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REPORT

Live coral cover may provide resilience to damage from the vermetid gastropod *Dendropoma maximum* by preventing larval settlement

N. E. Phillips · J. S. Shima · C. W. Osenberg

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Abstract *Dendropoma maximum* is a vermetid gastropod (a sessile tube-forming snail) commonly associated with living corals throughout shallow-water reefs of the Indo-Pacific. Recent work suggests that, once established, this species can adversely affect growth and survival of corals. Here, we test the hypotheses that disturbances to live coral substrates (e.g., creation of bare patches) facilitate successful larval settlement and subsequent population growth of *D. maximum,* and conversely, that live coral inhibits *D. maximum* settlement. In the shallow lagoon of Moorea, French Polynesia, we selected patch reefs where *D. maximum* was either present or absent (to evaluate potential effects of resident adult conspecifics on recruitment) and established focal quadrats on each reef. In each quadrat, we either experimentally removed 50 % of live coral cover or left the quadrat with 100 % live coral cover. In addition, we deployed units of bare substrate (coral rubble) to each reef. We conducted a census of deployed substrates and quadrats after 6 months and found that *D. maximum* settled irrespective of resident vermetid populations, and only onto nonliving surfaces (i.e., cleared patches in quadrats, coral rubble, and marine epoxy). In laboratory experiments, we exposed larvae of *D. maximum* to live coral and found species-specific effects on survival of *D. maximum* larvae. *Porites lobata* and *Pocillopora* sp. killed larvae of *D. maximum*, *Porites rus* caused weaker mortality, and *Millepora* sp. had no effect on larval survival. Collectively, these results suggest that *D. maximum* requires disturbances that create bare patches to successfully settle onto reefs, and that a high cover of living corals contributes resilience to reefs by limiting settlement opportunities of a species known to reduce coral growth and survival.

Keywords Coral reefs · Disturbance · *Dendropoma maximum* · Larval settlement · Larval mortality

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N. E. Phillips (✉) · J. S. Shima
School of Biological Sciences and Coastal Ecology Laboratory (VUCEL), Victoria University of Wellington,
P.O. Box 600, Wellington, New Zealand
e-mail: Nicole.phillips@vuw.ac.nz

C. W. Osenberg
Department of Biology, University of Florida, Gainesville, FL, USA

Present Address:
C. W. Osenberg
Odum School of Ecology, University of Georgia, Athens, GA, USA

Introduction

Coral reefs are under increasing threats from a suite of environmental stressors including global change (Hoegh-Guldberg 1999; Carpenter et al. 2008; Maina et al. 2011), which can exacerbate effects of biotic factors such as competition and disease (Bruno et al. 2003; Gardner et al. 2003). Indeed, synergisms among stressors could add to the challenges faced by coral, possibly speeding their decline (Nyström et al. 2000; but see Darling et al. 2010). Further, feedbacks driven by biotic and abiotic interactions are important in both triggering and stabilizing shifts between healthy coral reefs and degraded ones (Mumby and Steneck 2008; Nyström et al. 2012).

One newly recognized biotic threat to corals is the vermetid gastropod, *Dendropoma maximum* (Shima et al. 2010, 2013). Vermetid gastropods (also known as worms-nails) are common constituents of coral reefs. Sessile as

adults, their shells form tubes that are often embedded in a matrix of live and dead coral and they have been found associated with a large number of coral species (Hughes and Lewis 1974; Smalley 1984). *Dendropoma maximum* is the largest known vermetid species and is widespread and abundant across its Indo-Pacific range (Hadfield et al. 1972; Hughes and Lewis 1974; Zvuloni et al. 2008). Observational and experimental evidence has shown that adult *D. maximum* can have strong deleterious effects on several species of corals, causing large reductions in survival and growth, altering reef morphology, and creating bare patches on reefs (Colgan 1985; Zvuloni et al. 2008; Shima et al. 2010, 2013).

