EFFECTS OF SEDIMENT ON GROWTH AND SURVIVAL OF VARIOUS JUVENILE MORPHOLOGIES OF THE SCLERACTINIAN CORAL, *OCULINA ARBUSCULA* (VERRILL)

by

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(Under the Direction of Daniel F. Gleason)

ABSTRACT

Sedimentation can play an important role in shaping tropical and temperate benthic marine communities. Here, I quantified sedimentation rates on a hard-bottom reef in the South Atlantic Bight (SAB) off the coast of Georgia, USA and assessed its effects on a conspicuous member of the benthic community: the scleractinian coral, *Oculina arbuscula*. I addressed the predictions that: 1) inorganic and organic sedimentation rates vary in relation to wind speed and wave height in the SAB, 2) the ability of juvenile *O. arbuscula* to shed sediment depends on skeletal morphology, and 3) inorganic sedimentation reduces growth and survival of encrusting *O. arbuscula* juveniles more than those with a branching morphology. The first prediction was tested by quantifying sedimentation rates from July 2008-October 2010 at J-Y Reef, a hard bottom reef at 18-20 m depth ~32 km off the coast of Sapelo Island, GA. Collected sediments were divided into inorganic and organic fractions and compared with wave height and wind speed from the region. Results showed that organic material comprised ~3% of total sediment. Inorganic sediments consistently exceeded 50 mg cm^{-2} day^{-1} and were positively correlated with wave height and wind speed. The second prediction was investigated by documenting passive and active sediment shedding abilities in

juvenile *O. arbuscula* with morphologies ranging from encrusting to branching. Laboratory

experiments showed that juveniles with greater branching morphology exhibited better

passive sediment shedding ability under both low (30 mg cm^{-2}) and high (100 mg cm^{-2})

sediment regimes. However, this morphological advantage was nullified when active

sediment shedding mechanisms were included. The third prediction was tested by

investigating the relationship between inorganic sedimentation and growth and survival of *O.

arbuscula* juveniles settled on artificial recruitment tiles. Mortality of coral recruits was

positively correlated with sedimentation. Juveniles with a branching morphology survived

best under sediment stress. Collectively, these results provide evidence that sedimentation

can affect the population structure of *O. arbuscula* via mortality at the juvenile stage and that

developing a branched morphology early in life provides a selective advantage for countering

the negative impacts imposed by the high sediment loads present on Georgia offshore reefs.

INDEX WORDS: Sedimentation, Morphology, Coral, South Atlantic Bight, Temperate reefs

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DEDICATION

This work is dedicated to my parents, Rick and Marsha Lott. They play a pivotal role in my ability to accomplish goals, both professional and personal. I cannot describe how much it means to have parents that provide unconditional love, support and guidance in all that I set out to achieve; I would not be where I am today without their continual support. My grandparents, Burdeane and Gordon Fair, were also very invested in this project and my development as a successful scientist. Years of summer vacations to various beaches in Florida with them fostered my interest in marine science.

I would also like to dedicate this thesis to my family, Tim and Brynn Sharp. There is no greater reward in this life than to know that they are proud of me. This project was not completed alone; they were with me every step of the way. I can only hope that the completion of this project is as special to them as it is to me.

ACKNOWLEDGMENTS

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CHAPTER 1

SPATIO-TEMPORAL VARIATION IN INORGANIC AND ORGANIC SEDIMENTATION RATES ON A HARD-BOTTOM REEF IN THE SOUTH ATLANTIC BIGHT, GEORGIA, USA

INTRODUCTION

Sediment deposition can exert influence over the structure of benthic marine communities by impacting the survival of sessile invertebrates. Adverse effects of high sediment loads have been well documented on coral reefs, sponge dominated communities, and within rocky subtidal and soft-bottom assemblages (Rogers 1990; Bell and Barnes 2000a; Airoldi 2003; Fabricius 2005). For example, Thomsen and McGlathery (2006) reported that sediment accumulation on temperate oyster reefs in soft-bottom lagoons leads to decreases in species richness and abundance and lowers oyster recruitment over time. Likewise, sedimentation serves as an important regulator of community structure in Maryland's Lower Chesapeake Bay by reducing richness to a few resilient species (Schaffner 2010). Sedimentation can affect organisms directly through burial (Babcock and Davies 1991; Wesseling *et al.* 1999; Babcock and Mundy 2006) and abrasion (Aller and Dodge 1974; Loya 1976; Rogers 1983; Miller *et al.* 2000), and indirectly via reduced light intensity (Maughan 2001; Irving and Connell 2002), reduced food capture (Bak 1978; Stafford-Smith and Ormond 1992; Anthony 1999), and decreased photosynthetic rates (Riegl and Branch 1995; Te 1997). Temperate regions generally receive much higher sediment loads than tropical systems (Riegl 1995) and can experience chronically high sedimentation that persists for weeks to months. An example of this type of temperate high-sediment system is the South Atlantic Bight (SAB).

