

INFLUENCE OF CURRENT SPEED, SUBSTRATE, AND PLANKTON ON THE DISTRIBUTION OF SUSPENSION FEEDERS IN MO'OREA, FRENCH POLYNESIA

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Abstract. Suspension feeders are sessile marine organisms dependent on plankton and organic particles transported by the water column for food. This study focused on the distribution of four suspension feeders (*Dendropoma maxima*, *Spirobranchus giganteus*, *Heteractis magnifica*, and *Tridacna maxima*) in Mo'orea, French Polynesia based on current, suspended particle abundance, and substrate type. Both *D. maxima* and *S. giganteus* were more frequently present at the site with highest current flow and suspended particle abundance. The positive correlation between current and suspended particle, or food, abundance suggests that a stronger current transports more organic particles to a set location than a weaker current. In comparison, *H. magnifica* and *T. maxima* abundance and occurrence was not related to current. This is because they are less reliant than *D. maxima* and *S. giganteus* on the current for suspension feeding. In comparison, all four species studied showed substrate preference. The distribution of the suspension feeders studied showed varying dependence on current and substrate type. Since suspension feeders regulate primary production by consuming plankton, their distribution and abundance greatly affects marine food chains. Understanding coral reef food chains is vital for comprehending the niche suspension feeders' fill in coral reef ecosystems.

Key words: sessile, filter feeder, water flow, detritus, coral reef, food web, primary production

INTRODUCTION

Marine suspension feeders are mostly sessile organisms that have evolved to capture food highly diluted in the water column (Jorgensen 1980, Gili and Coma 1998). Suspension feeders are widespread across the ocean, from coral reefs to kelp forests, and found in almost all animal classes including bivalves, worms, ascidians, bryozoans, and sponges (Duggins and Eckman 1994). The two main types of suspension feeders include organisms that feed on plankton large enough to be caught individually, such as anemones, and organisms that feed on items obtained by processing the surrounding water, including different worms and mollusks (Gili and Coma 1998). Both types of suspension feeders are important because they regulate primary production and indirectly regulate secondary production, therefore connecting phytoplankton to higher trophic levels in marine food chains (Gili and Coma 1998). To fully understand marine food webs, the energy flow between all trophic levels must be considered (Moloney *et al.* 2011). Suspension feeders' significant role in marine food chains illuminates the importance of studying these unique organisms.

There are multiple factors that influence the distribution of suspension feeders in marine environments. Some of these factors in coral reef environments include substrate type, coral abundance, larvae preference, current flow and particle abundance in the water column (Gili and Coma 1998). In particular, sessile suspension feeders are reliant on current flow for transport and accumulation of food. Studies suggest that stronger currents correlate to greater plankton and detritus abundance, and subsequently greater suspension feeder density (Brolund *et al.* 2004, Ribak *et al.* 2005, Hattori 2006). In addition, many suspension feeders are morphologically adapted to high flow environments, and cannot effectively filter feed without substantial current flow (Zuschin and Piller 1997, Fierce and Campbell 2004, Zuschin and Stachowitsch 2007). Therefore, a stronger current should correlate to higher species density. In addition, studies suggest that substrate type can impact suspension feeder distribution. This is due to larval preference for certain coral species over others (Marsden 1987, Hunte *et al.* 1990, Marsden *et al.* 1990, Nishi and Kikuchi 1996, Hattori 2006). Although there are multiple factors that determine the location of suspension feeders in coral reef environments, current and

substrate type appear to play the dominant roles.

Many studies research how current and substrate type affect individual suspension feeders, yet few investigate the effect on multiple suspension feeders within the same microhabitat. This study expands on the current knowledge of suspension feeders by investigating how current flow, substrate type, and plankton abundance affect four major macro-suspension feeders in Mo'orea, French Polynesia. The four suspension feeders studied were *Dendropoma maxima*, *Tridacna maxima* (small giant clam), *Spirobranchus giganteus* (Christmas tree worm), and *Heteractis magnifica* (magnificent sea anemone).

All four filter feeders are abundant within the coral reefs around Mo'orea. Studying the abundance of these suspension feeders will provide insight to understanding habitat preference. This information will enhance the understanding of coral reef ecosystems, and how different factors, such as current, effects suspension feeder distribution. For this study, suspension feeder abundance was studied at three sites: Temae Beach, Hilton Beach, and Pineapple Beach. Each site represented a different current flow, ranging from high to low current velocity. At each site, the abundance of the four suspension feeders was studied. The hypothesis was that coral reefs with higher current flow transports more plankton and detritus to suspension feeders, and thus increase their abundance. In addition, substrate type was hypothesized to play another, though less potent, role in determining suspension feeder distribution.

To determine why current flow is vital for

D. maxima, a field manipulation was preformed. The manipulation examined mucus net production of *D. maxima* with and without current. For this experiment, the hypothesis was that the production of mucus nets by *D. maxima* without a current is significantly reduced because there is no current to spread out the mucus net and facilitate feeding.

Overall, the distribution of four suspension feeders in Mo'orea was studied to learn more about how current flow, plankton abundance and substrate type contribute to their abundance and location. This knowledge will contribute to future research on coral reef ecosystem and food web dynamics.

METHODS

Study site

The distribution of *S. giganteus*, *D. maxima*, *H. magnifica*, and *T. maxima* was studied on Mo'orea, French Polynesia at three different sites: Temae Public Beach, Hilton Hotel Beach, and Pineapple Beach (Fig. 1). The survey was conducted during October and November 2010.

Temae Public Beach is located in northeast Mo'orea, French Polynesia (17°29'51.12"S, 149°45'29.66"W). The beach is composed of coral-derived sand and has a fringing reef offshore and lagoon along the shoreline. The currents vary from strong to medium-strong, providing an excellent gradient for examining the effects of currents on suspension particle distribution. There is a high abundance of corals, especially *Porites*, *Montipora*, and *Pocillopora*.

