Assessing Coral Health in Moorea After a Regional Die-Off of the Coral Antagonist, *Dendropoma maxima*

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Abstract. Coral reefs are under pressure from numerous anthropogenic and natural threats. A species of vermetid worm, *Dendropoma maxima*, has a negative interaction with the corals it lives on. Vermetid worm interactions result in structural homogeneity of reef habitats, reduced coral growth, and increased coral death. *Dendropoma maxima* and corals have a naturally evolved competitive relationship. Therefore, it is inherent that removal of *D. maxima* from the environment would alleviate stress to coral associated with vermetid worm activity and lead to increased coral growth and survival. A 2015 die-off of *D. maxima* in French Polynesia is likely to have had direct positive effects to coral and cascading effects on reef community structure. The aim of this investigation was to contribute to the understanding of vermetid worm and coral interactions by quantifying the extent of stress on corals under reduced vermetid worm densities. This study measured *D. maxima* size and abundance on several coral types and assessed *Porites* coral health by the presence of pink lesions and growth along edges of coral. Surveys of *D. maxima* size and Porites coral health occurred at Temae Reef, Moorea in October and November 2016. Live *D. maxima* were less than half the size of dead *D. maxima*. Average size of live *D. maxima* was different between *Porites* coral and dead coral substrates and between Top or Side positions. There was a strong positive correlation between number of live *D. maxima* and number of lesions on *Porites* coral and positive correlation between live *D. maxima* and percent of coral death. A positive but insignificant correlation between number of live *D. maxima* and length of new growth was observed. The die-off of *D. maxima* in 2015 appears to have positively impacted coral health and the results are important to understanding shifts in community structure and ecological health, especially as environmental changes become more frequent in the future.

Introduction

Species interactions influence the habitat and community structure of ecosystems (Sale *et al*, 1977; Naeem, 1997). The species diversity of an environment is influenced by the structural complexity of the environment and level of species interactions. (Larsen, Williams, and Kremen, 2005). Understanding relationships that underlie the ecological workings of an environment is important to anticipate impacts to a habitat following a major shift in abundance of a pervasive species (Naeem, 1997). The cascading effects of fluctuations in abundance of a singularly important species can have important consequences to the availability of resources for other organisms (Larsen, Williams, and Kremen, 2005). Coral reefs are biodiverse and productive ecosystems and are home to complex interspecies interactions (Sale 1977; Connell 1978).

A well-documented interaction exists between *Porites* corals and the vermetid gastropod "worm," *Dendropoma maxima*, on the fringing and back reefs of Mo'orea, French Polynesia (Shima and Osenberg and Stier, 2010). Vermetid worms anchor themselves to hard substrate, grow cylindrical shells, and cast mucus nets into the current to capture food particles (Phillips, 2011). *Dendropoma maxima* is the largest species of vermetid worm and is found throughout warm shallow reefs of the Indo-Pacific (Zvuloni *et al*, 2008). *D. maxima* growth rate depends on

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the availability of food, exposure to water flow, and density of conspecifics (Smalley, 1984). *Dendropoma maxima* aperture size and shell length generally increase with age (Shima and Osenberg and Stier, 2010) but can also be limited by the proximity of other vermetid worms and ability to expand mucus nets to capture food (Smalley, 1984; Shima *et al*, 2013). *Dendropoma maxima* prefer habitat with high wave energy or current to help facilitate the extension of mucus webs used to capture food (Zvuloni *et al*, 2008; Shima *et al*. 2010; Kappner *et al*. 2000). The mucus webs of vermetid worms are negatively buoyant and remain in contact with coral (Kloppel *et al*, 2013). Corals compete with mucus webs to filter plankton, detritus, and other food particles (Kloppel *et al*, 2013). Periodically, mucus webs full of particles are retracted and consumed (Funsten, 2014; Kloppel *et al*, 2013). Mucus web retraction has been hypothesized to be abrasive and stress inducing to coral (Kloppel *et al*, 2013). The sticky mucus webs also contain bioactive compounds that cause coral necrosis and capture metabolites from the surface of coral (Kloppel *et al*, 2013).