Vermetid densities are highly variable among and within patch reefs, possibly owing to factors that drive settlement of vermetid larvae. Furthermore, recruitment dynamics of *D. maximum* likely play an important role in their interactions with coral (Shima et al. 2010). Yet, little is known about the process of vermetid settlement in the field, although laboratory experiments demonstrate *D. maximum* larvae successfully settle and metamorphose on coral rubble (Phillips 2011).

Here, we hypothesize that live coral cover may deter recruitment of *D. maximum*, providing a measure of resistance to vermetid population establishment. Corals have been reported to feed on a variety of particulates and zooplankton, including invertebrate larvae (reviews by Muscatine 1973; Houlbreque and Ferrier-Pages 2009). Most reports on coral feeding have focused on the contribution of zooplankton to coral energetics, whereas little is known about the degree to which corals are a source of mortality for invertebrate larvae or potentially reduce the recruitment of coral-associated species. If the settlement of *D. maximum* larvae requires nonliving substrates, then disturbance may play an important role in opening space for larval settlement, as is widely observed in other marine systems (Gaines and Roughgarden 1985; Pineda and Caswell 1997; Cifuentes et al. 2007). A variety of abiotic and biotic agents can damage coral, resulting in bare patches that might facilitate vermetid settlement: storms, bleaching events, disease, fish predation, and anthropogenic disturbances (reviewed by Nyström et al. 2000). Once established, *D. maximum* populations may contribute to a cycle of feedbacks that could accelerate coral declines, e.g., established populations of vermetids would be predicted (based upon results of Shima et al. 2010, 2013) to increase the production of bare patches, which may then facilitate further vermetid settlement.

As adults, these animals are often embedded in large, live coral heads, completely surrounded by living coral tissue except for the opening of the tube; therefore, it is possible that *D. maximum* larvae are able to settle and metamorphose on live coral similar to the tubeworm *Spirobranchus* sp. (Smith 1985) and the boring date mussel *Lithophaga lessepsiana* (Mokady et al. 1991). Although it is well known that many tropical reef invertebrates settle in response to cues such as crustose coralline algae and biofilms in laboratory experiments and to artificial substrates in the field (Morse et al. 1988; Harrington et al. 2004; Price 2010; Arnold and Steneck 2011; Hadfield 2011), explicit examination of live, intact coral as a potential settlement substrate is rare.

Many marine species, especially invertebrates, are also known to settle in response to conspecific cues, e.g., barnacles (Raimondi 1990), polychaetes (Minchinton 1997), crabs (Donahue 2006), ascidians (Rius et al. 2010), and fish (Lecchini et al. 2005; review by Pawlik 1992). *D. maximum* is patchily distributed (Shima et al. 2010), so it is possible that they settle in response to conspecific cues. If resident (e.g., adult) populations of *D. maximum* provide conspecific cues that enhance settlement of subsequent cohorts, then this could intensify the deleterious feedback loop.

The first aim of this paper is to evaluate whether disturbances and/or resident adults facilitate larval settlement in the field, allowing *D. maximum* to gain a foothold on reefs. Secondly, we evaluate whether living corals facilitate or deter vermetid settlement, using laboratory experiments to examine the interaction between several common Indo-Pacific coral species and *D. maximum* larvae.

Materials and methods

D. maximum settlement in the field: effect of resident adults and coral disturbance

This study was conducted in the shallow (2–3 m depth) lagoon on the north shore of Moorea, French Polynesia (17.488°S, 149.818°W). *Dendropoma maximum* settlement was examined in two ways: (1) using pieces of coral rubble as settlement substrates, and (2) in focal, permanently marked quadrats that were either covered in ~100 % live coral or manipulated to create patches of bare substrate (~50 % live, ~50 % bare) on large colonies of the coral, *Porites lobata* (see below). The latter approach tested the hypothesis that settlers require bare patches (as opposed to live coral) for successful establishment. During our field studies, several species of vermetid were observed (*D. maximum*, *Serpulorbis variabilis*, *Dendropoma platypus*, and a few individuals that could not be identified). However, *D. maximum* was the most abundant species with the others represented by only a few individuals.