Hilton Hotel Beach is located in north-central Mo'orea, French Polynesia at a point between Opunohu and Paopao Bay (17°29'5.82"S, 149°50'42.29"W). The beach, lagoon, and fringing offshore reef are similar to that of Temae. The currents range from medium to medium-weak currents. Therefore, Hilton Beach continues the current flow gradient and provides valuable information on the distribution of filter feeders.

Pineapple Beach is located along the western coast of Mo'orea, French Polynesia near the town of Haapiti (17°32'38.79"S, 149°53'35.88"W). Pineapple Beach has a similar beach, lagoon, and fringing offshore reef as the other two sites. The current varies from medium-strong to medium-weak, and thus represents another site location that measures current variation.

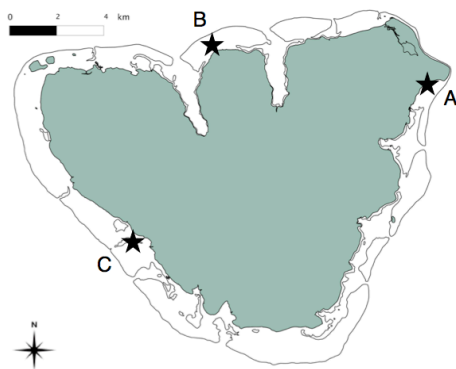


FIG. 1. Locations of study sites. A) Temae Beach, B) Hilton Beach, C) Pineapple Beach.

Study species

The four suspension feeders studied were *Dendropoma maxima*, *Tridacna maxima* (small giant clam), *Spirobranchus giganteus* (Christmas tree worm), and *Heteractis magnifica* (magnificent sea anemone).

D. maxima are marine mollusks that burrow into hard substrates (Fig. 2). *D. maxima* live in calcareous tubes, and secrete a mucus net spread by wave action over the substratum (Hughes and Lewis 1974, Ribak *et al.* 2005, Gagern *et al.* 2008). Plankton and detritus material fall on the web, which is then retracted back and digested by the worm (Kappner *et al.* 2000, Gagern *et al.* 2008). Thus, these suspension feeders not only affect plankton particle abundance, but also impact coral reef food webs by consuming detritus.



FIG. 2. Photograph of *D. maxima*. Photograph taken by Courtney Hann.

Another suspension feeder studied was *T. maxima*, small giant clams, which are small sessile bivalves that embed into hard substrate (Fig. 3). *T. maxima* rely on both their symbiotic relationship with photosynthetic algae and filter feeding for growth and survival (Yonge 1980, Klumpp *et al.* 1991, Ellis 1998). In addition, *T. maxima* require cryptic coral habitats for protection from predators and consistent light exposure for their symbiotic algae (Lucas *et al.* 1989). Therefore, the abundance of *T. maxima* is predominately dependent on current flow and habitat characteristics.

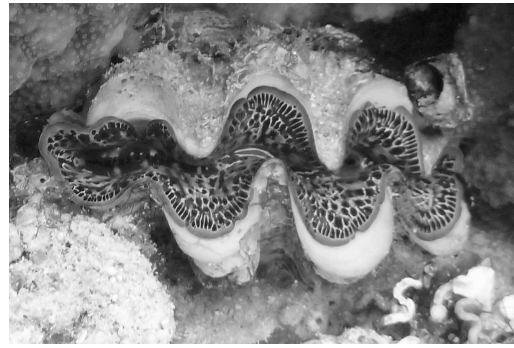


FIG. 3. Photograph of *T. maxima*, small giant clam. Photograph taken by Courtney Hann.

The third suspension feeder studied was *S. giganteus*, Christmas tree worms, which are tropical serpulid polychaetes that live in calcareous tubes on live coral heads (Hunte *et al.* 1990, Dai and Yang 1995) (Fig. 4). *S. giganteus* have two spiraled radiole crowns that each resembles the shape of a “Christmas tree”, which is where the common name is derived from (Fierce and Campbell 2004). The spiraled radiole require external flow to filter plankton for feeding, making the distribution of *S. giganteus* dependent on current flow (Fierce and Campbell 2004). The dispersal of *S. giganteus* is also dependent on larval preference for certain coral substrates (Marsden 1987, Hunte *et al.* 1990, Marsden *et al.* 1990, Nishi and Kikuchi 1996). Overall, studies suggest that *S. giganteus* prefer certain coral substrates and high flow reef environments.

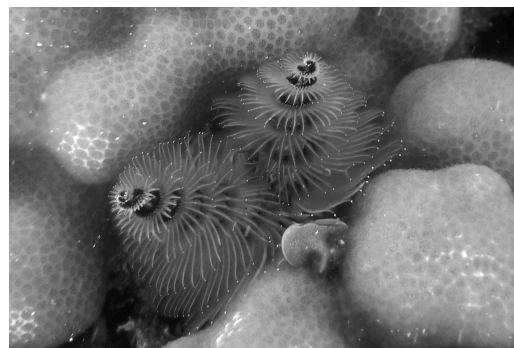


FIG. 4. Photograph of *S. giganteus*, Christmas tree worm. Photograph taken by Courtney Hann.

The fourth suspension feeder studied was *H. magnifica*, giant sea anemones, which are relatively sessile echinoderms that inhabit the

tropical Pacific (Fig. 5). *H. magnifica* feed by capturing plankton, and are relatively sessile, making them dependent on current for the dispersal of plankton prey (Holbrook and Schmitt 2005, Hattori 2006). Current also varies with depth, and studies suggest that *H. magnifica* density and size are positively correlated with depth (Brolund *et al.* 2004, Hattori 2006). Thus, the abundance of *H. magnifica* depends on current flow and depth.

