due 100% CM cover. CM cover continued to decline for several days following treatment to < 10% as dead tissue was removed from the reef by wave action. After 15 months post treatment, CM had recovered from 100% bleached and dead to an average of 43.3%, and CCA (Fig. 2d) cover had recovered from 100% bleached and dead to an average of 19.7% (Table 1). Placement of intact chlorine tablets under the first tarp failed to kill more than 20% of CM (trial 1); however,

kill rate was far more effective (87–97%) using crushed chlorine in the three subsequent tarp trials (Fig. 2b, c). Based on the four trials, we empirically determined that a minimum of ca. 3 kg of crushed chlorine/m² was needed to effect > 90% kill of CM over a 3 × 3 m area. Chlorine concentration from water collected under the tarps just prior to removal the morning after application ranged from 0.1 to 0.5 mg/L.

Discussion

Our initial survey in 2007 found 1 km² area surrounding the shipwreck infested with invasive CM (Work et al. 2008). By 2011, CM occupied a 3 km² area giving a spread rate of approximately 0.5 km²/year. This rate of spread may be due to the highly prolific replication of CM, which reproduce frequently using at least three modes that include sexual production of planktonic larvae, and clonal production via fission and budding (Chadwick-Furman and Spiegel 2000; Chen et al. 1995). In the red sea, an average of 9% of polyps in aggregations of *Rhodactis rhodostoma*, were observed to be actively replicating at any point in time (Chadwick-Furman and Spiegel 2000). Using a 2-month doubling rate for individual polyps, it was estimated that an aggregation could become 2.8× larger in a year (Chadwick-Furman and Spiegel 2000). Our removal plots that increased in CM cover from 25 to 43% over a year suggests the doubling rate on Palmyra is slower than the hypothetical extreme. Our prior work (Work et al. 2008) estimated the number of

Fig. 6 Frequency distribution of mean weekly current speed (m/s) and directions for 1/3° intervals in the vicinity (– 162.3 W, 5.6 N to – 162 W to 6 N) of Palmyra 1993–2015

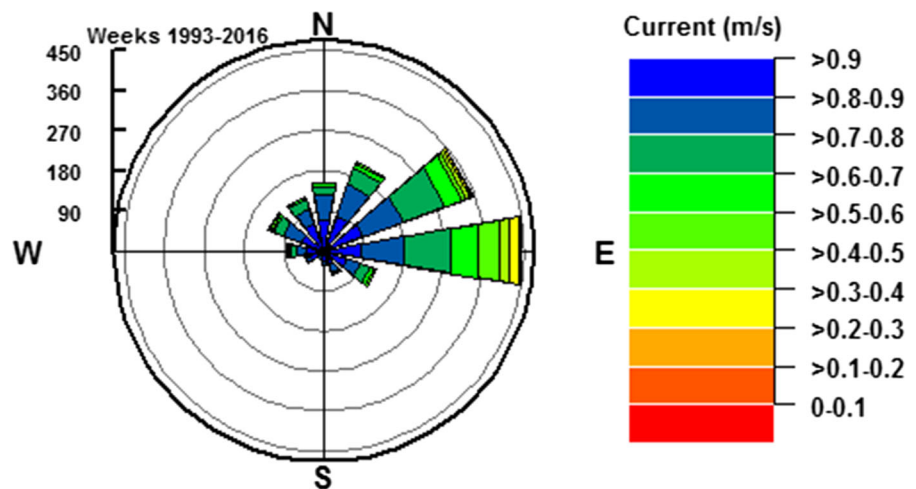


Fig. 7 **a** Mean (line) \pm SD (shaded) monthly current speed (m/s) and **b** sea surface height (cm) in the vicinity (-162.3 W, 5.6 N to -162 W to 6 N) of Palmyra 1993–2015

