# Canopy Effects of Octocoral Communities on Sedimentation: Modern baffles on the shallow-water reefs of St. John, USVI

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**Keywords:** Canopy, Animal forest, Sedimentation, Caribbean, Gorgonian, Clod card

## Abstract:

Recent shifts in the presence and abundance of species on shallow Caribbean coral reefs have left octocorals as the dominant functional group on some reefs, creating an “animal forest” with an associated canopy. This transition changes the reef profile potentially affecting flow and sedimentation. We examined the effects of an octocoral forest on the depositional environment on a shallow-water fringing reef system on the south shore of St John, USVI. The depositional environment was characterized as canopy or non-canopy based on octocoral density. The effect of the octocoral canopy on flow and sedimentation was assessed using clod cards and sediment traps at 15 paired locations. The octocoral canopy altered flow resulting in greater levels of turbulence within the canopy. Sediment traps in areas of dense octocoral canopy accumulated greater amounts of sediment, with coarser, more rounded grains. Organic content of sediments collected in the traps was greater within the canopy than outside of it. The increase in turbulence within the canopy was likely due to wave driven oscillatory flow interacting with the octocoral colonies. Sediment traps in the canopy likely had greater sediment accumulation due to both resuspension of sediments from within the canopy and deposition of imported sediments as flow decreased within the canopy. The presence of octocoral canopies and the reworking of sediment within them may affect the success of settling larvae and the evolution of reef structure.

## Introduction:

Although most attention has been focused on the interplay between scleractinian corals and macroalgae (Hughes 1994; Bruno et al. 2009; Roff and Mumby 2012), Caribbean coral reefs have also undergone shifts in the abundance of sessile macroinvertebrate other than scleractinians (Norström et al. 2009; Ruzicka et al. 2013; Edmunds and Lasker 2016; Sánchez et al. 2019). Among these shifts, octocoral species at some sites have increased or maintained their abundance (Ruzicka et al. 2013; Lenz et al. 2015; Tsounis and Edmunds 2017) while scleractinian species have experienced declines in population density. Octocorals now dominate some of these systems forming animal forests, living three-dimensional structures, that have canopies analogous to those of terrestrial forests (Rossi et al. 2012; Guizien and Ghisalberti 2016). Given the apparent resilience of octocorals, there is a growing need to understand how octocoral forests alter their environment. Studies of flow over and through scleractinian coral reefs have found that oscillatory flow over a reef structure increases mixing within its canopy (c.f., Reidenbach et al. 2007; Lowe et al. 2008). However, unlike scleractinians, octocorals are flexible and likely to have different canopy effects on resuspension and local deposition of sediments. This research focused on understanding the effects these modern octocoral forests have on the depositional environment.

Canopies have the ability to alter flow structure and depositional patterns. Flow through a canopy is affected by the density and morphology of individuals that compose it. The presence of a canopy in the turbulent boundary layer reduces flow, and if dense enough, creates a shear zone with an inflection point in flow speed just above the canopy that can cause flow instability and generate canopy-scale turbulence that may reach the substratum (Nepf and Vivoni 2000; Nepf 2012; Guizien and Ghisalberti 2016). This change in flow velocity within the shear zone increases mixing at the top of the canopy (Nepf 2012). Some marine canopies, such as seagrass beds, have an inflection point within their shear layer; canopy scale turbulence may not reach the substratum in these systems due to their density, thus reducing resuspension (Nepf 2012). The densest of octocoral canopies differ from seagrass beds in that typically, they are not as dense, and canopy-scale turbulence may reach the substratum.

In habitats dominated by unidirectional flow, sediments carried over the reef that enter the shear zone may enter the canopy through vertical turbulent diffusion. The effect is more complex in systems characterized by wave-driven oscillatory flow (Guizien and Ghisalberti 2016), which applies to many reef environments. Oscillatory flow leads to greater water movement within the canopy than occurs in a unidirectional flow environment (Lowe et al. 2008), and wave driven flow is associated with greater turbulence (Koehl and Powell 1994).

We characterized relative water flow and sedimentation within and outside of the octocoral canopy on a shallow water reef system on St. John, USVI. If areas of dense canopy alter flow patterns (Fonseca et al. 1983; Eckman 1987; Fonseca and Cahalan 1992), then sedimentation rate in those areas may increase (Scoffin 1970; Ward et al. 1984) along with differences in grain size (Ginsberg and Lowenstam 1958; Lynts 1966; Granata et al. 2001) and the organic content of the deposited sediments (Burrell and Schubel 1977). Such affects can have implications for sedimentation on modern reefs, on the associated community and in interpretations of ancient sedimentary regimes.

## Methods:

Research was conducted along the southern shore of St. John, USVI parallel to the eastern shore of Grootpan Bay. The study area, referred to as East Cabritte in other publications (see Fig 1 in Tsounis et al. 2018), is a fringing reef with an abundant animal forest. Water flow is predominantly wave-driven. The sediments in Grootpan Bay likely have minimal terrestrial input. The watershed of the bay is within the Virgin Islands National Park. There is no development within the park, and a salt pond and mangroves inland of the bay act as a settlement pond for drainage from the watershed.

Sedimentation and hydrodynamic regime were measured using sediment traps and clod cards attached to cement bases (henceforth bases) positioned either within or outside of the canopy (Fig 1 and 2). Bases were spread along the East Cabritte study area over approximately 100 m. Depth of the bases ranged from 7-9 m. Fieldwork was conducted between June and August 2018, and was broken into 6 data collection periods, or deployments. Deployments were planned to last 6 days, but the first deployment lasted 10 days due to sea states that precluded field work.

Positioning of the sediment traps and clod cards was based on a visual assessment of the octocoral canopy. Areas with 12 or more octocorals present within 1 $m^2$ were classified as canopy and those with less were classified as non-canopy. The cutoff density for canopy was based on preliminary data suggesting that the depth vs. water velocity profile shows an inflection point at a canopy density of 12 colonies per $m^2$ or more (L. Bramanti, personal communication, see also Figure 1 in Nepf, 2012 for an example of such a profile). Fifteen paired canopy and non-canopy locations were selected. Within each pair, bases were an average of 3.75 m apart (range, 1.9-6.2 m). Density of octocorals above 10 cm tall was recorded in the four 1 $m^2$ quadrats surrounding each base.