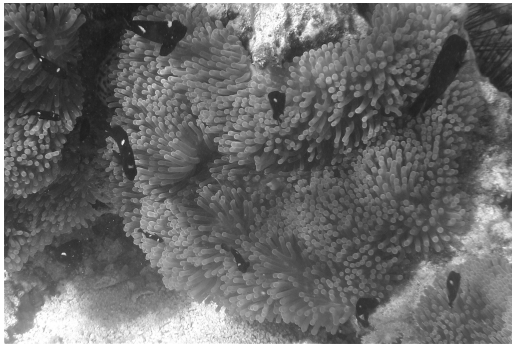


FIG. 5. Photograph of *H. magnifica*, magnificent sea anemone. Photograph taken by Courtney Hann.

Sampling

Several methods were used to investigate what factors determine suspension feeder distribution and abundance. All observations occurred at three field sites: Temae Beach, Pineapple Beach, and Hilton Beach. At each site, five 100 meter transects with ten 0.25 m² quadrats per transect were measured. Their location was randomly chosen using a random number generator. Each quadrat was recorded with a 2007-2008 Garmin Ltd. GPS and a photograph. Temperature was also recorded.

Current and particle abundance

Instantaneous current velocity was measured three times at each quadrat. To measure instantaneous current velocity, a stopwatch was used to record the time it takes a thallus from *Padina boryana* or *Turbinara ornata* to travel 0.25 meters. Both algae, *P. boryana* and *T. ornata*, were used because they are neutrally buoyant in the water, making it feasible to measure the current within the water column. To account for diurnal tidal fluctuations and changing wind velocities, transect and quadrat samples were taken throughout the day and on different days.

Plaster of Paris (clod cards) were used to measure average current velocity (Thompson

and Glenn 1994). Clod cards were placed on the top/front, top/back, bottom/front, and bottom/back of five coral heads at each site. After 24 hours, the molds were collected and weighed. The average current velocity was estimated by comparing the weight before and after.

Plankton tows were used to evaluate plankton and detritus particle abundance at each site. Three plankton tows were taken at each site, and the abundance of plankton and detritus particles was estimated by counting twenty-five randomly determined sub-samples from each sample.

Location on substrate

The species location on a 3D coral structure (top/front, top/back, bottom/front, bottom/back) was recorded. Colored dye was used to determine current direction. Once current was confirmed, the “front” and “back” side of the coral head was determined. The “front” side refers to the side of the coral head that faces the current, and the “back” refers to the opposite side of the coral that does not face the current. Average depth (distance from the organism to the surface) of each species was also measured.

Species distribution

The abundance of all four species (*D. maxima*, *T. maxima*, *H. magnifica*, and *S. giganteus*) was recorded within each quadrat. There were 50 quadrats per site.

Substrate preference

Species abundance on each substrate was recorded to estimate substrate preference. A photograph was taken of any unknown coral substratum, and later identified in the laboratory.

Dendropoma maxima manipulation

To analyze why current flow affects the feeding process of *D. maxima*, a clear glass 0.25 by 0.5 by 0.3-meter aquarium was placed over ten coral heads with one *D. maxima* per coral head. The first ten *D. maxima* that were alone on a coral head that could fit under the clear aquarium were chosen for the experiment. The size of the mucus net with and without the clear box was recorded every 10 minutes, for 30 minutes total, to determine production rate. The mucus net was collected before and after

each manipulation, and then weighed in the laboratory. This information was used to examine the difference in mucus net production with and without current flow.

Statistical analysis

Several analyses were made regarding the affects of current velocity, suspended particle abundance, and substrate type on species distribution. When analyzing current, a one-way ANOVA was used to evaluate the difference in instantaneous current velocity, average current, suspension feeder abundance, and suspended particle abundance between sites (Temae Beach, Pineapple Beach, and Hilton Beach). A one-way ANOVA was used to determine the relationship between suspension feeder abundance with substrate and location on substrate (top/front, top/back, bottom/front, and bottom/back). It was also used to compare the four locations on the substrate with clod card weight differences and species abundance. A linear regression was used to evaluate species abundance compared to suspended particle abundance and current velocity. A linear regression was also used to analyze the relationship between instantaneous current and suspended particle abundance. A t-test was used to compare the presence or absence of each suspension feeder with particle abundance. A Chi-square test was used to analyze the presence or absence of each suspension feeder in relation to site

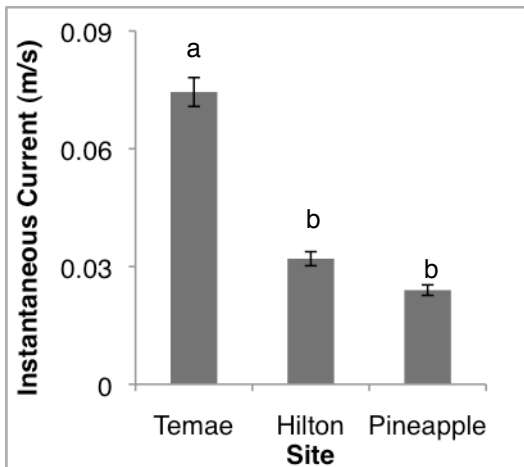


FIG. 6. The average instantaneous current for October through November 2010 at Hilton Beach, Temae Beach, and Pineapple Beach (Mo'orea, French Polynesia). Data are means \pm SE and $n=50$ for each site.

location, substrate, and location on substrate. A Matched Paired Analysis was used to determine the control and experimental difference between mucus net area and weight produced. This was used for two experiments, one with an aquarium present and one without an aquarium present. All data were inputted into Excel. All graphs were made in Excel. JMP software was used for all statistical analyses.