Pieces of coral rubble, approximately elliptical in shape and similar in size (average maximum length × width × height ± SD = 12 ± 1.2 × 8 ± 1.6 × 7 ± 1.7 cm), were collected from the lagoon on 01 October 2008. Rubble was soaked in freshwater overnight, scrubbed with brushes to remove fouling organisms, and dried in full sun for 3 d.

On 02 October 2008, ten pairs of small focal patch reefs ($\sim$2–6 m^2 in area) were selected that were predominately (>80 %) live *Porites lobata* and separated from nearest neighbouring reefs by at least 0.5 m of sand. One member of each pair of reefs lacked populations of adult *D. maximum;* the other member of the pair had *D. maximum* adults present. Although these were not quantified, densities appeared approximately similar to densities on *P. lobata* reefs reported elsewhere (e.g., Shima et al. 2010). These reefs also had corresponding morphological differences: i.e., reefs without vermetids were rounded, and those with vermetids were flattened (see Shima et al. 2010). It was hypothesized that reefs with resident *D. maximum* would have higher settlement if larvae were attracted to conspecific cues. A single piece of rubble (whose surface area was estimated using the equation for an ellipsoid) was attached to each reef on 04 October 2008 with cable-ties that were affixed to the reef using marine epoxy. The pieces of coral rubble were collected from the reefs after 6 months (in April 2009, $n = 17$ due to three rubble pieces missing) and examined in the laboratory, where vermetid settlers were counted and identified to species. Data were normal and homoscedastic, therefore, we used a one-way ANOVA to examine the effect of reef type (i.e., presence/absence of resident *D. maximum*) on *D. maximum* settler density.

On the same reefs, and over the same time period, two haphazardly positioned 15 × 15 cm quadrats (each with 100 % live coral cover) were marked on each reef by embedding a cable tie into marine epoxy in each of the four corners. One quadrat on each reef was left with 100 % coral cover (called 'unmanipulated'). In the other, $\sim$50 % of the live coral (evenly distributed through the quadrat) was chipped and scraped away with a geology hammer to mimic disturbance to live coral (e.g., due to fish grazing or anchor chains); we refer to these as 'scarred' quadrats. Each quadrat was photographed. Six months later (April 2009), quadrats were photographed again, the vermetids were counted and identified, and the substrate they were on (e.g., live coral, bare/dead patch, marine epoxy) was recorded. Because this is a split-plot design, we used a partly nested linear model to analyse the data, where reef type (presence/absence of resident *D. maximum*) and quadrat treatment (scarred or unmanipulated) were each fixed factors and reef identity was nested within reef type as a random factor (Quinn and Keough 2002). The count data were log-transformed prior to analysis (Zar 1984).

Effect of live coral on *D. maximum* larvae

Collection of D. maximum larvae and coral fragments

Three laboratory experiments, designed to assess the effect of live coral on larvae of *D. maximum*, were conducted in October 2008 at the University of California Gump Research Station, Moorea, French Polynesia. In all three experiments, *D. maximum* larvae were obtained from field-collected adults. Individual adult *D. maximum* were chiselled from the coral matrix intact in their tubes, transported to the laboratory in coolers of seawater, and their brooding status ascertained by gently poking each snail until it retracted deep into its shell. If late-stage capsules were observed attached to the inside of the shell, a mesh-sided cage (mesh = 150 μm) was secured around the tube with cable-ties, and the adult (with mesh enclosing the openings to their tubes) was then placed in a large tank with flowing seawater. Swimming larvae were released by females after 1–3 d.

Fragments (approximately 2 × 3 cm) of live coral were collected from the lagoon on the morning of each experiment and left for 2 h in flowing ambient seawater to recover. Fragments were examined under a microscope prior to each experiment to ensure that polyps were extended.