**Clod Cards:** Hydrodynamic regime was assessed using clod cards (Doty 1971). Dissolution rates of clod cards are related to mass transfer (Jokiel and Morrissey 1993), and thus integrate the effects of net flow and turbulence over time. Using dissolution rate as an indicator of water movement was first proposed by McConnel and Sigler (1959). Clod cards used in this study were rectangular solids made with dental plaster (Gibralter Green Dental Die Stone). Dental stone undergoes slower dissolution than plaster of Paris due to its lower porosity.

Clod cards were made to be approximately 225 g using a ratio of 5.25 g of die stone to 1 g of water. The mixture was poured into cubic silicone molds, and the head of a stainless-steel screw was placed in each to facilitate attachment in the field. After removal from the molds, the clod cards were dried to a constant mass in a drying oven at 50° C. Initial mass of the clod cards averaged 227.18 ± 15.45 g (mean ± SD). Clod cards were manufactured in multiple batches, due to the speed at which the dental plaster sets. The clod cards from the different batches were distributed randomly across bases and treatments.

Once completely dry, clods were weighed and attached to a plastic petri dish with glue (Gorilla glue™). The cap from a plastic water bottle was attached to the bottom of the petri dish with a washer and nut, and the clod card deployed in the field by screwing the bottle cap to a bottle that had been embedded in a concrete base (as in Clements et al. 2018). The clod cards were approximately 20 cm above the seafloor.

Following retrieval, clod cards were dried to a constant mass and dissolution reported as the change in mass. Sea state and thus water movement on the reef varied both during and between deployments. Changes in surface to volume ratio as the plaster dissolves also affects the rate of dissolution over the course of each deployment. Visual observation of the clod cards indicated that the rate of dissolution varied between days. Thus, total dissolution instead of a daily dissolution rate is reported.

**Sediment Traps:** Sediment traps were 20 cm tall with a 5 cm diameter, a 4:1 height to width ratio as in Gray et al. (2012) and Tsounis et al. (2018). Traps typically sat below the height of the surrounding octocorals in order to measure sedimentation and resuspension within the canopy. Sediment traps were constructed out of PVC pipe, capped and sealed with PVC glue at their bottom and fitted with screw tops for transport of collected sediments. Traps were attached perpendicular to the substratum on a rod fixed in the concrete base using elastic cords. The top of the sediment trap was approximately 20 cm higher than the clod cards to reduce effects of the clods on waterflow around the trap opening. The trap and base were placed on small patches of soft substratum within each area to minimize damage to the reef.

At the end of each deployment, traps were capped underwater and brought to the surface. Traps were maintained upright overnight to allow fine sediments to settle. The content of each trap was filtered under suction onto Whatman GFA glass fiber filters (47 mm). In cases in which large amounts of sediment were present at the bottom of the trap, the water in the trap was decanted and filtered, and the remaining sediment was deposited into aluminum weigh boats. All sediment was dried to constant mass at $50^{o}$ C and weighed. Sediment samples were stored in aluminum foil envelopes inside of plastic freezer bags, frozen and transported back to Buffalo, NY for further analysis.

Organic content of 20 samples from each of the 6 deployments was measured based on loss on ignition (LOI). Ten canopy/non-canopy pairs from each deployment were randomly selected using a random number generator. Subsamples of the collected sediment were used in LOI analyses for some of the larger samples and for samples whose packaging was damaged in transport. Larger biological material, i.e. shells from living gastropods and hermit crabs, were separated from the original sample prior to analysis. The remaining material was weighed, and open aluminum foil envelopes were placed in a Paragon high fire kiln and organic matter combusted at a temperature of 550° C for 3 hours (Heiri et al. 2001).

Grain size of sediments reflects the conditions under which sediments are deposited and provides insight to the origin of the sediments. Five pairs of sediment samples from each deployment were randomly selected for sediment analysis. Slides were prepared by dispersing a small subsample of sediment onto a glass slide and then sealing the slide and coverslip with Permount. 150 grains were randomly chosen from multiple views under an Olympus BX51 petrographic microscope at a magnification of 100x. Grains were measured along the longest dimension using the program Infinity Analyze 3 (Lumenera Corporation) and categorized by roundness using an US GeoSupply grain size card. Rounded and well-rounded grains were categorized together due to the limited number of well-rounded grains. Sieve analysis was not possible due to the small amount of sediment collected in many of the samples.

Frequency distributions of sediment sizes were created using GRADISTAT (Blott and Pye 2001). Samples were analyzed using both phi scale ($\phi$) and in micrometers ($\mu$m) (Krumbein 1934). Characteristics of frequency distributions were compared between deployments following Folk and Ward (1957). These characteristics included: average grain size (median), grain sorting, symmetry of distribution (skewness) and peakedness (kurtosis). Most grains could not be definitively identified. Grains that were identified were typically foraminifera and fragments of the plates of green alga *Halimeda* spp.

**Environmental Conditions:** Parameters that could affect sedimentation such as precipitation, wave height and direction were compared between deployments. These environmental factors were considered because precipitation and wave action from storms may be correlated with times of greater turbulence. Wave height provides a more direct measure of conditions affecting turbulence within the canopy. Wave height can show the association between larger waves and an increase in the size and amount of sediments resuspended (Storlazzi et al. 2011). However, the wave height data only provide a generalized characterization of conditions at the study site because data from St. John were unavailable. Both precipitation and wave height and direction data from nearby St. Thomas were downloaded from the website windguru.com. (A complete dataset from NOAA buoy station number 41052, south of St. John, was unavailable for the entirety of the study.)

**Data Analysis:** Dissolution data were not collected from Deployment 1 as almost all of the dental plaster dissolved during the 10-day deployment. Clod card mass loss data were log transformed and analyzed using a linear mixed model analysis (SPSS, version 25). Treatment (canopy or non-canopy) and deployment number (2-6) were modelled as fixed effects and base pair (1-15) was treated as a random effect. The mass of sediments collected in the traps in canopy and non-canopy areas was compared using a linear mixed model analysis (SPSS, version 25). The data were log transformed, with treatment and deployment as fixed effects and base pair as a random effect.

The percent of organic matter of the sediment samples was analyzed using a linear mixed model analysis (SPSS, version 25). Treatment and deployment were modeled as fixed effects and base pair nested within deployment as a random effect.

A non-parametric hierarchical log-linear test was used to compare the similarity in the grain size frequency distributions (Fig 8). Small sample sizes precluded incorporating all 3 categorical variables simultaneously. In the first analysis, treatment, i.e., canopy vs. non-canopy, was the main effect, and base pair was the lower order effects and grain size ($\phi$) was the categorical variable. A second analysis was conducted with deployment instead of base as a main effect. Grain roundness was analyzed with a non-parametric hierarchical log-linear test similar in structure to the grain size analysis. A second analysis was conducted with the variable deployment, rather than base pair.