RESULTS

Current and particle abundance

Instantaneous current velocity and particle abundance varied between sites, but average current velocity did not. For example, Temae Beach showed the strongest instantaneous current velocity, followed by Hilton, and then Pineapple (Fig. 6). Between sites, Temae Beach had the strongest instantaneous current velocity (one-way ANOVA, $F_{2,107}=83.30$, $P<.001$). Comparatively, the average current velocity, measured with plaster of Paris clod cards, did not differ between sites (one-way ANOVA, $F_{2,11}=2.19$, $P=0.16$).

Plankton and organic particle abundance was correlated to instantaneous current velocity, and sometimes correlated to the presence of filter feeders (Fig. 7). For instance, particle abundance followed the same trend as instantaneous current such that Temae had greater plankton and organic particle

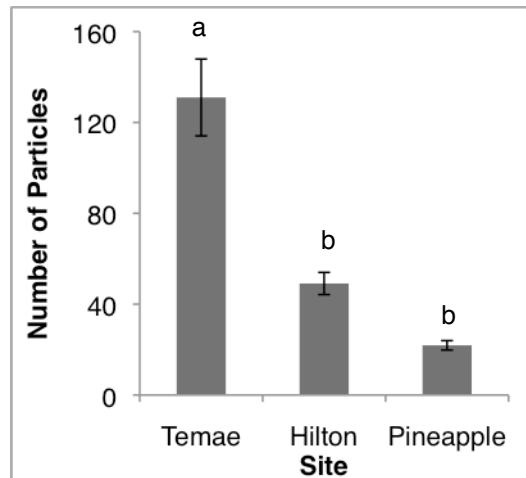


FIG. 7. The average plankton and detritus particle abundance for October through November 2010 at Hilton Beach, Temae Beach, and Pineapple Beach (Mo'orea, French Polynesia). Data are means \pm SE and $n=75$ for each site.

abundance than Hilton and Pineapple (one-way ANOVA; Hilton, $F_{2,222} = 30.89$, $P < 0.001$; Pineapple, $F_{2,222} = 30.89$, $P < 0.001$ respectively). Particle abundance from the plankton tows was positively correlated to instantaneous current velocity (linear regression, $R^2 = 0.08$, $P < 0.001$). Consequently, particle abundance was positively correlated to the presence of *D. maxima* (t-test, $t_{126.38} = 3.83$, $P < 0.001$) and *S. giganteus* (t-test, $t_{27.74} = 2.66$, $P = 0.01$), and the abundance of *D. maxima* (linear regression, $R^2 = 0.10$, $P < 0.01$).

Location on substrate

Although current does not differ based on location, certain locations on the coral head, such as the top, correlate to greater species abundance (Fig. 8). Current does not differ based on location because the change in weight of the plaster of Paris clod cards was not significantly different (one-way ANOVA, $F_{3,50} = 2.53$, $P = 0.07$). When examining the relationship between suspension feeders, *D. maxima* were more abundant at the top/front over the bottom/front and bottom/back (one-way ANOVA; bottom/front $F_{3,340} = 4.85$, $P < 0.01$; bottom/back $F_{3,340} = 4.85$, $P = 0.02$). The presence of *D. maxima* did not vary between coral head locations (one-way ANOVA,

$F_{3,340} = 2.44$, $P = 0.06$). *S. giganteus* were also more abundant at the top/front over the bottom/front of the coral head (one-way ANOVA, $F_{3,92} = 3.19$, $P < 0.05$). In addition, the presence of *S. giganteus* was greater at the top/front over the top/back, bottom/back, and bottom/front (one-way ANOVA; top/back $F_{3,92} = 5.17$, $P < 0.01$; bottom/back $F_{3,92} = 5.17$, $P < 0.01$; bottom/front $F_{3,92} = 5.17$, $P = 0.03$ respectively).

In correlation, both the abundance and presence of *T. maxima* was greater at the top/bottom of the coral head over the bottom/front or bottom/back (one-way ANOVA; bottom/front abundance, $F_{3,80} = 3.70$, $P = 0.02$; bottom/back abundance, $F_{3,80} = 3.70$, $P = 0.03$; bottom/front presence or absence $F_{3,80} = 4.06$, $P = 0.01$; bottom/back presence or absence $F_{3,80} = 4.06$, $P = 0.03$). Unlike the other three suspension feeders, the abundance of *H. magnifica* did not vary between coral head locations (one-way ANOVA, $F_{3,8} = 0.91$, $P = 0.48$). The presence of *H. magnifica* also did not vary between coral head locations (one-way ANOVA, $F_{3,8} = 0.33$, $P = 0.80$).