The South Atlantic Bight (SAB) extends from Cape Hatteras, North Carolina to Cape

Canaveral, Florida and spans approximately 130 km from the coastline to the edge of the continental shelf (Hyland *et al.* 2006). A majority of the SAB (>70%) is characterized by large expanses of smooth or rippled sand substrate (Hyland *et al.* 2006). Scattered but relatively common within this landscape are limestone hard-bottom reefs dominated by sponges, cnidarians, bryozoans, and ascidians (Hopkinson *et al.* 1991). Biodiversity and biomass on these reefs are concentrated within a narrow 2- 4 m wide zone paralleling hard-bottom ledges with 1-2 m vertical relief (hereafter referred to as the "scarp") (Wenner *et al.* 1983; Hopkinson *et al.* 1991; Ruzicka and Gleason 2009). The elevated side of ridges transition into expanses of soft sand substrata with a sediment layer up to 5 cm thick (Ruzicka and Gleason 2009). Sediments within the SAB are comprised primarily of sand grains with a mean diameter of 250-500 μm (Gorseline 1963). Coastal rivers and marshlands are the largest source of organic particles and fine sediment input into the SAB (Gorseline 1963; Hopkinson *et al.* 1991). Sedimentation in the SAB has been investigated previously; however, these studies did not seek to elucidate the role of sediment in shaping or maintaining benthic community dynamics (Gorseline 1963; Hunt 1974; Mathews and Pashuk 1986; McCarney-Castle *et al.* 2010). Due to the numerous sources of sedimentation in the SAB, it is probable that sedimentation is a factor shaping the community structure of temperate hard-bottom communities in this region.

For the present study, I investigated spatio-temporal variation in inorganic and organic sedimentation rates at J-Y Reef, a temperate live-bottom reef off the coast of Georgia, USA. I predicted the mass of inorganic sediments and organic particles settling out of the water column would increase with wave height and wind speed. These variables have been used in previous studies as predictors for increased sedimentation in marine systems (Dobrynin *et al.*

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2010). Average wave height and wind speed were taken daily from 1988 to 2008 at a data

buoy within Gray's Reef National Marine Sanctuary, located approximately 15 km from J-Y

Reef. Mean wave height and wind speed are generally highest from September-October and

December-January, thus sedimentation rates should be highest during the fall and winter

months (NOAA 2011). Sessile invertebrate biomass and biodiversity vary over a small

spatial scale (within meters), with highest abundance and diversity occurring in the first 2 m

of the reef ledge, also called the "scarp" (sensu Ruzicka and Gleason 2009). I predicted that

sediment would vary on a similar spatial scale across the reef, with lower sedimentation in

the first 2 m of the scarp than 5 m back from the scarp. Additionally, I investigated the grain

size composition of sediments to determine if seasonal changes in granular characteristics

(i.e. percent of various grain sizes, percent organic content) occurred because the effects of

sedimentation on benthic organisms are partially related to sediment composition (Lasker

1980; Riegl and Branch 1995).

METHODS

Study Site

The study was conducted at J-Y Reef (31° 36.056 N, 80° 47.431 W), a temperate

hard-bottom reef located approximately 32 km off the coast of Sapelo Island, Georgia, within

the SAB (Figure 1). J-Y Reef occurs at 18 to 20 m depth and hosts a diverse assemblage of

sponges, hard and soft corals, anemones, tunicates, bryozoans, and mollusks (Hyland *et al.*

2006). The rocky reef topography of J-Y Reef is characteristic of hard-bottom reefs within

the SAB and attracts numerous benthic and pelagic fishes as well as populations of protected

species such as the loggerhead sea turtle (Hyland *et al.* 2006).

Quantification of sedimentation rates

Sediment trap data were gathered at J-Y Reef from July 2008 to October 2010.