Laboratory experiment 1: one day exposure to coral

Treatments were established in 1-l plastic tubs filled with filtered seawater (FSW; mesh size = 0.5 μm). Each tub contained one of five treatments: fragments of live *Porites lobata*, *Pocillopora* sp., or *Porites rus,* coral rubble (fragments had been scrubbed and dried in full sun for 2–3 d prior), or a control of FSW only ($n = 4$ replicate tubs per treatment). Twenty 2-d posthatch *D. maximum* larvae from a single female were gently pipetted into each tub, released a few cm above the substrate. In all cases, the velum (the ciliated larval swimming structure) was extended. Tubs were maintained in a flowthrough seawater table and examined after 24 h under a dissecting microscope. The tub and each fragment were thoroughly searched for any settlers, and all larvae scored as either live or dead. If larvae were dead, it was noted whether the larval shells were empty of tissue (i.e., presumably consumed by the coral). This experiment was repeated 3 d later with 1-d posthatch larvae from a different female, and with the addition of a treatment of live *Millepora* sp. (referred to as run 2). Proportional mortality data were arcsin square-root-transformed, and each run analyzed with a separate one-way ANOVA. We used Tukey post hoc tests to further examine significant effects.

Laboratory experiment 2: several hours of exposure to coral

In this experiment, larvae were exposed to treatments for a shorter time period. Four treatments of live coral were established: *Porites lobata, Pocillopora* sp., *Porites rus*,

and *Millepora* sp. A single coral fragment was placed into each of ten replicate plastic containers of each treatment with approximately 200 ml FSW. To each container, we added 1 larva (1-d post-hatch) as described above for *Laboratory experiment 1*. Of the ten larvae for each treatment, five were from each of two females. We examined larvae after 4–6 h, and they were scored as live or dead. We used a logistic regression model to test for treatment effects.

Laboratory experiment 3: brief contact with coral

For this experiment, the three coral species that caused the highest mortality in the previous experiments were used: *Porites lobata*, *Pocillopora* sp., and *Porites rus*. Fragments of each species were placed into tubs with 500 ml FSW ($n = 4$ replicate tubs for each treatment). Twenty 3-d posthatch larvae from a single female were added to each tub. Larvae were pipetted out very slowly and released a few cm above the coral, ensuring the velum was extended and that larvae would exit the pipette swimming in a trajectory that would bring them slowly into contact with the coral polyps. A dissecting microscope was used to observe as many larvae as possible as they came into contact with coral polyps. After approximately 5 min, as many larvae as could be found were collected from each dish with a pipette and scored as live or dead. Live larvae were placed in a petri dish with FSW for 2 h and then examined for recovery. Larvae were observed for several min before a determination was made about their recovery status. Larvae were considered 'recovered' if they were swimming, or if the velum was extended or was in the process of being extended, and the velar cilia were visibly beating. Larvae scored as dead were also retained in a petri dish with FSW and examined after a further 2 h to ensure they had not been mistakenly scored as dead. In all cases, larvae judged to be dead had not recovered after 2 h. We used a one-way ANOVA and post hoc Tukey tests on arcsin square-root-transformed proportional mortality to examine treatment effects.