By a variety of antagonistic methods, *D. maxima* activity has been shown to directly diminish the structural complexity of corals, indirectly impacting biodiversity in coral reef ecosystems (Zvuloni *et al*, 2008; Shima and Osenberg and Stier, 2010; Shima *et al*, 2013). The negative effects of vermetid activity on coral health are evolved strategies of *D. maxima* to create advantages for all life stages of *D. maxima* (Shima *et al*, 2010). Scarring and coral death resulting from *D. maxima* activity leads to increasing morphological uniformity in coral reef ecosystems (Zvuloni *et al*, 2008). As corals react to D. maxima antagonists, they exhibit melanized areas that appear pink containing high concentrations of immune cells to boost the health of coral polyps that are stressed (Petes *et al*, 2003; Palmer, Mydlarz and Willis, 2008; Lance, 2012). Corals also have melanized pink areas where there is new growth and coral edge extension (Reed, Muller, and van Woesik, 2010; Benzoni, Galli, and Pichon, 2011).

Previous surveys on the abundance of *Dendropoma maxima* at Temae Reef, Mo'orea revealed high densities of vermetids on *Porites* corals (Funsten, 2014). Pink lesions on *Porites* corals were shown to be positively correlated with the presence of *D. maxima* and other coral boring invertebrates (Lance 2012). Between June and August 2015, an unknown environmental change or pathogen led to an extirpation of *D. maxima* on all the reefs of the Society Islands, French Polynesia (Brown *et al*, 2016). The mass mortality of *D. maxima* in 2015 created an opportunity for corals to improve their condition while alleviated from a major natural stressor in their environment (Brown *et al*, 2016). This study investigates the size and density of *D. maxima* at Temae Reef to estimate the recovery of D. maxima populations and to investigate how corals have responded in the absence of *D. maxima*.

Methods

Study site

Surveys were conducted at the back-reef of Temae Beach, Moorea French Polynesia. The reef is included within a Marine Protected Area that prohibits harvesting fish and other organisms in its boundaries. Temae was chosen as the study site due to its accessibility from shore and many coral outcrops, called bommies, found at shallow depths. Additionally, prior investigations into abundance of lesions and vermetid density on *Porites* coral have been conducted at Temae Reef. The similar current and depth across the reef minimized environmental differences that could affect coral health and vermetid settlement. Surveys on coral health and *Dendropoma maxima* size were conducted parallel to shore along the transition between sandy flat bottom and coral bommies. The first day of surveying began from the yellow boundary marker of the MPA at the northwest end of Temae Beach and the last day ended by the Sofitel Bungalow Resort (17.498677S, 149.756481W – 17.502525S, 149.761575).

Field Sampling

Data were collected between October 13 and November 8, 2016. Coral bommies located midway between the algal crest and shore were selected for the study based on several qualifying criteria. Corals were surveyed in the order they were encountered. Depth of surveys varied between one half and two meters. Surveys on subsequent days of field work began approximately 25 meters southwest from the end of the previous day of surveys and continued parallel to shore to avoid repeating surveys of the same coral bommies. *Porites* coral bommies were surveyed for number of pink lesions, percent dead coral and extension of new growth along edges of healthy coral. *Porites* coral bommies were surveyed for level of health associated with the Top and Side of the coral column. Vermetid worms were distinguished as *Dendropoma maxima* by the dark brown or black opercula covering of the aperture; other vermetid worm species were ignored. Sizes of *D. maxima* were collected from quadrat surveys on Top and on the Side of coral bommies. Coral or substrate selected for the study met the following criteria: 1) single coral species type or categorized as dead coral, 2) past or present vermetid worm habitation, 3) coral bommie area greater than 50 cm^2 for positional surveys of *D. maxima* average size and *Porites* coral health estimates. The last survey requirement was made to determine differences between *D. maxima* size and *Porites* coral health on coral Tops and Sides. Quadrats were placed on the Tops of coral bommies to include as many vermetids as possible and then repeated on the coral's vertical or slanted Side facing the direction of oncoming current. Photographs were taken and time recorded at the start of each quadrat to reference data with photo time stamps.