Sediment traps consisting of PVC pipes measuring 15 cm (height) x 5 cm (diameter) were zip-tied to 30 stainless steel rods. Rods were epoxied into holes drilled approximately 10 cm deep into the substrata in 2007 (D.F. Gleason, pers. communication). Collecting tubes had an aspect ratio (height: diameter) of 3:1 thus exceeding the minimum aspect ratio of 2:1 as recommended by Gardner (1980). The tube was positioned vertically in the water column so that sediments were collected approximately 15 cm above the substrata. Rods were placed 1 m apart on top of a rocky ledge along transect lines that were 1, 2, and 5 m from the scarp. These distances were chosen to address the prediction that sedimentation rates varied on a small spatial scale (within m) because benthic invertebrate abundance and diversity also vary on this scale. A total of 10 sediment traps were deployed along each transect for each date. Traps were retrieved one to five months after being deployed, capped, and placed on ice for transport to the lab. All samples were stored at –20 ºC until processing. I collected sediment traps on 12 dates: July 29, October 17, and December 5, 2008; February 6, June 23, July 24, September 9, and November 23, 2009; and May 10, June 14, July 21, and October 8, 2010. I was not able to collect traps at regular intervals because of the variability in sea surface conditions that prevented dive operations on many days.

Total collected mass was divided into inorganic and organic fractions because organic material may serve as a food source for filter-feeding invertebrates (Lehman 1976; Richmond 1997; Anthony 1999). Each sample was wet-sieved into the following grain sizes: >500 μm, 250-500 μm, 125-250 μm, 63-125 μm, and <63 μm. Silt fractions (<63 μm) were measured volumetrically by removing a 40 ml subsample from each sediment trap after stirring for 1 min and 56 sec and filtering the contents on 0.45 μm filter papers (Type HAWP, Millipore, Bedford, MA, USA). Salt content was removed by rinsing sediments with deionized water as

they were collected on filter papers (approximately 30 sec) (Gleason 1998). Sediments were placed in preweighed and precombusted aluminum weigh boats and dried at 60 ºC for at least 24 h to remove water. Dried samples were weighed to the nearest 0.1 mg on an APX-60 analytical balance (Denver Instrument, New York, USA). Organic fractions were removed by combusting samples for at least 1 h at 500 ºC, cooling to room temperature, and reweighing. The difference in mass before and after combustion, after aluminum pan and filter weight were subtracted, represented the amount of organic material present in each sample. Inorganic and organic particle masses were divided by the total number of days traps were in the field to determine daily sedimentation rates for each fraction (mg cm^{-2} day^{-1}).

All data were tested for normality and homogeneity of variance. Any data that did not meet normality were square root transformed and retested. Inorganic and organic sedimentation rates met assumptions after transformation, thus a two-way repeated measures ANOVA was used to determine differences in sedimentation rates at various distances from the scarp (1, 2, and 5 m) across all time intervals.

Historical Data

Wave heights (m) and wind speeds (m/s) from July 2008-October 2010 were downloaded from the National Oceanic and Atmospheric Administration's National Data Buoy Center website (www.ndbc.noaa.gov). These variables were chosen because they were readily available and have been previously used as a representative measure of turbidity (Dobrynin *et al.* 2010). These variables were obtained from a 3 m diameter discus buoy moored within the boundaries of Gray's Reef National Marine Sanctuary (Station 41008, 31°24.9 N, 80°52.9 W), approximately 23 km from J-Y Reef. The buoy measures wave height as the average of the highest one-third of all waves each minute during a 20 min

sampling period (for a total of 20 measurements), and the 20 min average is reported every hour for 24 h. Wind speed is measured from 4 m above sea level once a minute for an 8 min sampling period (for a total of 8 measurements), and the average of the 8 min period is reported every hour for 24 h. I distilled these data down to daily wave height and wind speed averages by computing the mean for each variable over 24 h. Wave height and wind speed were not available June to mid-July 2009 because the buoy was dislodged from its anchor.

Linear regressions were used to determine the relationships between wave height and wind speed and inorganic and organic sedimentation rates. The median grain sizes for inorganic and organic fractions of sediment were determined for each time interval by plotting the cumulative percent of all grain sizes. First, I $\log_{10}$ transformed all grain size categories using the smallest grain size that would have collected in the corresponding sieve size for all categories (i.e., 501 µm, 250 µm, 125 µm, 63 µm) except for the smallest size category (<63 µm) where I used the largest particle size that would have been collected (62 µm). The point at which each line intersected the y-axis at 50% of the total sediment composition was back transformed to give the median grain size for each time interval that traps were in the field. I then used linear regressions to determine if median grain size was dependent on wind speed and wave height.