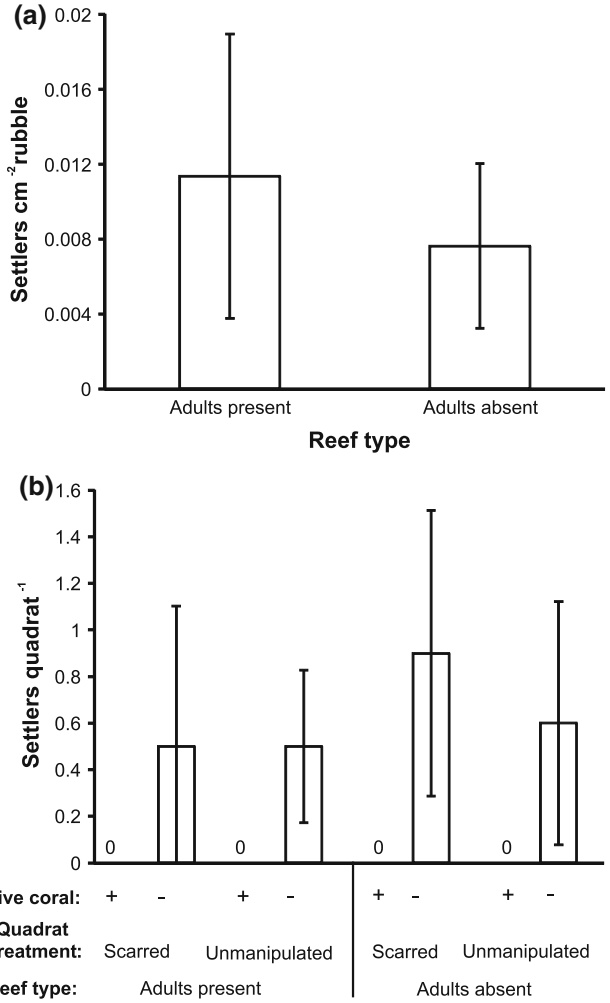

Fig. 1 *Dendropoma maximum* larval settlement (mean ± 95 % CI) observed after 6 months in the field on reefs which either had resident adults or did not: **a** Settlement on pieces of coral rubble attached to the tops of reefs ($n = 8$–9); and **b** in experimental quadrats that were either 50 % bare from scarring, or 100 % live coral cover (unmanipulated; $n = 10$). '+' indicates portions of quadrats that are comprised of live coral; '−' indicates portions of quadrat that are nonliving coral substrates. Larvae only settled onto nonliving substrates, but in all cases, there was no significant effect of quadrat treatment or reef type on settlement (see 'Results' section)

Results

D. maximum settlement in the field: effect of resident adults and coral disturbance

After 6 months of deployment in the field, each piece of rubble had 0–6 settlers of *D. maximum* (mean ± SD = 2.59 ± 2.00). To examine differences in settlement between reef types, and to control for variation in the size of the rubble, the number of settlers was standardized per surface area of rubble (cm^2). There was no difference in settlers cm^{-2} between reefs with or without resident *D. maximum* populations (one-way ANOVA: $F_{1,15} = 1.29$, $p = 0.274$; Fig. 1a).

No *D. maximum* recruits were found on live coral in either plot type (Fig. 1b). Recruits only occurred in scarred areas of manipulated plots, and in both plot types, recruits were also found on nonliving substrates such as marine epoxy or plastic cable-ties used to demarcate plot boundaries (Fig. 1b). Thus, all *D. maximum* recruits were found on nonliving substrates. Settlement to nonliving substrates was not affected by whether there were resident adults on the reef ($F_{1,18} = 0.65$, $p = 0.429$), nor whether quadrats had been scarred or not ($F_{1,18} = 0.45$, $p = 0.512$), nor the

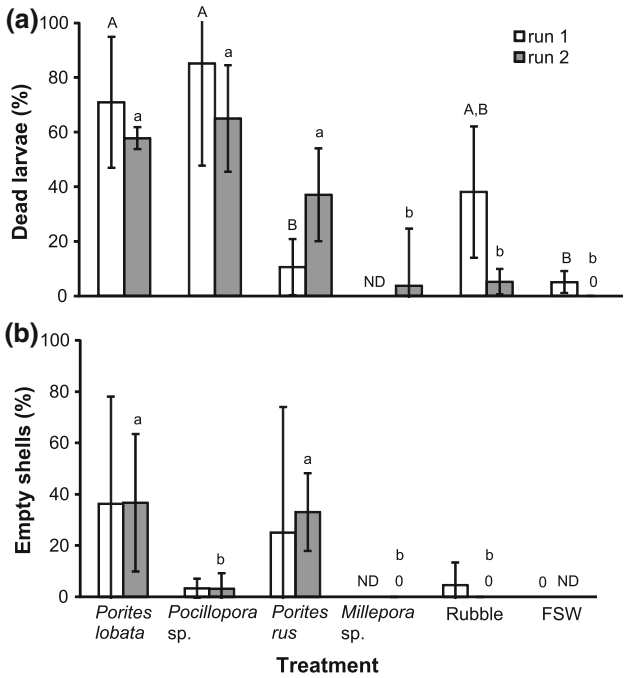

Fig. 2 Responses of *Dendropoma maximum* larvae after 24 h in each treatment in laboratory experiment 1 (mean ± 95 % CI): **a** percentage mortality; and **b** percentage of dead larvae that were empty shells ($n = 4$ replicate containers per treatment, 16–20 larvae per container). *Letters over bars* indicate significant differences (Tukey HSD, $p < 0.05$) within runs. *Capital letters* are used for run 1 and *lower case letters* for run 2. 'ND' indicates no data for that treatment