Vermetid snail surveys

Dendropoma maxima were counted within quadrats and sized with a ruler. Surveys were performed on three substrate types: *Porites*, *Montipora*, and dead coral rock. The number of live and dead vermetid worms and their corresponding sizes were recorded. Photographs of each quadrat were used to reference and verify counts. Notes on a dive slate were later transcribed to a hand-written data sheet and excel document upon return from the field.

Coral health surveys

The study chose to survey *Porites* coral health since previous studies had noted a correlation between *Dendropoma maxima* and stress on this coral genus (Lance, 2012). *Porites* coral health was quantitatively assessed based on number of pink lesions, percent dead coral, and extension of new coral growth. The number of pink lesions, from 0.4 to 2 cm occurring on the surface of healthy coral within quadrats, were recorded and tested for a correlation with number of live *D. maxima*. Percent of dead coral within quadrats was recorded and tested for a correlation with number of live *D. maxima*. Coral stress was inferred from the number and size of dark pink lesions on *Porites* coral. Coral extension along the edge of healthy coral areas was identified by a thin white line with pink melanization and measured lengthwise using a centimeter ruler. Photographs were used to reference and complete field notes.

Data analysis
An ANOVA was used to compare sizes of all live and dead *Dendropoma maxima* on the three coral substrates surveyed. An ANOVA was also performed to test for differences between size of vermetid worms on Tops and Sides of coral bommies. A Tukey's HSD was run to determine pairwise differences between substrate types. *Porites* bommies with one or more pink lesion were included in an analysis of linear regression between number of live vermetids and the presence of pink lesions. Similarly, regression analyses were run between number of live vermetid worms and percent dead coral and new coral extension. A comparison of live *D. maxima* density on *Porites* and *Montipora* coral was made to assess changes to vermetid worm populations after the 2015 die-off event. Additionally, the total number of pink lesions at Temae Reef in 2016 and 2012 were compared to gauge changes in level of coral stress (Lance, 2012). Statistical tests were performed in *R* (R Core Group 2013) and variance reported as 95% confidence intervals.

Results

Size of Dendropoma maxima
There was a difference in aperture size by coral type, Fig. 1, (ANOVA $F_{(2,1388)}$ =10.8, Tukey HSD test, $p<0.0001$). Average aperture size of live D. maxima on Dead Coral was more than 0.05 cm larger than on *Porites* or *Montipora* (0.46 vs 0.40 or 0.39, respectively; ANOVA Tukey HSD $p<0.001$). Average aperture size of dead *D. maxima* on *Porites* was nearly 0.2 cm larger than *Montipora* (1.04 vs 0.86 cm, respectively; ANOVA Tukey HSD $p<0.0001$).

The average size of live *Dendropoma maxima* on all substrates was 0.403 ± 0.011cm, n=957, which is smaller than the average of 1.1 cm in 2014 (Funsten, 2014). On all substrates, there was a difference in aperture size between live and dead vermetids, Fig. 1, (ANOVA $F_{(1,1388)} = 967$, $p<0.00001$). The size of live vermetids was less than half the size of dead vermetids (Tukey's HSD, adj. p=0).

There was a difference in average size of live and dead *D. maxima* by quadrat positioning, Fig. 2. Live *D. maxima* in quadrats on Top of coral bommies were on average 0.02 cm smaller than on the Side of coral bommies, (0.40 vs. 0.42cm, respectively, ANOVA $F_{(1,1390)}$ =5.4, $p<0.05$, Tukey's HSD). Dead *D. maxima* on Tops were 0.11 cm smaller than on Sides (0.96 vs. 1.07 cm, respectively).

Density of Dendropoma maxima
The average density on *Porites* and *Montipora* coral was 40.9 ± 7.1 vermetid/m^2 and 36.9 ± 11.0 vermetid/m^2, respectively. There is an observable difference in *D. maxima* density on *Porites* and *Montipora* corals between 2014 and 2016.

Porites Coral Lesions
There were 99 lesions counted on 78 corals surveyed. There was a positive linear correlation between number of live *Dendropoma maxima* and pink spotted lesions on *Porites* coral, Fig. 3. (Regression analysis, $F_{(1,37)}$ =46.4, $p<0.0001$, R^2= 0.5445).