## Results:

**Clod Cards:** The average mass loss from clod cards during the other deployments averaged 129.5 g (57%) over 6 days. There was significantly greater mass loss in canopy areas (135.1g, 58.2%) than non-canopy (124.2g, 53.5%) areas ($p= 0.001$, $F= 10.975$, $df= 1, 123$), and significantly different mass loss between deployments ($p< 0.001$, $F= 64.028$, $df=4, 123$) (Fig 3). The random effect, base pair, did not add significant variance to the model ($p= 0.375$, Wald $Z= 0.888$) (Online Resource 1).

**Sediment Traps:** Sedimentation was greater in sediment traps within the canopy than in non- canopy positions ($p= 0.001$, $F= 10.52$, $df= 1, 154$). Sedimentation in the canopy (mean= 7.4g, stdev=23.3g) was significantly greater than in non-canopy areas (mean=3.7g, stdev=7.7g) in all deployments ($p= <0.001$, $F= 75.90$, $df= 5, 154$) (Fig 4). The random effect, base pair, added significant variance to the model ($p= 0.019$, Wald $Z= 2.349$) (Online Resource 2). There was a general trend of increasing sedimentation with increasing clod card mass loss ($r=0.273$, $p<0.001$, $n=150$) (Fig 5). The cases of greatest clod card mass loss and sedimentation were from deployment 3. As is evident in Fig 5, sedimentation rates when clod card dissolution was high were particularly variable. The relationship between clod card mass loss and sedimentation differed between bases, even when clod card dissolution was included as a covariate, reflecting a position effect independent of flow (ANOVA, rank transformed sedimentation, effect of clod card, F=100.534, p<0.001, df=1, 116; effect of base, F=2.522, p<0.001, df=29, 116). Although there was a significant canopy effect on sedimentation when analyzed as paired comparisons, that did not correlate with simple variation in numbers of colonies in the four quadrats surrounding the sediment traps (sedimentation and colony density, r=0.001, p=0.989, n=180) (Fig 6).

The percent of organic matter was greater within the canopy (6.2%) than in the non-canopy (5.3%) positions (p= 0.023, F= 5.51, df= 1, 53). In all deployments, the proportion of organic matter in the sediments collected in canopy areas was significantly greater than in non-canopy areas (p= <0.001, F= 6.41, df= 5, 53) (Fig 7). The random effect, base pair, did not add a significant amount of variance to the model (p= 0.405, Wald Z= 0.833) (Online Resource 3).

**Grain Analysis:** Sediment that accumulated in the sediment traps in canopy areas during deployments 2, 4 and 5 had larger mean grain sizes than the sediments from non-canopy areas. The largest mean grain sizes were observed in both the canopy and non-canopy treatments from deployment 3. Sediments in the traps in both canopy and non-canopy treatments were dominantly fine and very fine sand sized (Online Resource 4). Eleven out of twelve treatment groups were poorly sorted (Online Resource 5). Distributions of grain sizes within the canopy appeared to be slightly skewed towards coarser grains while the distribution of non-canopy grain sizes was skewed towards finer grains (Online Resource 6).

Comparison of the grain size frequency distributions showed that the interactions between grain size and base pair ($\chi^2(1) = 3096.0$, $p < 0.001$) and grain size and treatment ($\chi^2(1) = 131.8$, $p < 0.001$) and the 3-way treatment by pair by grain size were significant. In a second analysis deployment instead of base was used as a categorical variable. The interactions between grain size and deployment ($\chi^2(1) = 1627.9$, $p < 0.001$) and grain size and treatment ($\chi^2(1) = 128.9$, $p < 0.001$) were significant.

Distributions of grain roundness were similar in canopy and non-canopy treatments (Online Resource 7). Grains from the canopy sediment traps were slightly skewed towards more rounded grains while the distribution of non-canopy grains appears to be skewed towards more angular grains. The interactions between grain roundness and base pair ($\chi^2(1) = 698.3$, $p < 0.001$) and between grain roundness and treatment ($\chi^2(1) = 30.0$, $p < 0.001$) were both significant. The interactions between grain roundness and deployment ($\chi^2(1) = 252.0$, $p < 0.001$) and grain roundness and treatment ($\chi^2(1) = 20.1$, $p < 0.001$) were significant.

**Environmental Conditions:** Cumulative rainfall was greatest during deployment 1. Deployment 1 was also 4 days longer than the other deployments, but as suggested from the maximum rainfall, most of the precipitation fell during a 1-day period (Online Resource 8). Deployment 2 experienced the lowest rainfall. Wave heights were greatest during deployments 1 and 3, which also had the greatest rates of sedimentation (Online Resource 9). Waves were generally out of the east/southeast throughout the deployments.

## Discussion:

The octocoral canopy interacts with flow on the reef by developing a zone of shear in the turbulent boundary layer above the canopy (Nepf and Vivoni 2000; Guizien and Ghisalberti 2016). This shear zone produces a substantial amount of canopy-scale turbulence that may reach the substratum (Nepf and Vivoni 2000; Nepf 2012). Turbulence is also produced, to a lesser degree, in the wakes of the individual canopy elements (Nepf and Vivoni 2000; Chang et al. 2009; Nepf 2012). Both modes of turbulence production are enhanced by oscillatory flow created by waves (Reidenbach et al. 2007). These effects on flow may enhance the deposition of sediments in two ways. First, the supply of sediments into the canopy is enhanced by the diffusion of sediments through the shear layer above the canopy and second, turbulence at the substratum can promote the resuspension and subsequent deposition of sediments within the canopy. The resuspension of sediments is particularly important in understanding the sediment trap data as the traps, by design, sample the downward flux of sediments, but prevent those sediments from being resuspended. These effects on water flow shaped the results that we observed at East Cabritte where, in canopy areas clod cards were subject to higher rates of dissolution and more sediment was deposited within traps.

Greater dissolution of clod cards within the octocoral canopy is consistent with increased turbulence within the canopy. Dissolution of the clod cards is a function of mass transport over the surface of the clod card; enhanced turbulence within the canopy would increase mass transport at the surface of the clod card even if net flow was reduced within the canopy. A reduction in net flow within the canopy is supported by velocity profile measures (RMS) taken using an acoustic doppler current profiler (ADCP) at multiple sites at our East Cabritte site (Guizien and Bramanti, personal communication).

Greater accumulation of material occurred in sediment traps located in canopy areas. This material likely had two sources, suspended sediment transported onto the reef which entered the canopy through turbulent diffusion in the shear layer and sediments that were resuspended due to within canopy turbulence and subsequently redeposited. Sediment traps minimize resuspension of sediments from within the traps.