interaction ($F_{1,18} = 0.45$, $p = 0.512$). Notably, by April 2009, 6 months after scarred quadrats had been established, live coral had regrown and covered 90–100 % of the bare patches in each quadrat and had also grown over much of the marine epoxy as well.

Effect of live coral on *D. maximum* larvae

Laboratory experiment 1: one day exposure to coral

Tubs and their contents were thoroughly searched after 24 h for larvae or settlers. Between 16 and 20 of the 20 larvae were recovered from each tub (mean = 18.9, SD = 1.1), so results are presented as percentage of larvae collected. No settlers were found. After 1 full day of exposure to coral, there was high mortality of *D. maximum* larvae (up to 85 % in run 1, and 65 % in run 2) in some treatments. For the first run, there was higher mortality with *Porites lobata* and *Pocillopora* sp. than with *Porites rus* or FSW ($F_{4,15} = 10.45$, $p = 0.0003$; Tukey HSD, $p < 0.05$; Fig. 2a), although mortality with rubble was intermediate and indistinguishable from the other treatments (Tukey HSD, $p > 0.05$). In the second run, *Porites lobata*, *Pocillopora* sp., and *Porites rus* resulted in higher mortality than FSW, rubble, or *Millepora* sp. ($F_{5,18} = 21.76$, $p < 0.0001$; Tukey HSD, $p < 0.05$; Fig. 2a). Empty larval shells, possibly indicating larval soft tissues had been digested, were also evident, and more common in the treatments with *P. lobata* and *P. rus* (Fig. 2b), although the effect of treatment was significant only in run 2 (run 1: $F_{4,15} = 0.88$, $p = 0.502$; run 2: $F_{5,18} = 13.98$, $p < 0.0001$).

Table 1 Responses of *Dendropoma maximum* larvae after 4–6 h of exposure to coral in laboratory experiment 2 ($n = 10$ per treatment)

Coral species	% Live	% Swimming (of live)	% Dead	% Empty shells (of dead)
Porites lobata	0	–	100	30
Pocillopora sp.	30	0	70	0
Porites rus	100	30	0	–
Millepora sp.	100	20	0	–

Laboratory experiment 2: several hours of exposure to coral

Exposure of *D. maximum* larvae to live coral for only 4–6 h still resulted in high mortality from some species of coral [χ^2 ($df = 3$, $N = 40$) = 42.33, $p < 0.0001$]. All *D. maximum* larvae exposed to *P. rus* and *Millepora* sp. were alive, with 20–30 % swimming (Table 1), but 100 and 70 % of larvae exposed to *Porites lobata* and *Pocillopora* sp, respectively, were dead. Of the dead larvae in *P. lobata* treatments, 20 % were empty shells, but there were no empty shells in the treatment with *Pocillopora* sp.

Laboratory experiment 3: brief contact with coral

When *D. maximum* larvae contacted polyps, they immediately withdrew into their shells. Many of these larvae remained adhered to the coral polyps such that it took quite a bit of flow from the pipette to dislodge them after 5 min. Larval mortality after 5-min exposure to live coral varied significantly among the three coral species ($F_{2,9} = 8.14$, $p = 0.0096$; Fig. 3). Exposure to *Porites lobata* led to greater mortality than exposure to *Porites rus* (Tukey HSD, $p < 0.05$) although *Pocillopora* was not significantly different from the other two species (Tukey HSD, $p > 0.05$). Nearly 50 % of larvae in direct contact with *Porites lobata* and 20 % exposed to *Pocillopora sp.* died almost immediately (Fig. 3).