Species distribution

Abundance differed among the four

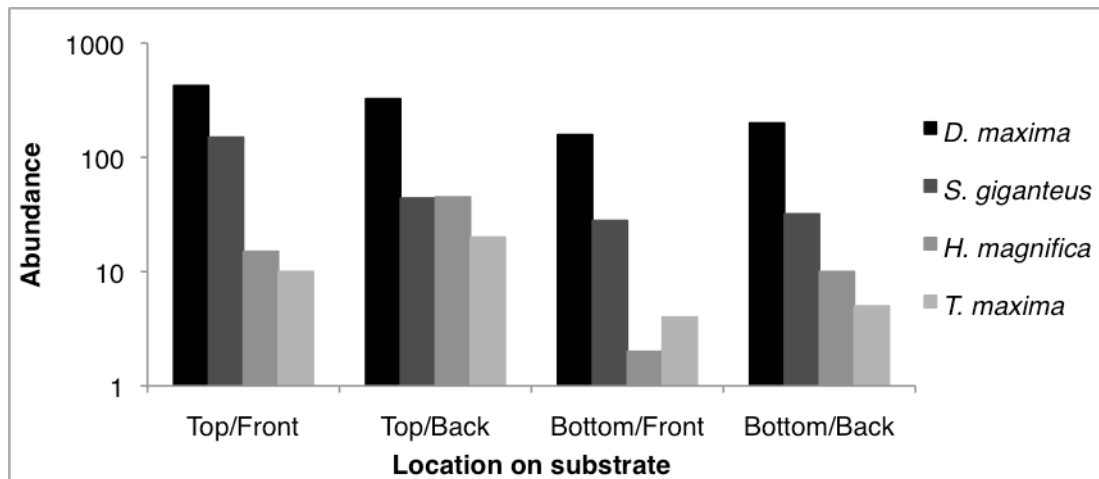


FIG. 8. The species abundance (number of individuals) on various coral head location (top/front, top/back, bottom/front, and bottom/back) for October through November 2010 at Hilton Beach, Temae Beach, and Pineapple Beach (Moorea, French Polynesia). Abundance (y-axis) scale is logarithmic. For each site, $n=50$ for quadrats recorded. "Top" refers to the top half of the coral head, versus "bottom" refers to the bottom half of the coral head. The "front" refers to the side of the coral that faces the current, versus the "back" refers to the opposite side that does not face the current.

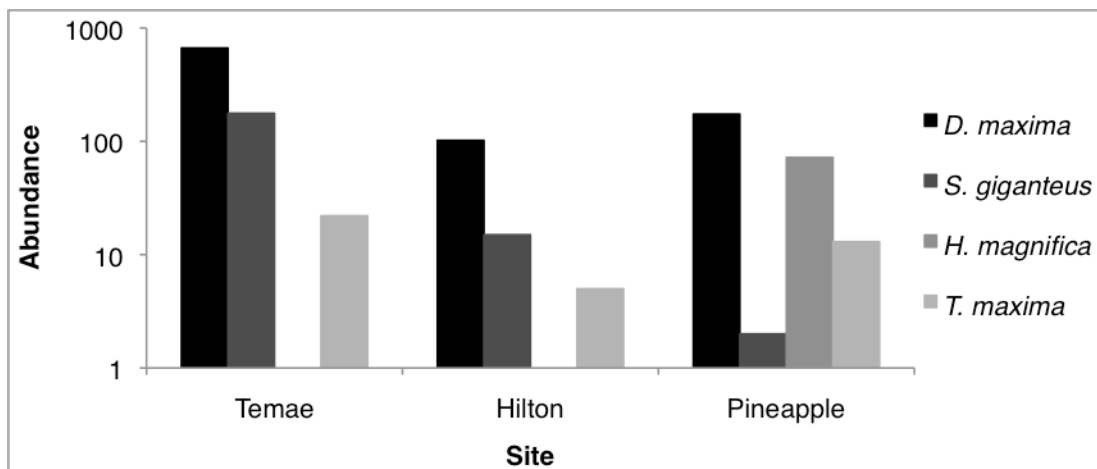


FIG. 9. The abundance (number of individuals) of four filter feeders (*D. maxima*, *S. giganteus*, *H. magnifica*, and *T. maxima*) for October through November 2010 at Hilton Beach, Temae Beach, and Pineapple Beach (Mo'orea, French Polynesia). Abundance (y-axis) scale is logarithmic. For each site, n=50 for quadrats recorded.

species examined at the three different sites (Fig. 9). The abundance of *D. maxima* and *S. giganteus* was not randomly distributed across sites (Chi-Square; *D. maxima*, $DF = 2$, Chi-Square = 9.63, $P = 0.008$; *S. giganteus*, $DF = 2$, Chi-Square = 18.38, $P < 0.001$). The abundance (number of individuals) of *D. maxima* was significantly greater at Temae Beach over both Hilton and Pineapple Beach (one-way ANOVA; Hilton, $F_{2,78} = 3.91$, $P = 0.02$;

Pineapple, $F_{2,78} = 3.91$, $P = 0.02$). *T. maxima* showed no preference for any site (Chi-Square, presence or absence, $DF = 2$, Chi-Square = 2.02, $P = 0.36$; one-way ANOVA, abundance $F_{2,19} = 1.61$, $P = 0.23$). *H. magnifica* was only present at Pineapple Beach. Overall, the abundance of suspension feeders was not randomly distributed across sites and was generally greatest at Temae Beach (Figure 5).