The importance of resuspension within this system is evident in both the amounts of sediment accumulated and their composition. Most of the sediment samples were classified as fine sand or very fine sand and were poorly sorted (Online Resource 5, Online Resource 6). Samples from the canopy included larger, more rounded grains and more organic material (Fig 8, Online Resource 7, Fig 7). Larger sediment sizes were likely present in the canopy area sediment traps because they were resuspended and subsequently deposited in nearby canopy sediment traps due to their greater settling velocity. The greater proportion of rounded particles deposited in the canopy could be a consequence of supply with the reworked sediments in the canopy being rounder and typically having a higher settling rate. Fine sands are typically well sorted (Inman 1949), however the sediment sizes collected in both canopy and non-canopy traps were almost always poorly sorted. This may reflect the distance sediments were transported. If the material always came from close by there would be little opportunity for sorting. This may also reflect the varying densities of the grains, where large, less dense grains such as those from *Halimeda* plates may be as readily transported as smaller denser grains originating from the erosion of shells or coral skeletons.

The balance between the two processes of deposition, through resuspension or transport into the canopy through the shear zone, were illustrated by the effects of sea state over the course of the deployments. Periods of winds and greater wave action occurred in deployments 1 and 3 (Online Resource 8, Online Resource 9). The larger grain sizes depositing under these conditions in both canopy and non-canopy areas were likely associated with increased turbulence across the reef. Greater wave action (height) increases both the grain size (Storlazzi et al. 2011) and amount of sediment that is resuspended (Ward 1984; Ogston et al. 2004; Storlazzi et al. 2004; Pang et al. 2020). At areas further within the bay, sediment traps that recorded the most sedimentation tended to be those closest to open sand patches at the edge of the reef system (Online Resource 2). The storms likely increased the volume of sediment in suspension moving onto the reef from those sand deposits. The suspended sediment was likely slowed in the shear layer due to the canopy effect and deposited on the reef.

Our findings may also have implications for larval settlement in the octocoral forest. shear layer. Although resuspension of larvae from the substratum mightreduce numbers attaching (Abelson and Denny 1997), but those that do attach may have enhanced success as recruits because the constant reworking of material may have the net effect of preventing them from being buried. These effects may influence the growth and distribution of octocorals as well as other reef organisms.

The greater amount of material collecting within sediment traps (located above the substratum) in canopy areas does not necessarily mean the canopy areas themselves will accumulate more sediments over time. Resuspension, which sediment traps do not directly measure, may intermittently clear the substratum except in places, such as holes, where sediment would be naturally trapped (Scoffin 1970). On reefs on which framework elements are present and growing, the presence of canopy producing taxa like octocorals will further promote resuspension which can keep exposed substratum available for settlement and facilitate the accumulation of sediments in depressions. This pattern of clearing and resuspension may be critical to the maintenance of octocoral forests on hardgrounds.

## Acknowledgements:

We thank Dr. Mary Alice Coffroth and Dr. Charles E. Mitchell for their feedback throughout this project. Angela Martinez-Quintana provided invaluable assistance in the field, and Zachary Hector assisted in the analyses of the sediment samples. This project was funded by

NSF Grant OCE 1756381 to HRL, The Geological Society of America Graduate Student Research Grant, the University at Buffalo Mark Diamond Research Fund, and the University at Buffalo Champion Award.

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**Figure Legends:**

**Fig 1.** Map of base positions at study site in Grootpan Bay St. John, USVI. Non-canopy bases are highlighted in red and include the letter 'A' after their pair number. Canopy bases are highlighted in yellow and include the letter 'B' after their pair number. Positions of the bases were mapped based on compass heading and distances between the bases.

**Fig 2.** Non-canopy (a) and canopy (b) bases positioned on the reef with sediment traps and clod cards attached. Sediment trap is indicated by white arrow in b. Clod card is indicated by yellow arrow in b.

**Fig 3.** Differences in mass loss between canopy and non-canopy bases in each deployment. Error bars represent ± 1 standard error.

**Fig 4.** Differences in sedimentation between canopy and non-canopy bases in each deployment. Error bars represent ± 1 standard error.

**Fig 5.** Differences in sediment mass in canopy and non-canopy bases for deployments 2-6 with clod card mass loss as a proxy for relative water flow.