Discussion

Although *D. maximum* adults can have deleterious effects on corals (Shima et al. 2010, 2013), this study shows that

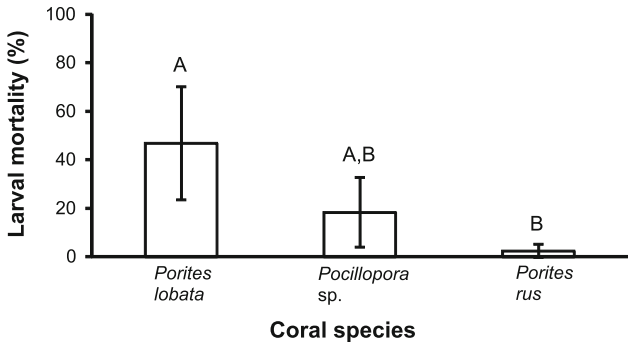

Fig. 3 Percentage (mean ± 95 % CI) of dead plus unrecovered *Dendropoma maximum* larvae after brief (<5 min) direct contact with coral polyps (laboratory experiment 3; $n = 4$ replicate containers per treatment, 20 larvae per container). *Letters over bars* indicate significant differences (Tukey HSD, $p < 0.05$)

corals also can have negative effects on *D. maximum* larvae, which may ultimately inhibit the establishment of adult populations of the gastropod. In the field, settlement of *D. maximum* occurred on a variety of natural and artificial substrates, but not on living coral. These, and the results of Phillips (2011), show that *D. maximum* larvae successfully settle to a variety of nonliving substrata (e.g., coral rubble, marine epoxy, plastic) and thus probably do not have highly specific settlement cues or requirements. There was also no evidence that settlement requires cues from established adult populations. Although many species do settle in response to cues from conspecific adults (e.g., Raimondi 1990; Pawlik et al. 1991; Minchinton 1997; Rius et al. 2010), many also do not. Gregarious settlement in response to conspecific cues often occurs in species that are highly aggregated as adults, e.g., ophiuroids, bivalves, polychaetes, crustaceans, and ascidians (Burke 1986; Toonen and Pawlik 1994; Tamburri et al. 2007). However, this does not appear to be the case for *D. maximum*, which although is patchy in distribution does not regularly attain extremely high densities. Without the requirement for a conspecific settlement cue, *D. maximum* is therefore able to take advantage of small local disturbances that result in coral death (e.g., from storms, abrasion, fish grazing) to opportunistically settle in otherwise unavailable habitat on live reefs, increasing potential dispersal into new areas and recruitment into newly opened microsites.

Previous work in Moorea has shown that *D. maximum* are reproductively active year round and that larvae are likely to persist (and potentially disperse) in the plankton for at least several days (Phillips and Shima 2010; Phillips 2011). Thus, a larval pool is probably always available, and dispersal potential between neighbouring coral patch reefs is likely relatively high. There was no statistically significant treatment effect of scarring of quadrats, although a small number of recruits did settle into those bare patches (while none settled into the live coral quadrats). This limited recruitment is likely due to the relatively quick regrowth of live *Porites lobata*, and the small scale of scarring, thus reducing available settlement habitat within the time frame of the study. The probability of *D. maximum* settlement into bare patches in a live coral matrix will therefore at least in part be determined by the areal extent of the damage and coral growth rates. Further, adult wormsnails are often observed surrounded by living coral; these patterns are likely a result of larval settlement to bare patches and subsequent regrowth of surrounding coral, despite the inhibitory effects of vermetids on coral growth (Shima et al. 2010, 2013).

The laboratory experiments showed that not only are *D. maximum* larvae unable to settle to live coral, but that several species of coral can be a significant source of larval mortality. Although this may be intuitive, it has rarely been directly observed. Further, some invertebrate larvae can settle directly on live coral (Smith 1985; Mokady et al. 1991; Loh and Pawlik 2012), in close proximity to polyps (Rawlinson et al. 2011; Hsu et al. 2013), or in response settlement cues from coral exudate (Hadfield et al. 2006). Therefore, tolerance to coral polyps by early life stages is species-specific and an area that requires further study to understand the fine-scale recruitment dynamics of reef-associated invertebrates.