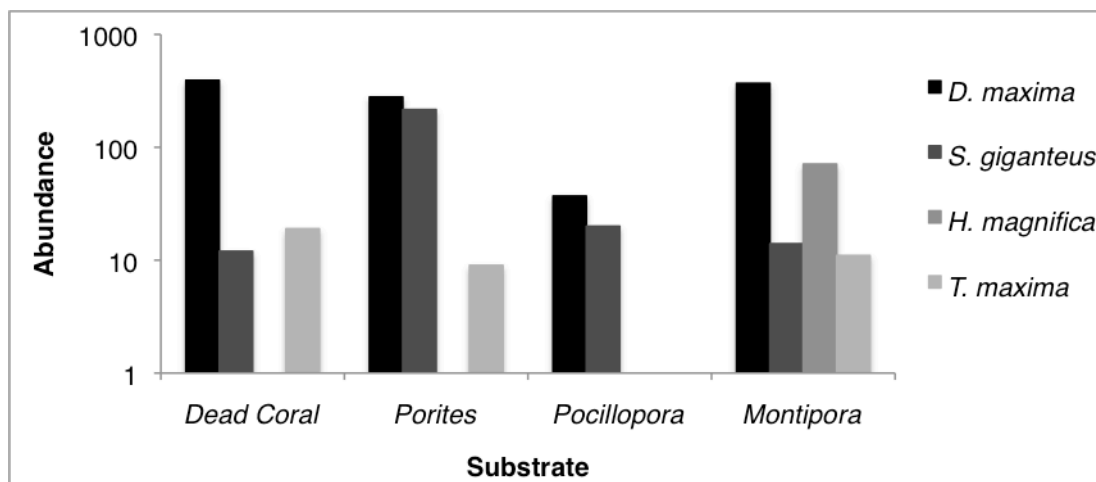


FIG. 10. The abundance (number of individuals) of four filter feeders (*D. maxima*, *S. giganteus*, *H. magnifica*, and *T. maxima*) on different coral substrates (dead coral, *Porites*, *Pocillopora*, and *Montipora*). This data was taken from October through November 2010 at Hilton Beach, Temae Beach, and Pineapple Beach (Mo'orea, French Polynesia). Abundance (y-axis) scale is logarithmic. For each site, n=50 for quadrats recorded.

Substrate preference

Different species showed distinctive preferences for substrate types (Fig. 10). Of the four species, the presence of *D. maxima*, *S. giganteus*, and *T. maxima* were correlated to specific substrates. The abundance of *D. maxima* was significantly greater for dead coral, *Montipora*, and *Porites*. For instance, the observed distribution of *D. maxima* presence across dead coral, *Porites*, and *Montipora* was not random (Chi-square; Dead Coral, Chi-square = 7.11, $P < 0.01$; *Porites*, Chi-square = 5.08, $P = 0.02$; *Montipora*, Chi-square = 12.40, $P < 0.001$). Yet, the abundance of *D. maxima* was greater for dead coral, *Montipora*, and *Porites* (one-way ANOVA; Dead Coral, $F_{6,581} = 14.00$, $P < 0.001$; *Porites*, $F_{6,581} = 14.00$, $P < 0.001$; *Montipora*, $F_{6,581} = 14.00$, $P < 0.001$).

Similarly, the presence of *T. maxima* was not random on dead coral (Chi-square, $DF = 3$, Chi-square = 16.74, $P < 0.001$). Yet, the abundance was greater on dead coral, *Porites*, and *Montipora* (one-way ANOVA; Dead Coral, $F_{6,140} = 11.23$, $P < 0.001$; *Porites*, $F_{6,140} = 11.23$, $P < 0.001$; *Montipora*, $F_{6,140} = 11.23$, $P < 0.001$).

The presence of *S. giganteus* was not randomly distributed on *Porites* (Chi-square, $DF = 4$, Chi-square = 7.70, $P = 0.006$). The

abundance of *S. giganteus* did not vary between substrates (one-way ANOVA, $F_{6,147} = 8.62$, $P = 0.86$). In addition, the presence of *H. magnifica* was not randomly distributed on *Porites* and *Montipora* (Chi-square; *Porites*, $DF = 1$, Chi-square = 12.65, $P < 0.001$; *Montipora*, $DF = 1$, Chi-square = 21.22, $P < 0.001$). Overall, the presence of three of the four species was dependent on a specific substrate, yet only *D. maxima* and *T. maxima* showed a greater abundance with specific substrates.

Dendropoma maxima manipulation

In the field manipulation, *D. maxima* mucus net production did not vary without an aquarium, but did when an aquarium was present and preventing current flow (Fig. 11 and 12). Mucus net area production did not change when there was not an aquarium present yet was smaller when there was an aquarium blocking the current (Matched Paired Analysis; No Aquarium, $t_9 = -0.07$, $P = 0.95$; Aquarium Present, $t_9 = -2.20$, $P = 0.05$). In comparison, the weight of the mucus net collected before and after each experiment was also different when an aquarium was present (Figure 6). When an aquarium was not present, the final weight of the mucus net did not change from the control weight (Matched

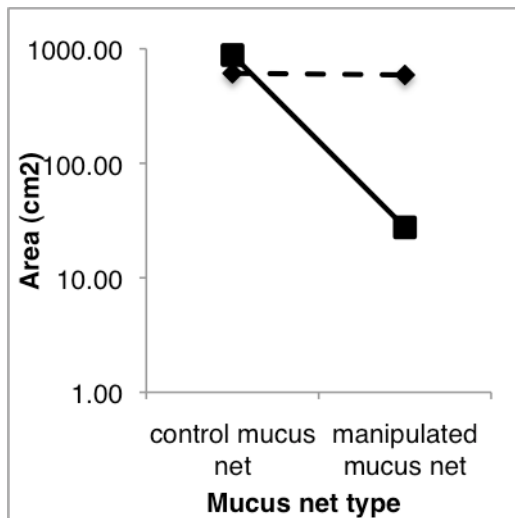


FIG. 11. Average change in mucus net area produced by *D. maxima* with an aquarium present (solid line) versus without an aquarium (dashed line). This data was taken from October through November 2010 at Hilton Beach, Temae Beach, and Pineapple Beach (Mo'orea, French Polynesia). There were ten mollusks used ($n=10$) for both manipulations.

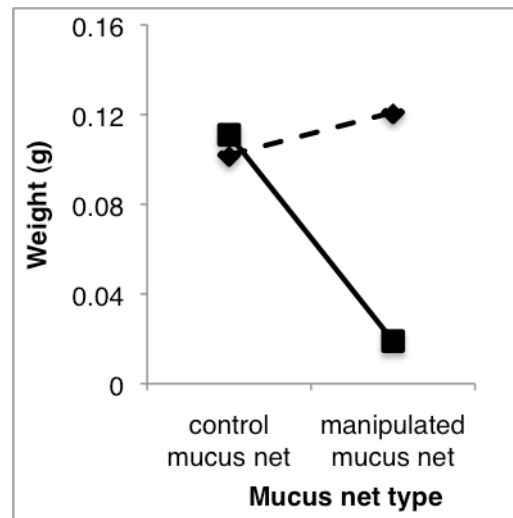


FIG. 12. Average *D. maxima* mucus net weight with an aquarium present (solid line) versus without an aquarium (dashed line), with $n=10$ for each manipulation. This data was taken from October through November 2010 at Hilton Beach, Temae Beach, and Pineapple Beach (Mo'orea, French Polynesia).