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Percent Dead Coral

There was a positive correlation between number of live *Dendropoma maxima* and percent dead coral on *Porites* bommies, Fig. 4. (Regression analysis, $F_{(1,43)}=10.3$, $p<0.01$, $R^2=0.174$).

Coral Growth

There was a positive correlation that was not significant between number of live vermetids and amount of coral edge extension on dead coral areas, Fig. 5 (Regression analysis $F_{(1,36)}=0.026$, $p>0.05$, $R^2=-0.02703$).

Discussion

The smaller average size and lower density of *Dendropoma maxima* on Temae Reef in 2016 suggests that *D. maxima* have been recolonizing the reefs of the Society Islands in the months since the 2015 mass-mortality event but are likely reproductively immature (Hughes and Lewis, 1974; Phillips and Shima, 2009). The origin of this newly recruited population of *D. maxima* is uncertain because the planktonic stage is just a few weeks, limiting the range of *D. maxima* dispersal (Phillips and Shima, 2009). However, research indicates the ability of *D. maxima* larvae to employ intermediate larval strategies to extend dispersal period and colonize distant reefs (Phillips 2011).

The average size of live *D. maxima* found on *Porites* and *Montipora* corals in this investigation was smaller than averages in 2012. *Dendropoma maxima* density on *Porites* and *Montipora* corals in 2012 was 162.7 ± 176.6 vermetid/m^2 and 288.0 ± 165.1 vermetid/m^2 (Funsten, 2014). Additionally, D. maxima densities on coral were not as great as in 2014 since vermetid worms are arriving by chance from distant reefs. Due to the 2015 die-off, there are greater numbers of dead *D. maxima* in 2016 than 2012.

Coral health has improved since 2012 as assessed by the presence of pink pigmented lesions on *Porites* coral at Temae back reef Moorea. The number of lesions found on *Porites* was less than reported previously, 40 ± 15 on 50 bommies, (Lance, 2012). The finding reinforces conclusions of previous studies that vermetid worms and corals interact negatively.

Complexity in the reef environment is important to attract and retain high biodiversity and subsequently high levels of organismal interactions contributing to a healthy ecosystem (Connell, 1978; Cottenie, 2005). Healthy corals are important to the diversity of the reef habitat and community structure of the ecosystem (Sale, 1977; Naeem, 1998). Coral reef health is affected by a variety of natural and anthropogenic factors (Pratchett *et al*, 2010; Chavanich *et al*, 2015). Antagonistic interactions between *Dendropoma maxima* and *Porites* corals indirectly impact the structural community and habitat of the surrounding reef (Kappner *et al*, 2000). The negative interactions of the vermetid worm *Dendropoma maxima* on corals have cascading effects to the reef community by altering available habitat (Zvuloni *et al*, 2008; Shima *et al*, 2013; Shima *et al*, 2015).

Vermetid worms and corals have an antagonistic relationship, so reduced density of vermetid worms is an opportunity for coral and other reef organisms to flourish. The change in abundance of *Dendropoma maxima* compared to 2014 is a benefit for coral reef diversity across French Polynesia. Increased coral growth in the year since the D. *maxima* die-off suggests that reef complexity and biodiversity is limited by vermetid worm interactions. The insignificant positive correlation ($p>0.05$) between *D. maxima* and coral growth was unexpected because previous research indicates vermetid worm activity deters growth and increases instances of coral death (Shima *et al*, 2010). A likely reason for the insignificant positive correlation was that there was a small sample size for *Porites* coral growth and one outlier that shifted the direction of the slope. The change in abundance of *D. maxima* in 2016 compared to 2014 is a benefit for coral reef diversity across French Polynesia. The results of this study indicate the need for continued long term research on the effects of reduced populations of vermetid worms on corals and how this alters ecosystem structure.

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Figure 1. There was a difference in overall vermetid size with coral type (ANOVA $F_{(2,1388)}$=10.8, p<0.001). The average size of live and dead vermetid worms was different (p<0.001), error bars represent 95% confidence intervals. The average size of all live *Dendropoma maxima* was 0.40 ± 0.01 cm, n=957.