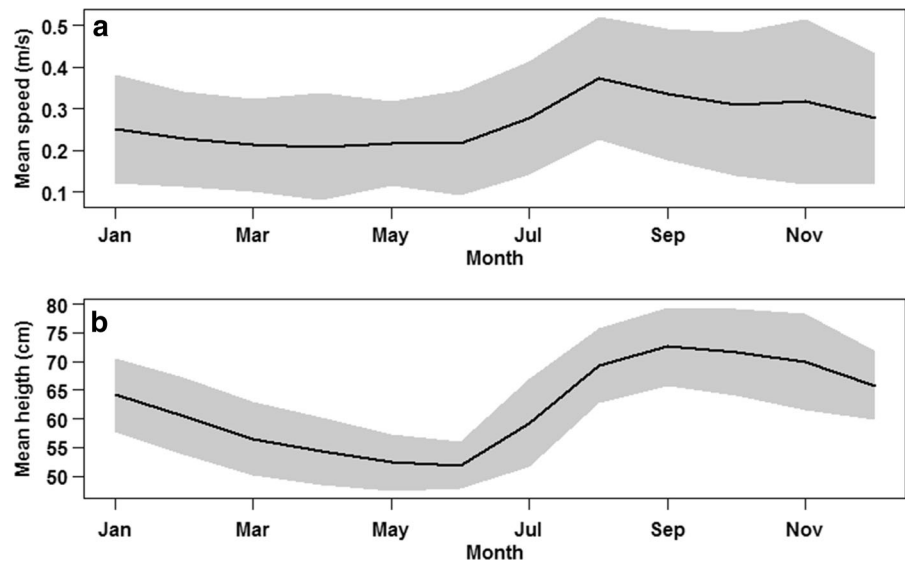


Table 1 Mean (\pm SD) percent of bare substrate occupied by crustose coralline algae (CCA), corallimorphs (CM), and macroalgae (MA), over time measured in four 9 m² plots treated with chlorine

Time	CCA	CM	MA
Day 0	0 (0)	100 (0)	0 (0)
Day 1	3 (5)	25 (2)	2 (2)
Day 7	2 (3)	14 (15)	2 (2)
1 year	20 (21)	43 (37)	8 (9)

CM surrounding the shipwreck at Palmyra to be between 52 and 141 million animals demonstrating considerable clonal and reproductive potential. If the clonal rate of *R. howesii* is similar to other CM, then it is not surprising to find that 4 years later, the aggregations had spread out over an additional 2 km² of reef.

Corallimorphs continue to spread at Palmyra with a 3.5 km² area found infested with CM in 2016 but at a slower rate (~ 0.06 km²/year). The proportion of highly infested areas ($> 67\%$ coverage) steadily decreased from $\sim 30\%$ in 2007 (Work et al. 2008) to 21% in 2011 and 14% in 2016. Initially, we thought that iron leaching from the shipwreck was helping to foster the rapid CM expansion (Work et al. 2008), so it is possible that as the CM spread further away from the source of iron, their spread rate slowed. Iron enrichment associated with shipwrecks was found as a driver

of a shift from coral domination to cyanobacteria on reefs in the Line Islands where iron concentrations in algal tissue near shipwrecks were six times higher than reference sites away from impacted reefs (Kelly et al. 2012). However, no relationship was found between proximity to the ship and iron levels in tissues of CM at Palmyra (Carter 2014), and doubts have been voiced as to how iron from the ship could influence growth of CM on the scale of many 100's of meters from the shipwreck site (Work et al. 2008).

There are several other factors that might limit the success of CM. Competition with other cnidarians for space or lack of suitable environmental conditions could have reduced the rate of CM expansion. Predation pressure could also be an influence, and we did observe butterflyfishes commonly feeding on CM around the shipwreck. Finally, CM are particularly successful in shallow habitats with high nutrients (Kuguru et al. 2007; Muhando et al. 2002). Differences in any of these variables among time periods (2007, 2011, 2016) or reductions in nutrients or other factors leaching from the now removed shipwreck might have contributed to the reduction in rate of spread. Logistical constraints of operating in Palmyra precluded doing surveys at the same month each year, so 2007 surveys were done in Sept.–Oct., 2011 in May–June, and 2016 in July–August. However, we think it unlikely that survey timings were contributory to the trends seen here. Supporting this assertion is the invariant presence of high infestation areas to the NW

and SE of the shipwreck site (Fig. 3). Presumably, if CM waxed and waned between months, this should have been reflected in those sites.

In 2007, the area directly around the shipwreck had the highest level of CM infestation, but following the removal of the ship in 2013, the 2016 survey showed that the infestation appeared to dissipate from that central area and split into a more pronounced NW and SE component. One would expect some direct mortality of CM from ship removal activities, but the area of CM disappearance extended beyond the reach of such activities. Removal of the ship resulted in a marked and rapid decrease of CM around the wreck site suggesting that something about the ship was contributing to growth of CM. Given that Palmyra is our only sample of this phenomenon, determining what drove CM around the shipwreck will be difficult, and clearly, invasive CM around shipwrecks seems a rare or under-reported phenomenon. For instance, over 13 million tons of shipping were sunk around tropical Western Pacific waters in WWII, yet the major concern for these wrecks is pollution from oil and munitions (Monfils et al. 2006). Given the popularity of shipwrecks as artificial reefs structures to enhance fish populations (Baine 2001), the situation at Palmyra could serve as a cautionary note to managers wishing to use these in tropical ecosystems. At the very least, careful monitoring around a newly established artificial reef for invasive cnidarians might be a priority to consider.