**Fig 6.** Sedimentation for each sediment trap as a function of the number of colonies per $4m^2$.

**Fig 7.** Mean percent organic mass in each of the deployments. Error bars represent ± 1 standard error.

**Fig 8.** Percent of grains within each treatment represented in phi-scale categories.

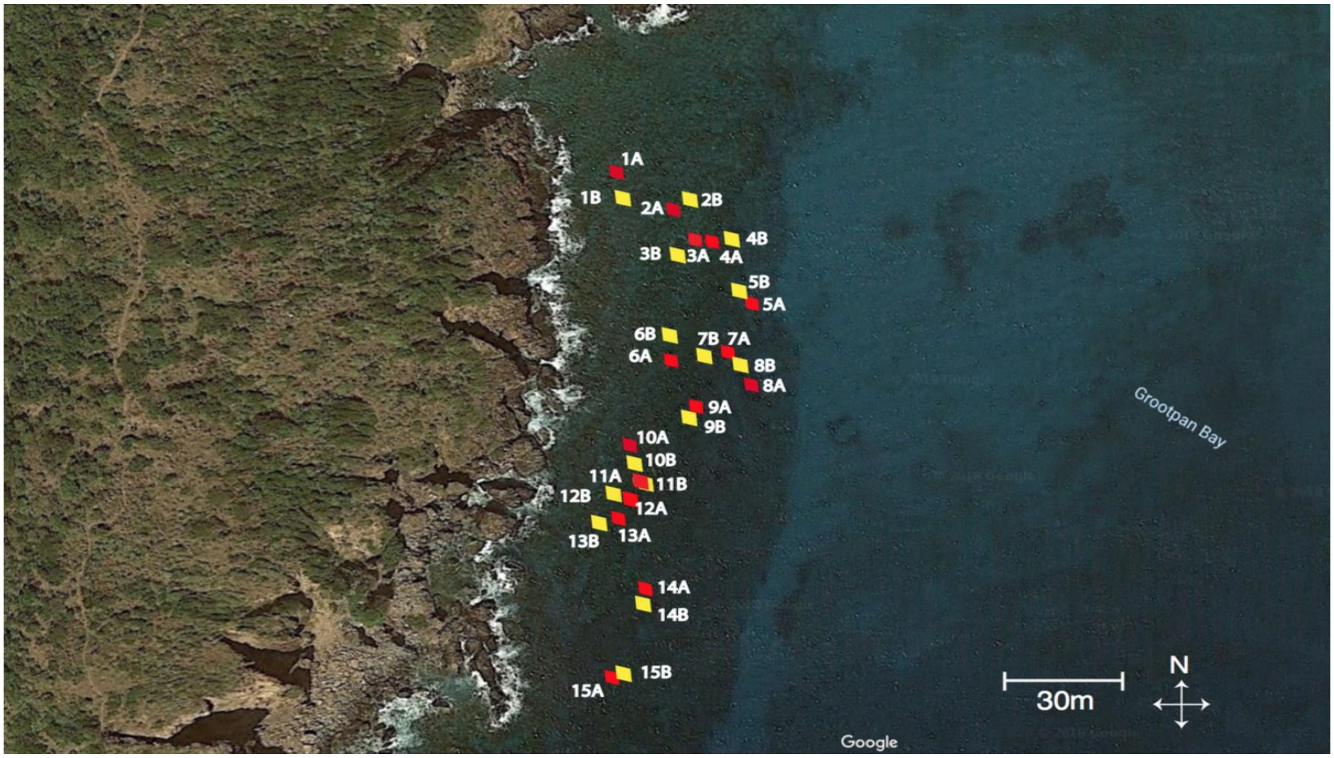

1A
1B
2A
2B
3B
3A
4A
4B
5B
5A
6B
6A
7B
7A
8B
8A
9A
9B
10A
10B
11A
11B
12B
12A
13B
13A
14A
14B
15B
15A
Grootpan Bay
30m
N
Google