Paired Analysis, $t_9 = 1.50$, $P = 0.17$). The weight of the final mucus net produced under an aquarium was less than that of the control (Matched Paired Analysis, $t_9 = -4.60$, $P = 0.001$).

DISCUSSION

In this study, I examined the factors responsible for distribution of suspension feeders in the shallow coral reef system. I found that current velocity positively correlates to the likelihood of two suspension feeders, *D. maxima* and *S. giganteus*, being present, and that substrate type affected the distribution of all suspension feeders. A higher current velocity also correlated to greater food abundance, including suspended phytoplankton, microorganisms, and detritus. Also, three of the four suspension feeders were more likely to be distributed on the top of coral heads, versus the bottom. In addition, my field experiment demonstrated the reliance of *D. maxima* on a current for spreading out its mucus net. These findings contribute to the understanding of which factors influence the distribution of suspension feeders, which play a vital role in regulating primary production within the coral reef ecosystem. Past studies have demonstrated primary production regulation by suspension feeders, such as the ribbed mussel *Geukensia demissa* and suspension feeders in the Bay of Biscay (Peterson *et al.* 1985, Leloch *et al.* 2008).

The main differences between the sites were instantaneous current velocity and suspended particle abundance. Instantaneous current and suspended organic particle abundance was greatest at Temae Beach, and not significantly different between Hilton and Pineapple Beach. This suggests that a stronger current correlates to a higher transport of suspended particles, which provides food for suspension feeders. These results are consistent with past studies relating higher current flow to greater suspended particle abundance (Wildish and Kristmanson 1979, Frechette *et al.* 1989). The lack of significant correlation to the plaster of Paris clod card measurements of current could have been from different storm and wind patterns when the clod cards were taken. Another study that used clod cards to measure current in Jamaican coral reefs encountered the same problem, where the differences in current were too small and dependent on daily wind fluctuations to show a significant difference

(River and Edmunds 2001). Because instantaneous current was measured over a 6-week period, the results represent a better average of current strength at each site. Thus, the rest of the data were compared to the instantaneous current measurements.

When examining the location of suspension feeders on their substrate, three of the four suspension feeders were more frequently present on the top of coral heads compared to the bottom. The clod card measurements of current did not vary with regards to location on the coral head, therefore these suspension feeders may favor the top of the coral heads for other reasons. These reasons could include a shallower depth, greater sun exposure, or enhanced exposure to organic particles. In addition, the current difference between the top and bottom of the coral head may not have been substantial enough to be recorded with the clod cards and may have been affected by external factors such as wind or storms.

D. maxima were more abundant at the top/front of the coral head than either the bottom/front or bottom/back of the coral head. This suggests that the top/front of the coral head, the area most exposed to incoming currents and generally at the shallowest depth, poses some advantage to this marine gastropod. This could be due to greater organic particle fall onto the organism's mucus nets, making suspension feeding more efficient and enhancing the organism's survival. This supports past studies that emphasize the importance of plankton and detritus particle abundance for mollusk survival (Gagern *et al.* 2008).

S. giganteus was also more abundant and more frequently present at the top/front than the bottom/front of the coral heads. *S. giganteus* preference for the top and front is consistent with past studies in Mo'orea (Song 2006). This greater abundance is most likely due to greater particle abundance. Higher suspended particle abundance enhances the feeding rates, and thus survival rates of *S. giganteus* (Fierce and Campbell 2004). This is supported by a study from South Africa that found a greater abundance of the worm on elevated coral heads (Floros *et al.* 2005).

Similarly, *T. maxima* also preferred the tops of the coral heads. The presence and abundance of *T. maxima* was probably greater at the top/back of the coral head over the bottom/front or bottom/back due to greater exposure to organic particles. This is important because *T. maxima* depend on

suspended organic particles for suspension feeding. In addition, when residing on top of the coral head, *T. maxima* receive more sunlight, which is important for the clam's symbiotic algae (Ellis 1998). The symbiotic algae, zooxanthellae, conserve and recycle essentially all nitrogen required for *T. maxima* tissue growth and metabolism (Hawkins and Klumpp 1995). Therefore, the clam's dependence on suspended particles and light for zooxanthellae make it advantageous for the organism to live at the top of a coral head. This is similar to other suspension feeding organisms that have a symbiotic relationship with zooxanthellae, such as *Plexaura homomalla* and *P. nina*, who are more abundant at shallower water depths, and therefore at the top of coral heads, than at deeper depths (Lasker *et al.* 1983). However, *H. magnifica* showed no coral head location preference. This contradicts past studies in which *H. magnifica* density and size are positively correlated with depth (Brolund *et al.* 2004; Hattori 2006). Perhaps this difference is due to the small number of *H. magnifica* recorded (n=72) in only three quadrats.