We doubt that the reduction of CM is a density-dependent decrease in population size as a result of resource consumption beyond carrying capacity. If that were the case, we would have expected the high density populations to the NW and SE of the wreck site (Fig. 3) to also be reduced which was not the case. The rapid response of CM to shipwreck removal contrasts with persistence of other invasive organisms surrounding removed shipwrecks. For instance, cyanobacterial mats at Rose Atoll in American Samoa associated with a shipwreck persisted for years within proximity of the wreck site (Schroeder et al. 2008).

We think it unlikely that *R. howesii* is a non-native species that somehow ran amok in Palmyra, because it has been anecdotally recorded during historical surveys of the reef as reported previously (Work et al. 2008), and this species has a cosmopolitan distribution in the Pacific (Chen and Miller 1996). Moreover, organisms do not necessarily need to be introduced or

non-indigenous to become invasive (Colautti and MacIsaac 2004; Norström et al. 2009). In most cases where natives become invasive, this follows some sort of human disturbance (Muhando et al. 2002; Valery et al. 2009). While human disturbance certainly applies to explain CM invasion in the vicinity of the ship and around mooring buoys (Work et al. 2008), it becomes more difficult to incriminate disturbance as a cause of infestation in areas far removed from the wreck (e.g. northwest). In coral reefs, phase shifts are usually attributed to fleshy macroalgae, often after anthropogenic disturbance that has resulted in loss of coral cover or reduction in coral health (Dudgeon et al. 2010). However, some phase shifts on reefs are also due to dominance by soft corals, sponges, or sea anemones (Chadwick and Morrow 2011; Norström et al. 2009). Corallimorphs have invaded benthic habitat in other regions outside of the Pacific, but only in the area where corals were previously extirpated. For instance, a low tide event on shallow reefs in Israel killed corals that were subsequently replaced by monocultures of *Rhodactis rhodosoma* (Chadwick-Furman and Spiegel 2000). An extensive survey of CM in Tanzania showed they dominated in reef areas disturbed by fishing, pollution, and other human activities (Muhando et al. 2002).

If CM were introduced into Palmyra, it would be unusual for a non native cnidarian to be so prolific. Historically, crustacea and molluscs are the most commonly documented introduced marine invasives with shipping, fishing, and aquaculture the likely vectors of introduction into susceptible habitats (Ruiz et al. 2000). Invasive cnidarians are less frequently documented, and those species that are introduced generally have a localized effect on the environment. Recent examples include the scleractinia *Tubastrea* in the Western Atlantic (Paula and Creed 2005), and *Oculina patagonica* in North Africa (Sartoretto et al. 2008). One exception is the invasive predatory Ctenophore (*Mnemiopsis*) in the Black Sea that led to massive decreases in zooplankton, loss of predatory fish, and dominance of the ecosystem by planktivorous fish (Shiganova 1998). What is happening in Palmyra is all the more surprising, because corals have presumably evolved to compete effectively against other cnidarians using a varied armamentarium of defenses such as sweeper tentacles and cnidae (Williams 1991).

Anatomical and behavioral aspects of CM help explain the successful overgrowth of intact reefs by CM at Palmyra. In general, soft bodied cnidarians are known to aggressively outcompete stony corals (Chadwick and Morrow 2011), a characteristic that makes them popular organisms for beginning aquarists (Fenner 2016). Corallimorpharians in particular can be dominant competitors known to aggressively kill stony corals using specialized marginal tentacles laden with nematocysts. These are produced within 2 weeks during interspecific competition and are very effective in killing certain coral genera such as *Acropora*. However, some species of corals such as *Platygyra daedala* (Langmead and Chadwick-Furman 1999a, b), and *Tubastrea* spp. (Hennessey and Sammarco 2014) can outcompete CM. The western terrace of Palmyra where the infestation originated was predominantly (80% cover) comprised of *Montipora* and *Acropora* (Williams et al. 2013). These two coral species are particularly susceptible to overgrowth by *Rhodactis* (Langmead and Chadwick-Furman 1999a, b) in spite of having the defenses (nematocysts, defensive tentacles) outlined above (Williams 1991) that would presumably allow them to fend off CM. Coralline algae can use chemical deterrents and shed surface layers as fouling defenses (Harrington et al. 2004). Clearly, however, coral and crustose coralline algae cover does not appear to dissuade the spread of CM at Palmyra, because the infestation continued to spread to the N and NW where coral cover ranged from 25 to 64% (Work et al. 2008) and CCA cover averaged 20% (Williams et al. 2013). Given the threat CM are currently posing to coral reefs at Palmyra, understanding environmental and host factors contributing to the pattern of invasion and rate of spread could shed light on ways to manage it.