RESULTS

Sedimentation rates, defined as the rates of downward flux of suspended particles, varied throughout the study for inorganic particles (Table 1). There was a strong interaction between collection date and distance from the scarp for inorganic particles, thus both of these variables contributed significantly to inorganic sedimentation rates observed during the study. Inorganic sediments ranged from <1 to >300 mg cm^{-2} day^{-1} (Figure 2A) and were

dominated by particles ranging from 125- 250 μm (~55 ± 11% S.D.) (see Table A2 for further detail). Seasonal trends in inorganic rates were not evident during the study. For example, both the lowest and highest rates of inorganic sedimentation were recorded in June-July, but in different years.

Organic particle mass varied temporally, but not spatially, throughout the study (Table 1). However, the analyses suggest there is a strong trend for an interaction between sample date and distance along the ledge. Quantities of organic sediments were over an order of magnitude lower than inorganic particles; however, the pattern of organic particle mass generally reflected inorganic sediment mass (Figure 2B). Organic particle mass composed 3 ± 0.7% S.D. of the total dry mass and was dominated by grains <63 μm (44 ± 6% S.D. of dry weight) (see Table A3 for further detail).

Mean wave height and wind speed were highly correlated (Figure 3), so I arbitrarily chose wave height to report relationships with sedimentation rates and median grain sizes in order to reduce redundancy. Wave height had a positive relationship with inorganic sedimentation rates at all distances from the scarp and explained 19-44% of the variation in inorganic sedimentation (Table 2; Figure 4 A). In contrast, organic sedimentation rates across the reef ledge were not influenced by wave heights during the study (Table 2; Figure 4B). Wave height explained only 8% of the variation in the mass of organic material for traps positioned 5 m from the scarp, and even less for traps 2 and 1 m from the carp. Wave height explained 38, 48, and 28% of the variation in median grain size for inorganic sediments at 1, 2, and 5 m from the scarp, respectively (Table 3; Figure 5A). Organic median grain sizes were independent of wave height during the study (Table 3; Figure 5B). Wave height explained 28% of variation at 5 m from the scarp, and <18% in the first 2 m of the scarp.

DISCUSSION

Sedimentation can exert control on the structure of benthic marine communities through numerous mechanisms that include preventing larval settlement, smothering organisms, and reducing growth rates and feeding efficiency (Rogers 1990; Irving and Connell 1992; Maida *et al.* 1994; Roberts and Davis 1996; Connell 2005; Schiel *et al.* 2006). Sedimentation rates reported in this study for J-Y reef, a temperate hard-bottom located approximately 32 km off the coast of Georgia, U.S.A., were an order of magnitude higher than those recorded in tropical locations where similar methods of collecting sediment were employed (review by Rogers 1990; Gleason 1998; Babcock and Smith 2000). In contrast, sediment rates comparable to those seen at J-Y reef have been observed in other healthy temperate reef systems (e.g., ~200 mg cm^{-2} day^{-1} on South African reefs, Riegl 1995). Organic mass rates, although comprising a small percentage of total sedimentation rates, were also higher than those recorded in tropical coral reef habitats (Gleason 1998; Wolanski *et al.* 2005). Organic particles may benefit organisms as a food source. A study of several benthic communities within the SAB off the coast of North and South Carolina reported that infaunal and filter-feeding species common on temperate offshore reefs are capable of consuming organic material falling from the water column (Blake and Grassle 1994). Thus, benthic invertebrates occupying hard-bottom reefs of the SAB must be well-adapted to deal with the high sediment loads that occur in this region, but may also benefit significantly from the influx of large quantities of organic material that occur.

Although sedimentation rates in the range of those observed here are harmful to most reef organisms in tropical regions (Loya 1976; Rogers 1990), many temperate reef organisms are capable of withstanding chronically high sediment loads (Maughan 2001). One aspect of