The role of benthic suspension-feeding predators on invertebrate larval settlement dynamics is not well understood, but has been documented in mussel beds, sponges, barnacles, and anemones (reviewed by Morgan 1995). Although studies of coral feeding on invertebrate larvae are relatively few, the best examples are for large ascidian larvae, for which mortality due to coral has been reported to range from 3 % in a temperate Australian system (Davis and Butler 1989) to 7.5–30 % in the Great Barrier Reef and Hawaii (Olson and McPherson 1987; Stoner 1992). Further, in the Caribbean, coral were able to filter 60 % of the zooplankton, including larvae, coming over the reef on an incoming tide (Glynn 1973). Other studies of zooplankton capture by coral have found that larger, relatively less motile taxa are captured in higher proportion (relative to their abundance) than smaller more mobile taxa, such as copepods (Sebens et al. 1996, 1998; Palardy et al. 2006, 2008). Thus, vermetid larvae, which are relatively large and have limited mobility, may be particularly vulnerable. For example, immediately upon contacting a polyp, *D. maximum* larvae retracted into their shells and were unable to free themselves from a polyp's tentacles. Thus, even a brief encounter with live coral polyps of some species can be an important source of mortality for *D. maximum* larvae.

Effects of corals on the survival of *D. maximum* larvae were species-specific, with minimal observable effects

from *Millepora* sp. and *Porites rus*, intermediate mortality from *Pocillopora* sp., and high mortality from *Porites lobata*. As a result, the aggregate effect of corals on larval survival will likely depend upon the composition of corals in the local vicinity where larvae attempt to settle. In this system, a variety of factors are likely to increase potential encounter rates between coral and larvae: *D. maximum* larvae are released from benthic mothers, are relatively poor swimmers, and have a relatively short larval duration (several days). Thus, these larvae are repeatedly negotiating a 'wall of mouths' (sensu Emery 1973). Further, much of Moorea's lagoon is shallow (1–5 m), contains patch reefs often exceeding 1 m in height, and is colonized by coral taxa that caused the highest mortality in these experiments: *Pocillopora* sp. and *Porites lobata* (Pratchett et al. 2011).

Although we did observe two empty larval shells after 24 h in one replicate of the coral rubble treatment (which may indicate decomposition), the high occurrence of empty larval shells after 4–24 h of exposure to coral are strongly suggestive of feeding and digestion. Indeed, digestion in other corals can occur within 4 h (Sebens et al. 1996). Feeding by *Porites lobata* was more consistent and prevalent than the other species examined. Other work has shown heterotrophy is a substantial carbon source for *P. lobata*. For example, in an experiment in Hawaii, feeding on zooplankton accounted for 47 % of daily metabolic carbon (DMC) requirements of *P. lobata* (Palardy et al. 2008). By contrast, *Pocillopora* sp. in our experiments appeared to kill but not necessarily eat *D. maximum* larvae (Fig. 2), although some species of *Pocillopora* are known to consume zooplankton (Palardy et al. 2006). Incidental death has also been found for ascidian larvae that were observed to be captured and killed by coral, but not necessarily ingested (Stoner 1992).

Our study, along with other recent work in this system, shows that life history strategies of *D. maximum* allow it to take advantage of disturbance events that open up bare patches in live coral reefs that are then suitable for settlement; larvae are available year round and nonspecific in their requirements. This suggests that *D. maximum* may capitalize on other factors (e.g., *Acanthaster* outbreaks: Pratchett et al. 2011; Kayal et al. 2012) that initiate coral decline to facilitate settlement and thus further limit the likelihood of coral recovery and growth through the deleterious effects of adult vermetids on corals (Shima et al. 2010, 2013). However, this negative feedback is countered by the fact that larval mortality caused by living corals may inhibit *D. maximum* recruitment and contribute to patchiness in adult vermetid distribution and interactions with corals. Thus, healthy reefs with high cover of live coral, particularly those species that are fast-growing, will likely be resistant to the expansion of *D. maximum* populations.

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