Corallimorph spread has occurred in an elliptical pattern with a NW to SE orientation. The spread of invasive species is largely controlled by their dispersal capacity, local environmental conditions and species interactions (Assis et al. 2015). We suggest that ocean currents and modes of reproduction of CM help explain the pattern of invasion at Palmyra. The NW to SE orientation of the infestation can be attributed to the way CM reproduce and oceanographic conditions. Satellite-tracked surface drifters and acoustic doppler current profiler measurements show a strong eastward setting North Equatorial counter current around Palmyra with maximum speeds exceeding 1 m/s at

80 m depth that turned southeastward on closer approach to Palmyra (Hamann et al. 2004) confirming our geostrophic current analyses. More recent fine scale modeling of currents around Palmyra confirmed this pattern (Rogers et al. 2017). Vortices occur to the south of the atoll as currents flow eastward with persistent circulation to SW forced by irregularities in atoll shape which may account for the new infestation at the SW corner of the atoll. Although flow across the western terrace of the atoll where the ship was located is mainly eastward, flow paths can diverge to various directions including West and North due to eddies and dispersion and outflow of current through the dredged shipping channel thereby accounting for the NW spread (Rogers et al. 2017). In summary, predominantly easterly currents are likely pushing clonal and sexual propagules of CM from the wreck site to the south and east of the atoll whilst localized flow irregularities are pushing CM to the North and West (Fig. 3). Currents seem to influence the spread of other invasive marine organisms. For example, the invasive mussel, *Mytilus galloprovincialis*, that was introduced to South Africa in the 1970s, has spread extensively via ocean currents colonizing ~ 2800 km of suitable coastal habitat (Assis et al. 2015).

Steps have been taken to remediate the situation with the removal of the shipwreck, a costly (ca. \$6M USD) undertaking because the atoll is remote with limited logistical infrastructure. This action underlined the importance of Palmyra's coral reef resources and the commitment of the FWS to coral conservation. Given likely continued expansion of CM due to reproduction by extant populations, and spread by ocean currents, it would seem advantageous to capitalize on recent management progress and undertake eradication of CM, especially in heavily infested regions in order to reduce sources of sexually and clonally reproductive propagules. Our trials with chlorine and tarps show that localized eradication of CM is feasible. Recolonization of trial plots by CM did occur with CM encroaching into cleared areas from the peripheral edges of the trial plots as well as apparent recruitment of water-dispersed CM to open space in the center of plots. However, our treatments were limited to four relatively small patches surrounded by 100% CM. Refining and scaling up this approach could conceivably decrease recolonization rates. Cleared substrate was rapidly colonized by CCA, an important substrate for coral recruitment

(Erwin et al. 2008; Price 2010) that would aid recovery of coral reefs. After 15 months, small Pocilloporids were found growing in trial plots. These trials were a proof of concept and show that eradication efforts could be successful with subsequent recolonization by reef-building organisms.

Like other CM, *R. howesii* are likely limited to shallower depths and more tranquil waters (Chadwick-Furman and Spiegel 2000), so focusing control efforts in such areas might be an effective strategy. Depth distribution of CM varies with species and host physiology. For instance, in Tanzania, *R. rhodosoma* grows more at shallower depths because its symbionts have photosynthetic adaptations to brighter light, and the host shifts symbionts deeper into tissues to protect them from irradiation (Kuguru et al. 2007). In contrast, another species *Discosoma unguja* relies more on movement to deeper depth to escape high irradiance (Kuguru et al. 2010). The depth limitation mechanisms of *R. howesii* most resembles those of *R. rhodosoma* and ensures that there will not be a pool of deeper animals serving as a source of colonizers in newly eradicated plots. Doing localized eradications during March–July when sea surface heights and current speeds are at their lowest would minimize chances of spread of any viable reproductive fragments that might be generated as plots are cleared. The alternative to localized eradication is to do nothing, particularly now that the shipwreck has been removed. However, the distribution of CM continues to expand at Palmyra, and given that sexual reproduction in CM increases with increasing water temperatures (Chadwick-Furman and Spiegel 2000; Chen et al. 1995), expansion of range may increase with global warming. Warmer water temperatures will also increase the frequency and severity of coral bleaching events, likely opening up new space for CM colonization and rendering surviving corals less able to compete. Without intervention, these mechanisms along with spread of propagules by prevailing currents may ensure continued overgrowth of corals with CM in Palmyra.

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