Figure 2. The average size of alive vermetids was 0.40 cm and 0.42 cm on Top and Side quadrats, respectively. The average size of dead vermetids was 0.96 cm and 1.07 cm on Top and Side quadrats, respectively. Error bars represent 95% confidence intervals. ANOVA $F_{(1, 1390)}$=22.3, p<0.00001, Tukey's HSD

Figure 3. There is a positive correlation between the number of live vermetids and number of lesions present on coral bommies. *Porites* corals with more *Dendropoma maxima* had more lesions present than coral bommies with fewer *D. maxima*. Regression analysis: $F_{(1,37)}$ =46.6, p<0.0001, y=0.40964x+0.15966. Residual standard error= 1.266, adjusted R^2=0.5445.

Figure 4. There was a correlation between percent of dead coral areas and number of alive vermetids. Regression analysis: $F_{(1,43)}$ =10.3, p=0.002552, y=9.4658x+0.6237. R^2=0.174.

Figure 5. There is an insignificant positive correlation between coral growth extension and number of alive vermetids. Regression analysis: $F_{(1,36)}$ =0.026, p>0.05, y=2.468657x+0.009303. R^2= -0.02703.

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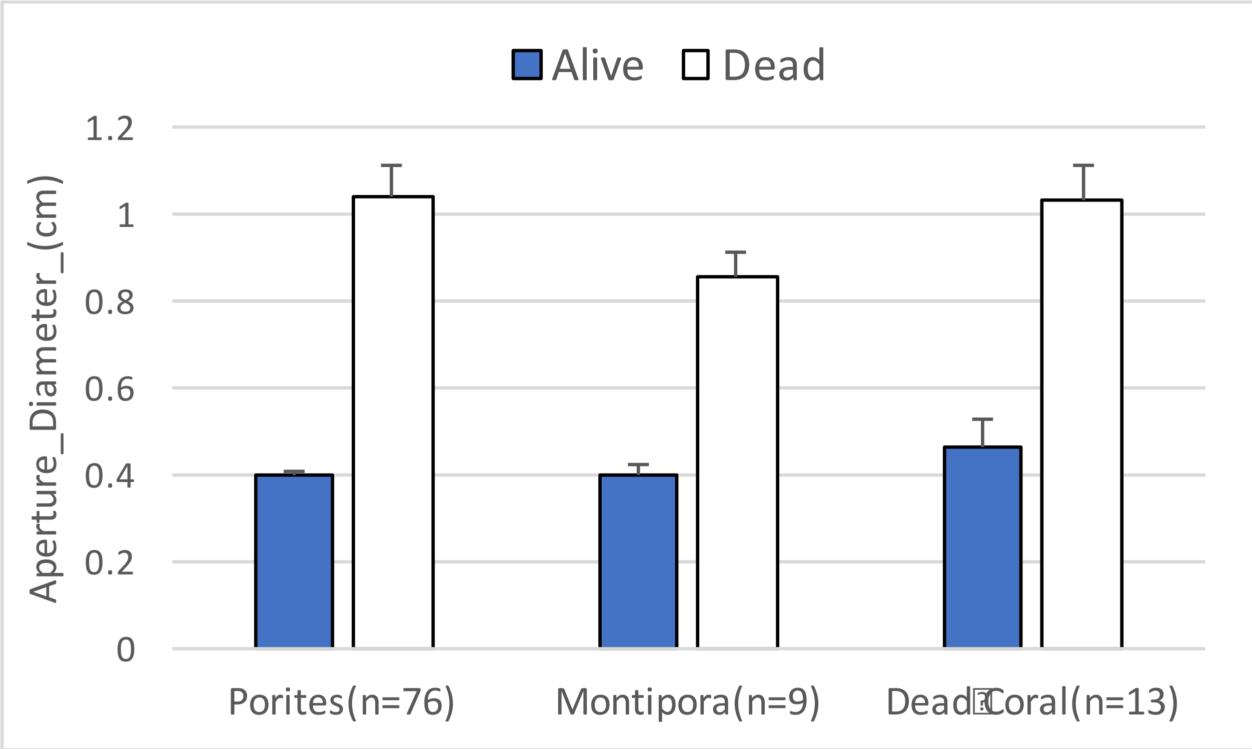
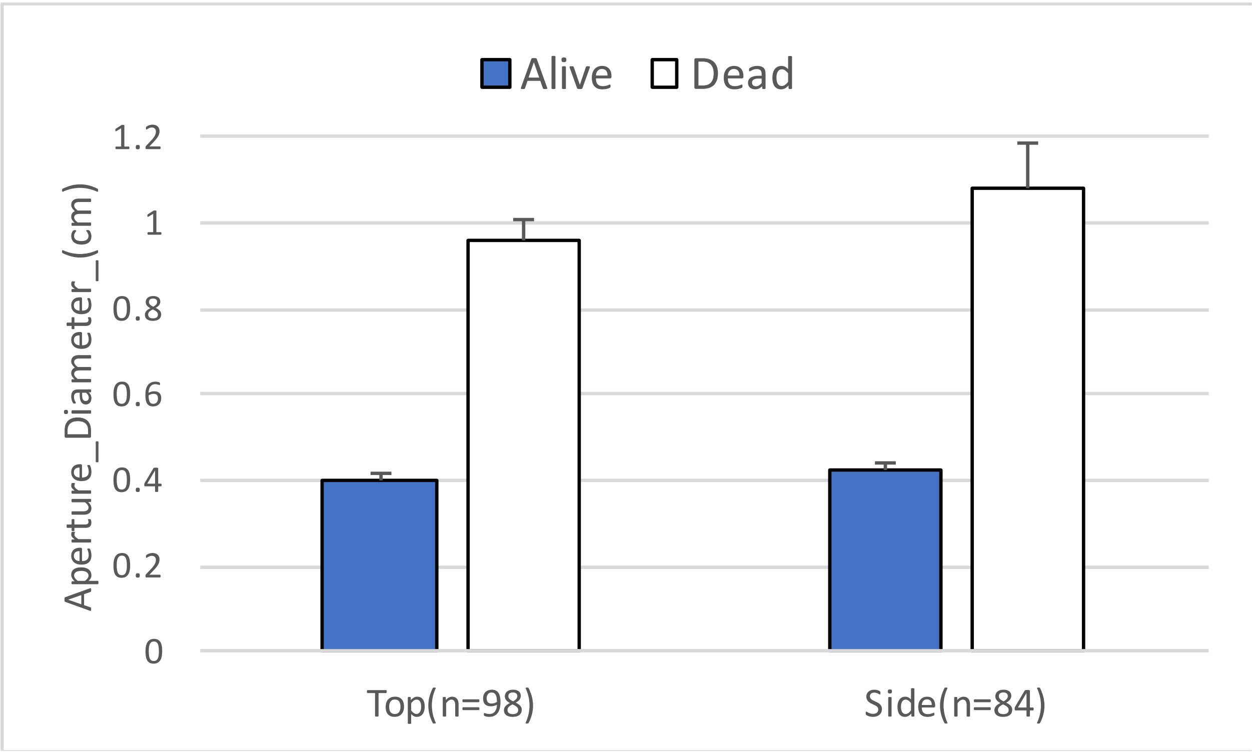

Alive
Dead
1.2
1
0.8
0.6
0.4
0.2
0
Aperture_Diameter_(cm)
Porites(n=76)
Montipora(n=9)
Dead Coral(n=13)