**Fig 1.**

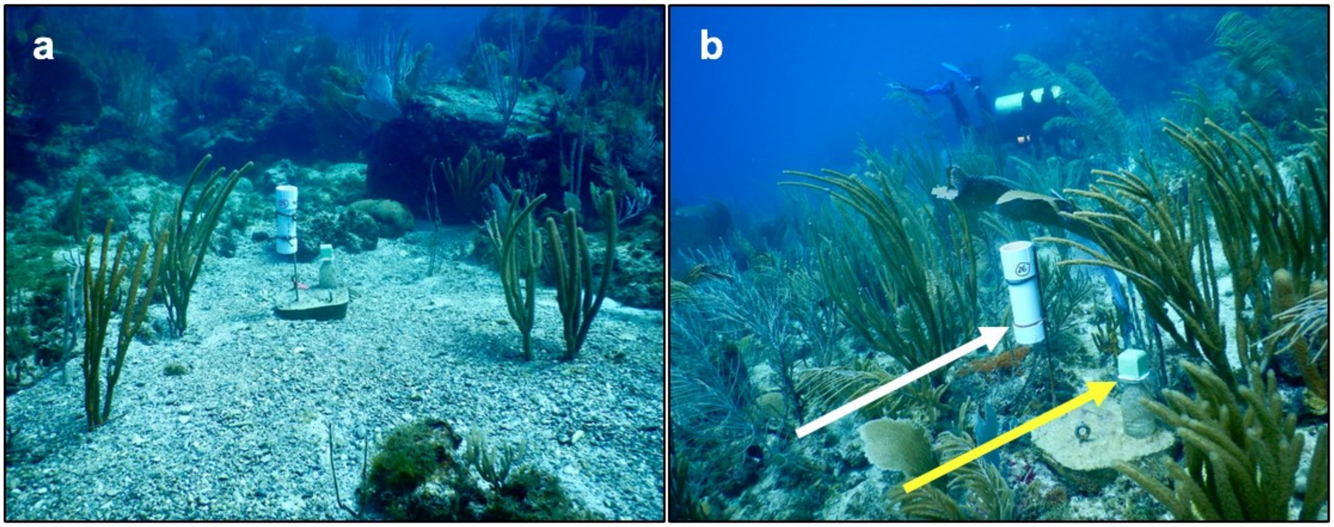



**Fig 2.**

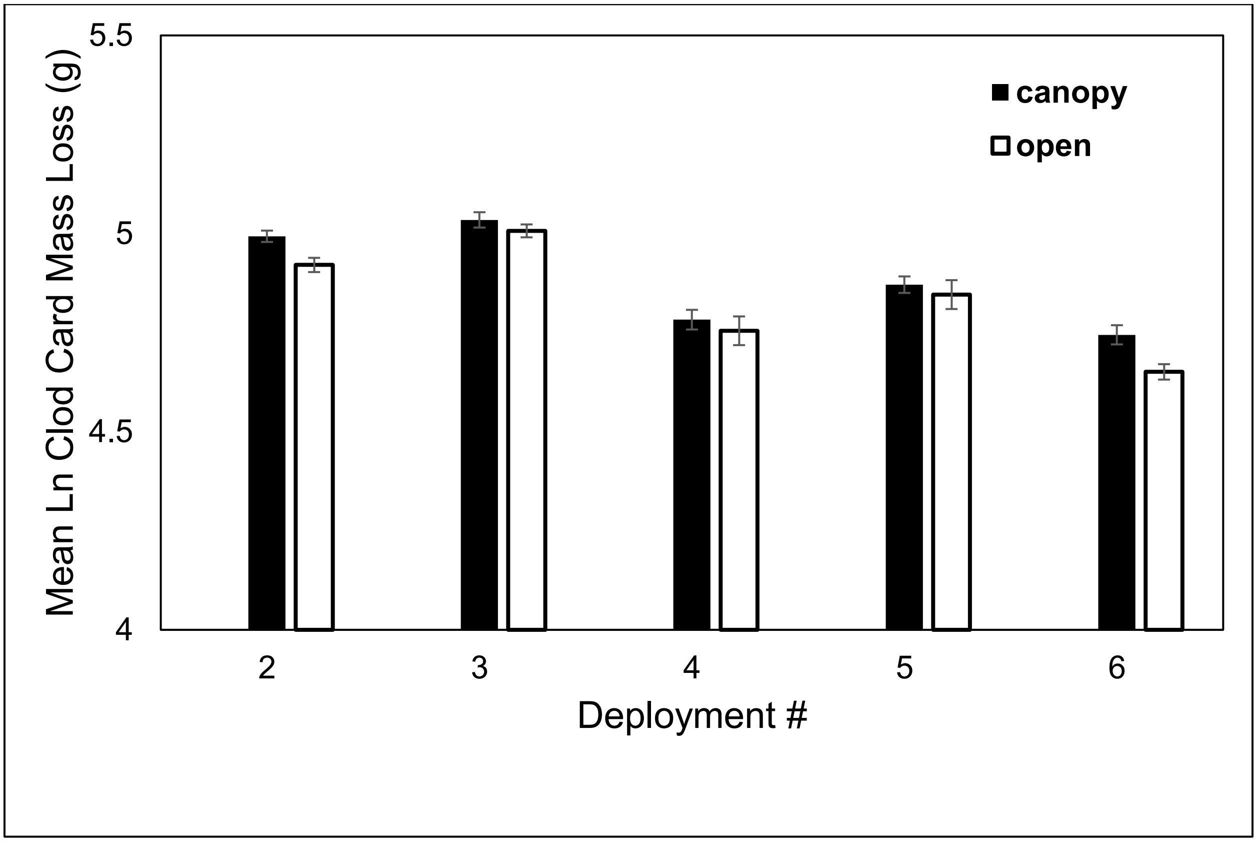

5.5
5
4.5
4
Mean Ln Clod Card Mass Loss (g)
canopy
open
2
3
4
5
6
Deployment #

**Fig 3.**

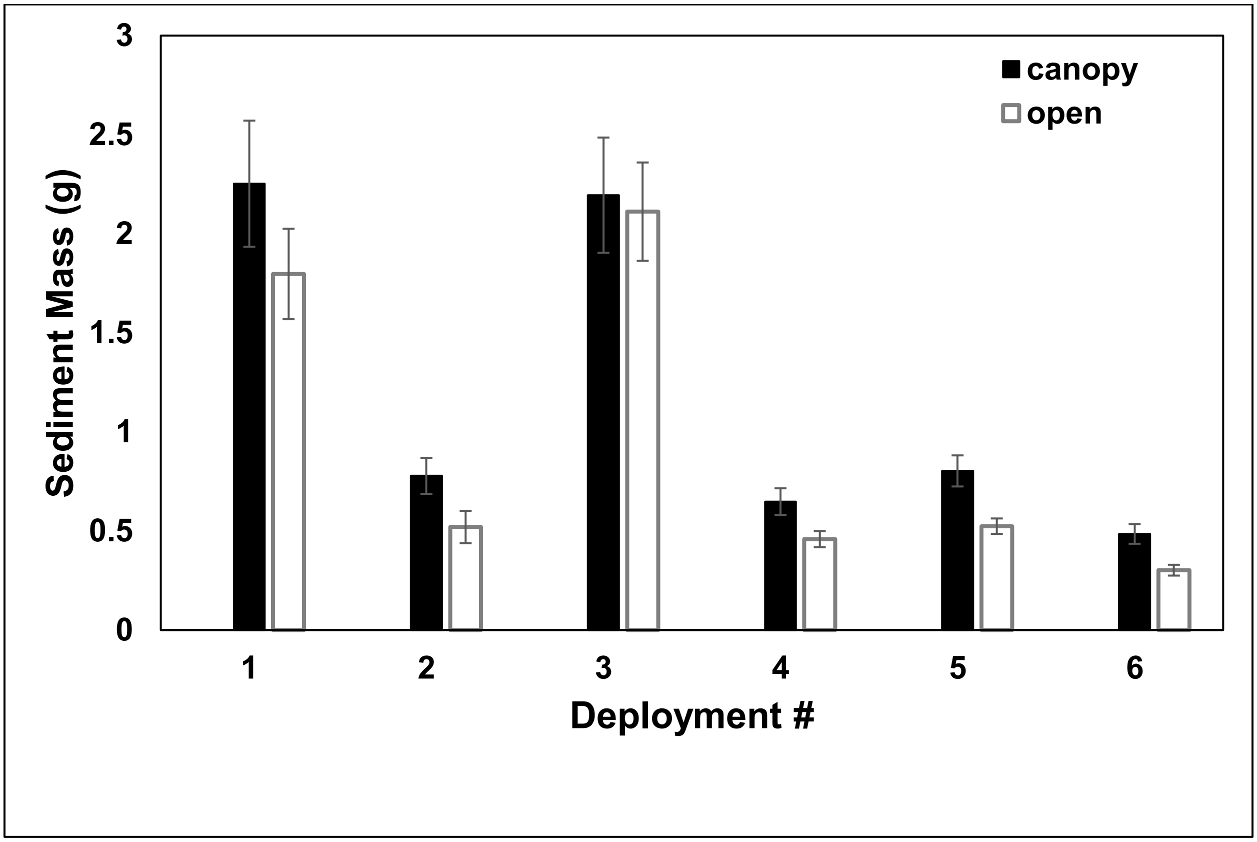



**Fig 4.**

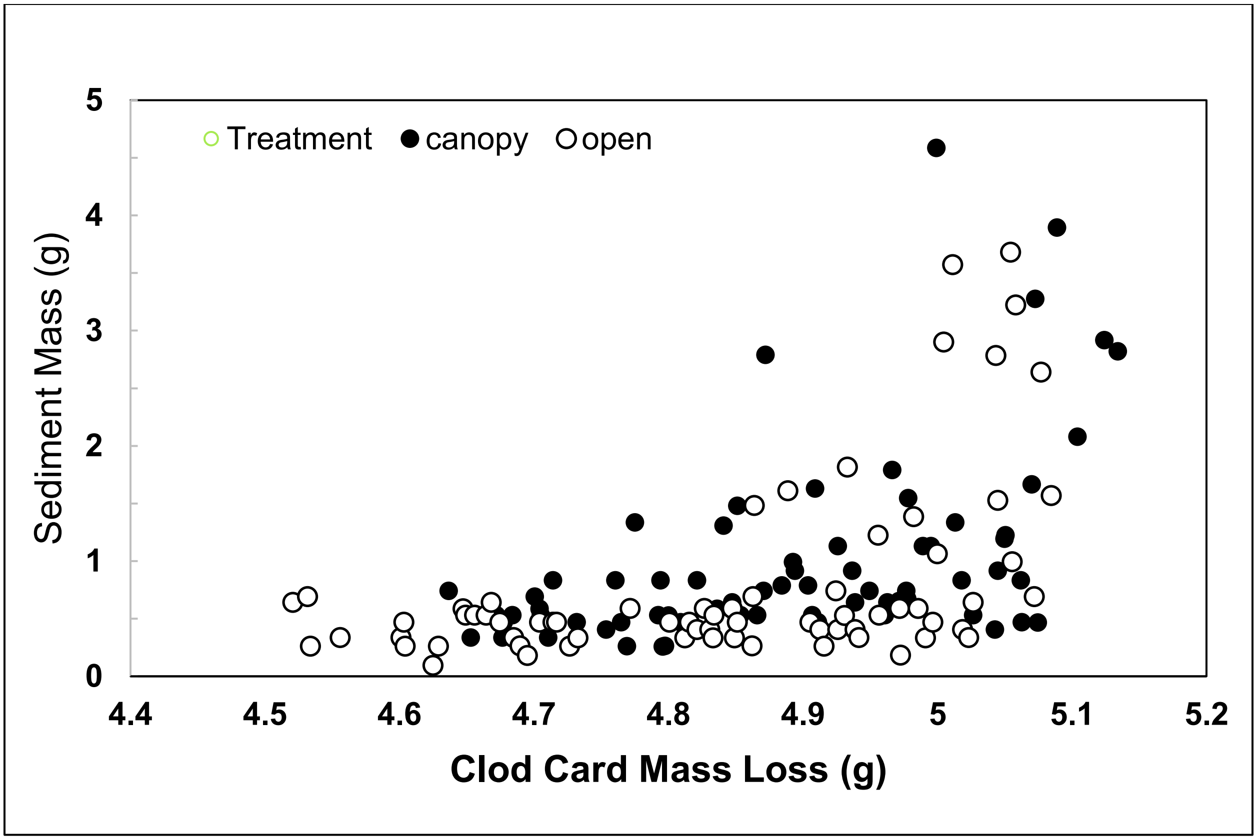