withstanding high sediment loads involves morphology. Arborescent, digitate or other erect growth forms inherently accumulate less sediment (Maughan 2001; Bell and Smith 2004; Todd 2008) reducing the amount of stress directly or indirectly associated with sedimentation (Irving and Connell 1992). Sponge communities on J-Y Reef provide support for morphological adaptations in response to high sediment loads. Ruzicka and Gleason (2009) reported that 90% of sponges located <2 m from the scarp had amorphous, massive, or encrusting growth forms while 80% of sponges >2 m from the scarp had more upright arborescent, digitate, or pendunculate morphologies. The substratum at the scarp is sloped and irregular resulting in the potential for higher flow velocities than 5 m back from the scarp and also the possibility for less sediment accumulation. Massive, amorphous, and encrusting morphologies are better suited to withstand abrasion or scouring which are more likely to occur in areas with higher flow velocities (Bell and Barnes 2000b). In contrast, at 5 m from the scarp, the substratum is relatively flat, allowing accumulation of a sediment layer up to 5 cm thick (Ruzicka and Gleason 2009). The arborescent, digitate, and pendunculate morphologies are favored farther back on the ledge because they reduce accumulations of sediment on organismal surfaces and prevent smothering (Lasker 1980; Bell and Barnes 2000a).

In addition to spatial variation, sedimentation rates were predicted to vary seasonally with highest sedimentation rates expected in the fall and winter months, as observed in previous studies (Jordan *et al.* 2010). Instead, the dependence of inorganic sedimentation rates and grain size composition on wave heights and wind speeds supersedes seasonal patterns. The lack of seasonal predictability in sedimentation rates is significant for sessile benthic organisms occupying off shore reefs of the SAB. For example, as Chapter 2 will

show, survival of juveniles of the stony temperate coral *Oculina arbuscula* can be impacted significantly by high sediment loads. The temporal unpredictability of these high sediment events, however, suggests that this parameter is, at most, a weak selective force in the reproductive timing and recruitment of *O. arbuscula*.

As a final methodological note, the sediment trap dimensions used in this study followed recommendations made by Gardner (1980) and Butman (1986) for unbiased sediment collection in high energy systems that experience multidirectional currents. A recent review by Storlazzi *et al.* (2011) indicated that sediment traps in turbulent systems may preferentially collect larger diameter grains with higher specific gravity, thus under-representing finer particles that can be carried past sediment traps before settling occurs. The dominance of the smallest organic grain size (<63 μm) across all sampling periods, despite variation in wave height and wind speed, suggest a size-based bias in sediment trapping did not occur. To verify that our trap design was unbiased, future studies may compare the grain compositions observed in the present study to sediments collected from the seafloor adjacent to reef ledges to determine the degree of similarity of sediments accumulated in traps to those that benthic organisms encounter.

This study provided insight into the sediment dynamics occurring on J-Y Reef, a temperate hard-bottom in the SAB. In Chapter 2, I investigate the effects of this sedimentation on a conspicuous member of these hard-bottom reefs: the temperate coral, *Oculina arbuscula*. Concentrating on the juvenile phase, I determine whether certain colony morphologies are more beneficial in coping with sediment stress and quantify the impact that sedimentation has on juvenile growth and survivorship.

Table 1. Two-way repeated measures ANOVA for inorganic and organic sedimentation rates collected from 1, 2, and 5 m from the reef ledge from July 2008- October 2010.

Inorganic	df	SS	F-Ratio	P-value
Collection Date	10	3083.78	49.92	<0.0001*
Distance from the scarp	1	17.09	2.77	0.10
Date*Distance	21	521.08	4.02	<0.0001*
Organic				
Collection Date	10	22.72	20.63	<0.0001*
Distance from the scarp	1	0.017	0.15	0.69
Date*Distance	21	3.72	1.61	0.05

Table 2. Linear regression reports showing the relationships between sedimentation rates across the reef ledge and wave height from July 2008- October 2010 at J-Y Reef, GA.

Inorganic sediment mass	R^2	P-value	Equation
1 m from scarp	0.25	<0.0001*	y= -170.52+ 295.02*wave height
2 m from scarp	0.19	<0.0001*	y= -135.46+ 265.07*wave height
5 m from scarp	0.44	<0.0001*	y= -260.73+ 395.53*wave height
Organic particle mass	R^2	**P-value**	**Equation**
1 m from scarp	0.01	0.35	y= 9.66- 7.32*wave height
2 m from scarp	0.04	0.07	y= -0.42+ 2.32*wave height
5 m from scarp	0.08	0.03*	y= -2.50+ 4.44*wave height

Table 3. Linear regression reports showing the relationships between median grain sizes across the reef ledge and wave height from July 2008- October 2010 at J-Y Reef, GA.