Alive
Dead
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1
0.8
0.6
0.4
0.2
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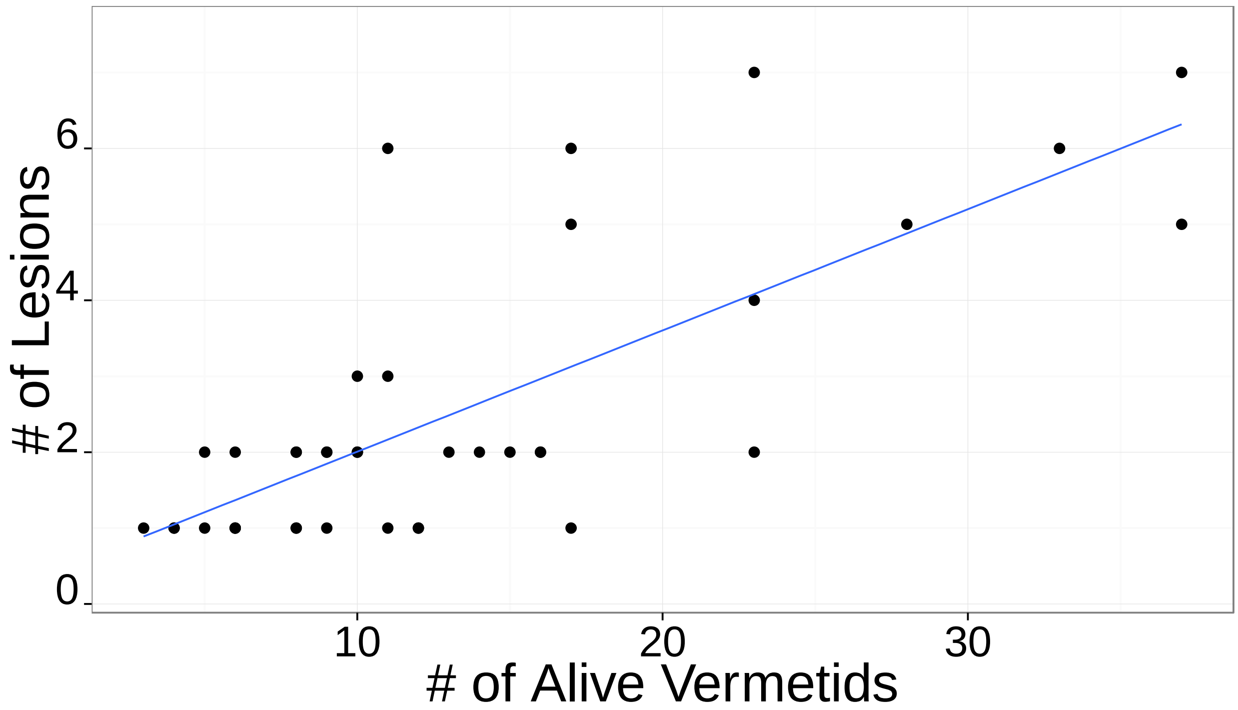
Aperture_Diameter_(cm)
Top(n=98)
Side(n=84)

332



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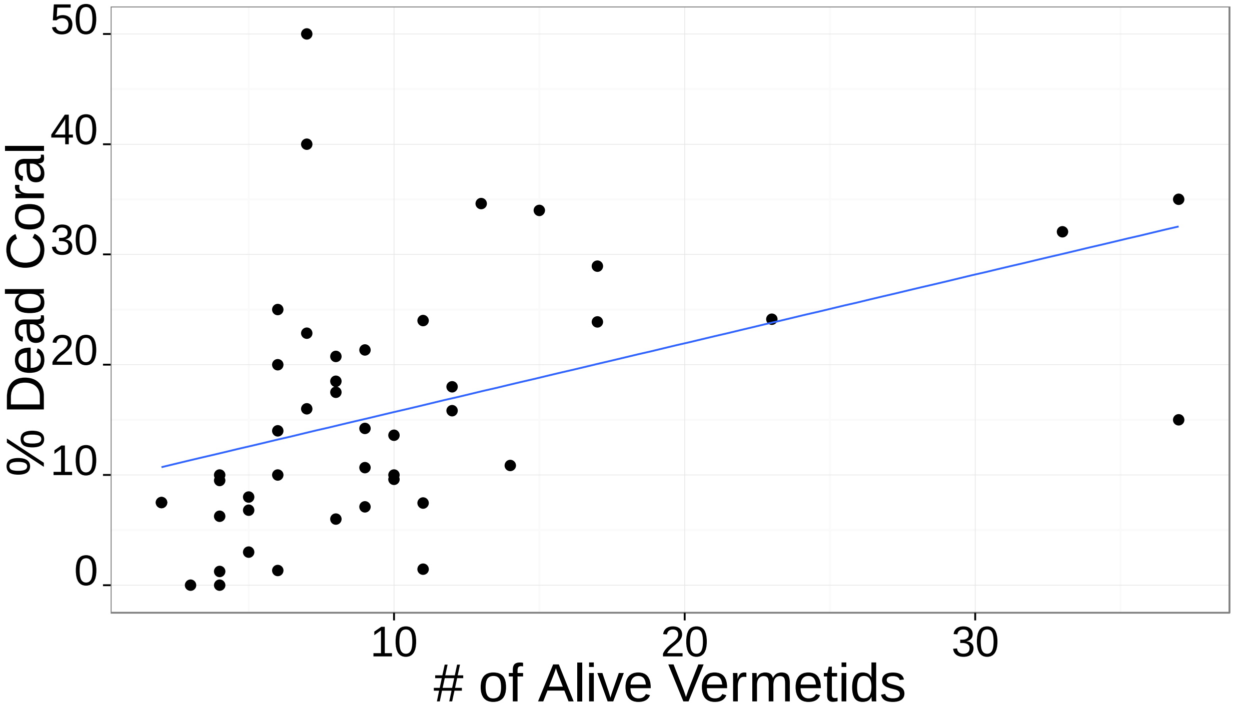