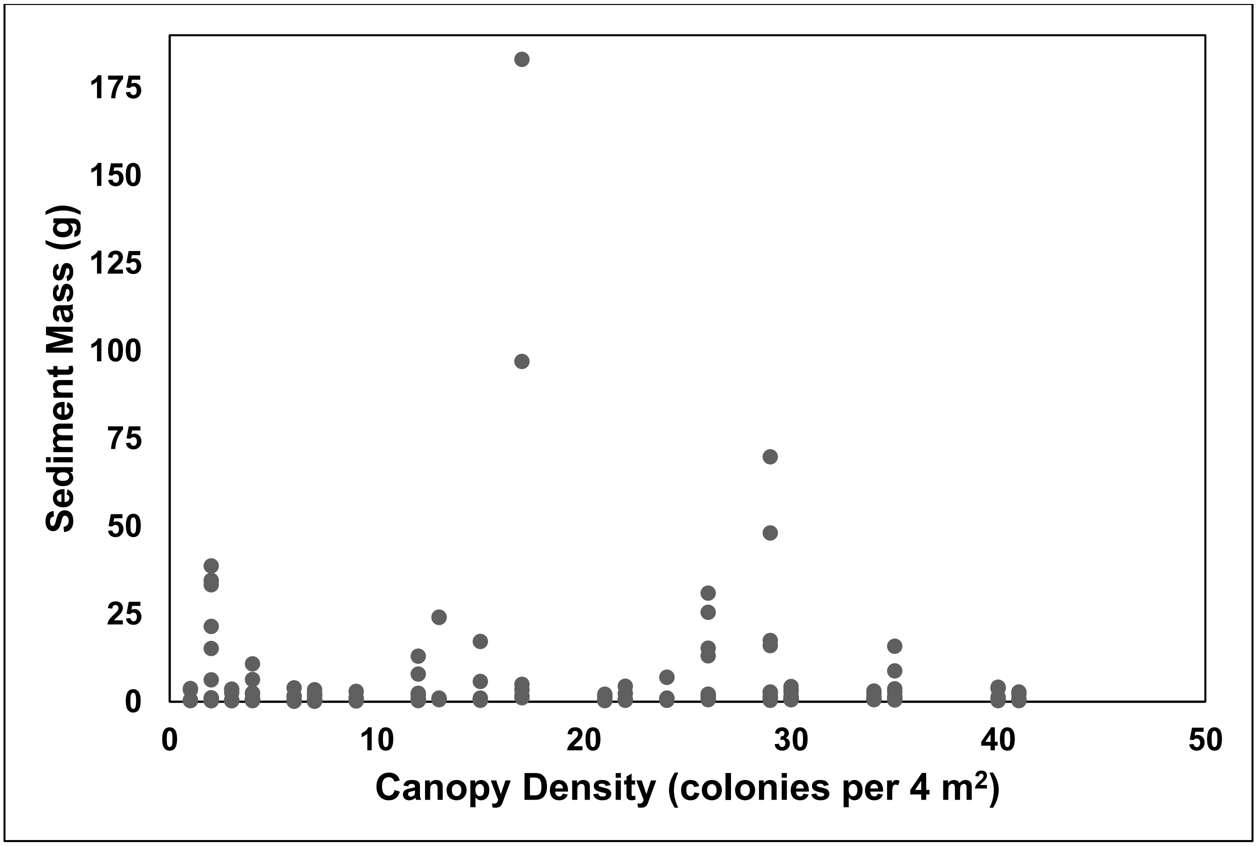

Treatment
canopy
open
Sediment Mass (g)
0
1
2
3
4
5
4.4
4.5
4.6
4.7
4.8
4.9
5
5.1
5.2
Clod Card Mass Loss (g)

**Fig 5.**



Sediment Mass (g)
175
150
125
100
75
50
25
0
0
10
20
30
40
50
Canopy Density (colonies per 4 m²)