The suspension feeders' dependence on suspension feeding for survival determined how reliant they were on current, and therefore site location. For instance, both *D. maxima* and *S. giganteus* were more frequently present at Temae where there is a greater current flow. Both of these suspension feeders are solely dependent on the water column for feeding. *D. maxima* requires a current to spread its mucus net for suspension feeding (Ribak *et al.* 2005), while *S. giganteus* requires a strong current for efficient filter feeding (Fierce and Campbell 2004). In addition, since greater suspended particle availability facilitates suspension feeder feeding (Lesser *et al.* 1994), *D. maxima* and *S. giganteus* may prefer a high current site. A study showed that sessile marine polychaetes, *Pseudopolydora paucibranchiata* and *P. kempji japonica*, ingest fewer large particles, and more small particles, in fast flow than they did in slow flow environments (Shimeta and Koehl 1997). Therefore, high flow environments are more advantageous for smaller suspension feeders, and less relevant for larger suspension feeders. This is presumably why the two smaller suspension feeders, *D. maxima* and *S. giganteus*, were more prevalent at the high flow site, while the larger suspension feeders, *T. maxima* and *H. magnifica* were not. *T. maxima* had no site preference, while *H. magnifica* was only present at Pineapple Beach,

which had a lower current velocity than Temae Beach. The lack of correlation of *T. maxima* with current could be due to the organism's reduced dependence on filter feeding with age (Klumpp *et al.* 1991). The greater abundance of *H. magnifica* at the low flow site contradicts past studies on sea anemone distribution. For example, the frilled sea anemone, *Metridium senile*, grows faster at higher flow sites due to greater food consumption and lower respiration rates (Lesser *et al.* 1994). *H. magnifica* recorded at Pineapple Beach can be compared to *M. senile*, which does not have a symbiotic fish, because all *H. magnifica* recorded did not have symbiotic fish. Therefore, perhaps the distribution of *H. magnifica* was only present at the low flow site due to the small number of *H. magnifica* recorded (n=72).

Each suspension feeder exhibited preference for specific substrate types. Both *D. maxima* and *T. maxima* were more abundant on dead coral, *Montipora*, and *Porites* over other coral substrates. Their relatively broad distribution suggests that neither species especially favors one substrate over the other. *D. maxima* require substrate to spread for its mucus net to attach to (Zuschin and Stachowitsch 2007). Therefore, perhaps the size of the coral head is more important than the particular coral species, thought this was not examined in this study. The large and abundant *Porites* coral heads and common encrusting *Montipora* would therefore provide optimum habitat for *D. maxima*. In comparison, *T. maxima* use coral for camouflage (Lucas *et al.* 1989), suggesting that live coral should be preferred over dead coral. In addition, because *T. maxima* embeds into coral, a flatter surface, such as one present on *Porites* and *Montipora*, would be preferred over a branching surface, such as *Acropora*. This is evident by the greater abundance of the clam on *Porites* and *Montipora*. Surprisingly, both *T. maxima* and *D. maxima* also preferred dead coral. This could be due to the fact they can survive on dead coral (Zuschin *et al.* 2001) or because the coral that today is dead was alive when the organisms originally embedded themselves. In comparison, *S. giganteus* was more often present on *Porites* than any other coral species. This preference is most likely due to larval preference for specific coral species. Studies suggest that *S. giganteus* prefers certain coral species to others, including two *Porites* corals, *P. lutea* and *P. lobata*, that are present at all three sites (Dai and Yang 1995, Nishi and Kikuchi 1996).

In comparison, *H. magnifica* was only present on *Montipora* and *Porites*. This is most likely due to the high abundance of *Montipora* and *Porites* at Pineapple Beach, the only site that *H. magnifica* was present. In addition, since no studies suggest substrate preference of *H. magnifica*, the larval distribution and depth most likely contribute to the distribution of *H. magnifica*. This correlates to studies of other anemones, such as the giant sea anemone *Actiniaria*, whose distribution is due to variation in water temperature, current, and depth (Richardson *et al.* 1997). Overall, substrate preference is an important factor for determining the distribution of *T. maxima*, *D. maxima*, and *S. giganteus*.

For *D. maxima*, the field manipulation demonstrated that mucus net area and weight produced in the absence of a current, when an aquarium was present, was smaller than when a current was present. This agrees with previous studies, which suggest that *D. maxima* utilize current for spreading out its mucus net (Hughes and Lewis 1974, Ribak *et al.* 2005). Consequently, a stronger current can spread the mucus net further, allowing more detritus and organic particles to fall on the net. This is why mucus nets produced with a current weighed more. Therefore, the presence of *D. maxima* is greater at Temae Beach, where the current is stronger and can facilitate in mucus net spreading.

To further understand the role of suspension feeders in coral reef food webs and ecosystems, future studies should focus on morphological differences in suspension feeders at various currents. For instance, *S. giganteus* seem to be larger and have a slower crown reaction time at low current sites. In addition, *D. maxima* tube diameter appeared smaller at low flow environments. This is possibly due to smaller mucus nets produced with a weaker current. This would provide more information on how current flow effects suspension feeder growth and survival. In addition, it would be important to examine community composition of suspension feeders with different current levels. This would provide insight into inter-species competition for preferred substrates and plankton availability. Overall, researching differences in suspension feeders' morphological and community composition with varying current levels would be important for understanding the ecological role of each suspension feeder. It would provide insight into what niche each species fills and enhance the present knowledge of coral reef ecosystems.

In conclusion, suspension feeders that are morphologically dependent on the water column for feeding, such as *D. maxima* and *S. giganteus*, are more frequently present at the site with the strongest current. A stronger current correlates to more plankton and detritus particles. In addition, substrate type plays a significant role for all suspension feeders studied. This is most likely due to larval preferences and coral species abundance, depth, size, and degree of camouflage provided. Therefore, both current flow and substrate affect the presence of suspension feeders and subsequently their effects on primary production of phytoplankton. Where stronger currents provide higher food quantity and more of the preferred coral species are present, suspension feeders are more abundant. Therefore, changes in current flow and nutrients would affect the pathways of energy flow and the survival of suspension feeders. The abundance of each suspension feeder affects the amount of plankton and detritus material taken out of the food web, which in turn regulates primary production (Gili and Coma 1998). As a result, suspension feeders are an important component of coral reef food webs.

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