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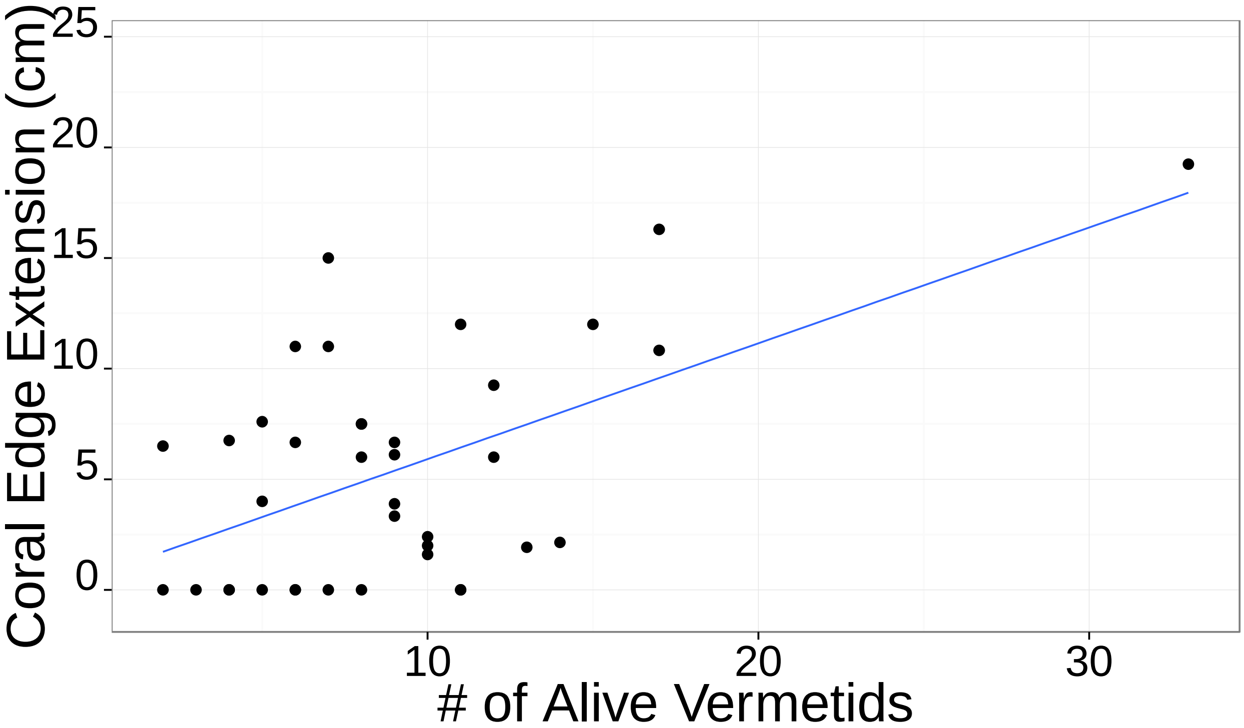
Coral Edge Extension (cm)
25
20
15
10
5
0
10
20
30
# of Alive Vermetids

335