**Fig 6.**

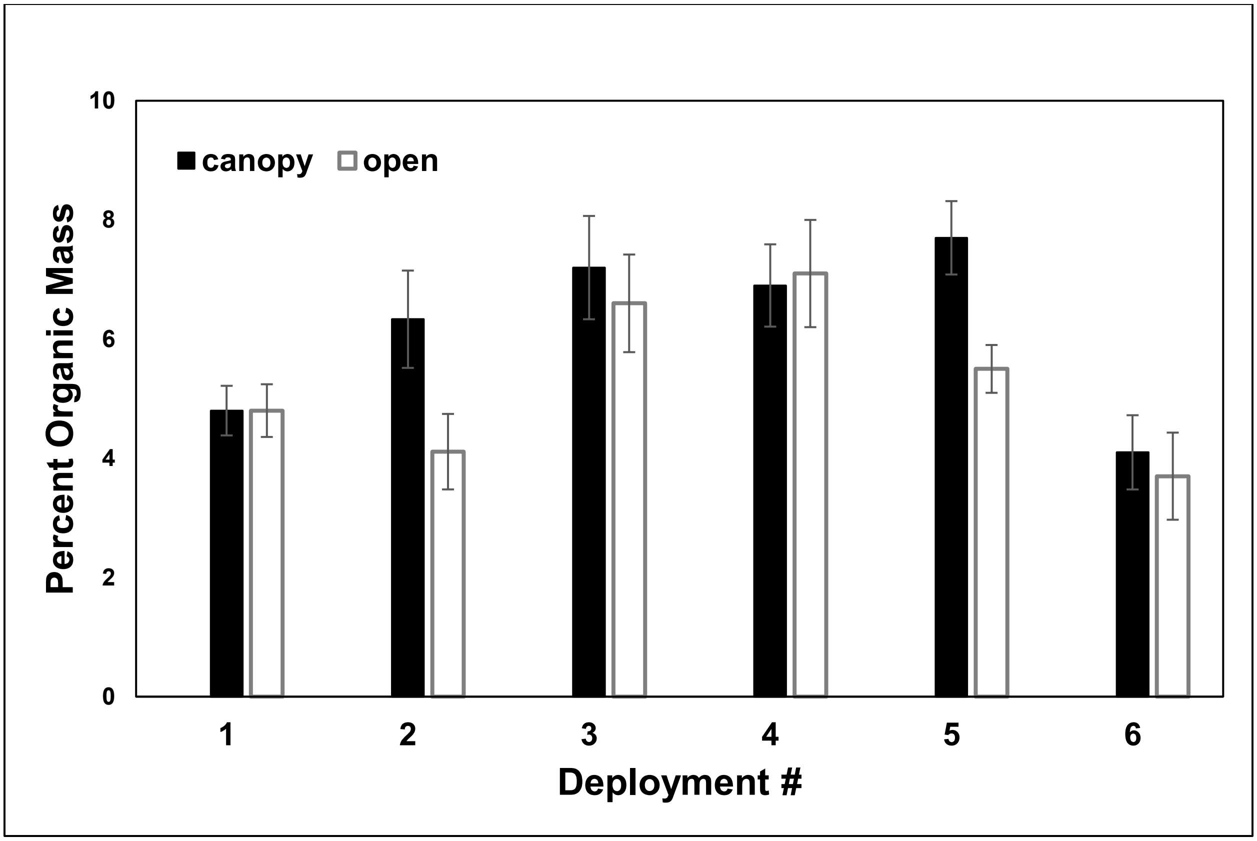

10
8
6
4
2
0
canopy
open
Percent Organic Mass
1
2
3
4
5
6
Deployment #

**Fig 7.**

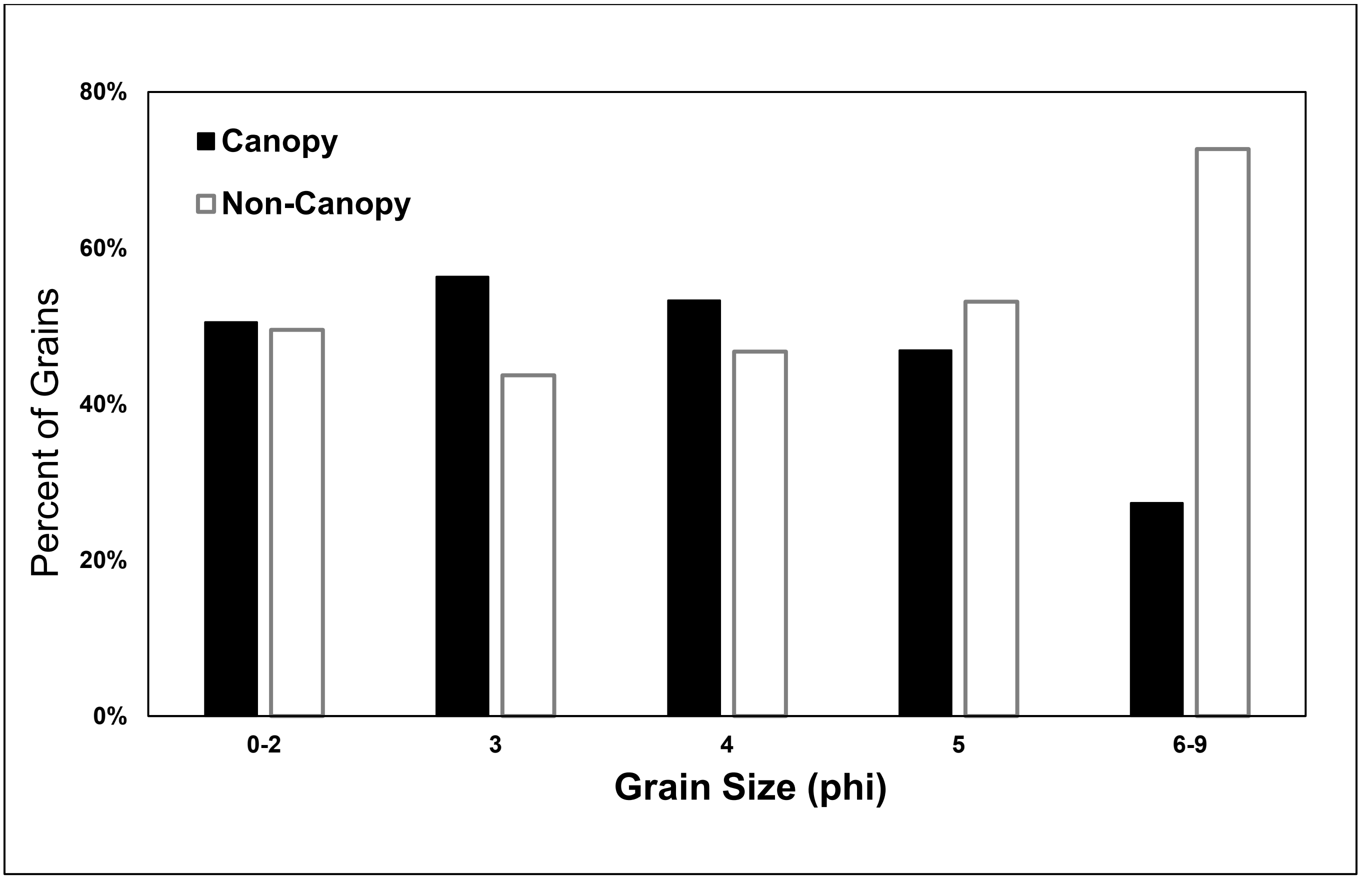

80%
60%
40%
20%
0%
Percent of Grains
Canopy
Non-Canopy
0-2
3
4
5
6-9
Grain Size (phi)

**Fig 8.**