Inorganic median grain size	R^2	P-value	Equation
1 m from scarp	0.38	0.03*	y= 1.44+0.08*wave height
2 m from scarp	0.48	0.01*	y= 1.47+0.06*wave height
5 m from scarp	0.28	0.09	y= 1.47+0.06*wave height
Organic median grain size	R^2	**P-value**	**Equation**
1 m from scarp	0.18	0.19	y= 0.89+0.46*wave height
2 m from scarp	0.12	0.28	y= 0.98+0.42*wave height
5 m from scarp	0.28	0.07	y= 1.02+0.43*wave height
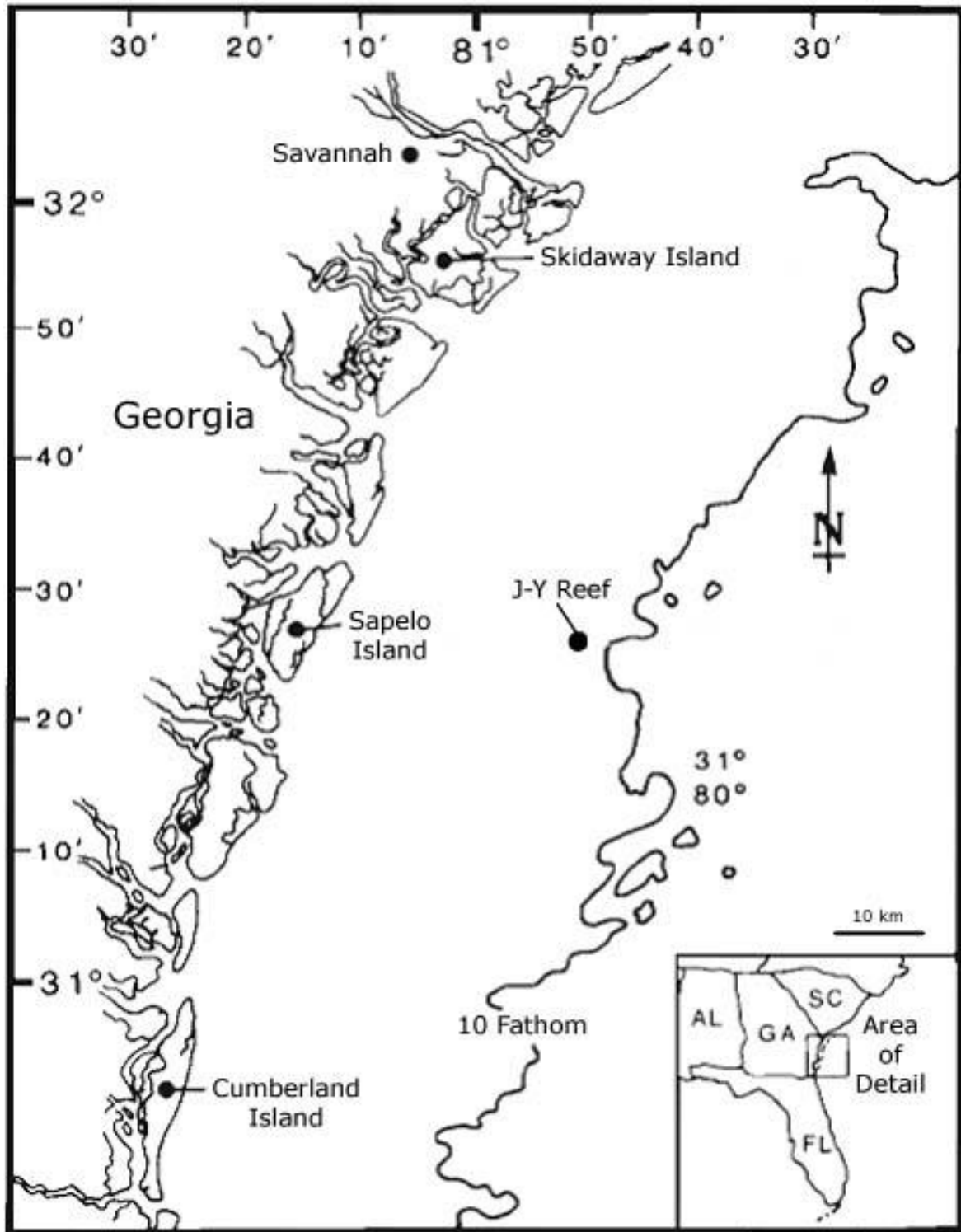
Figure 1. J-Y Reef is located approximately 32 km off the Coast of Sapelo Island, Georgia, USA, within the South Atlantic Bight.
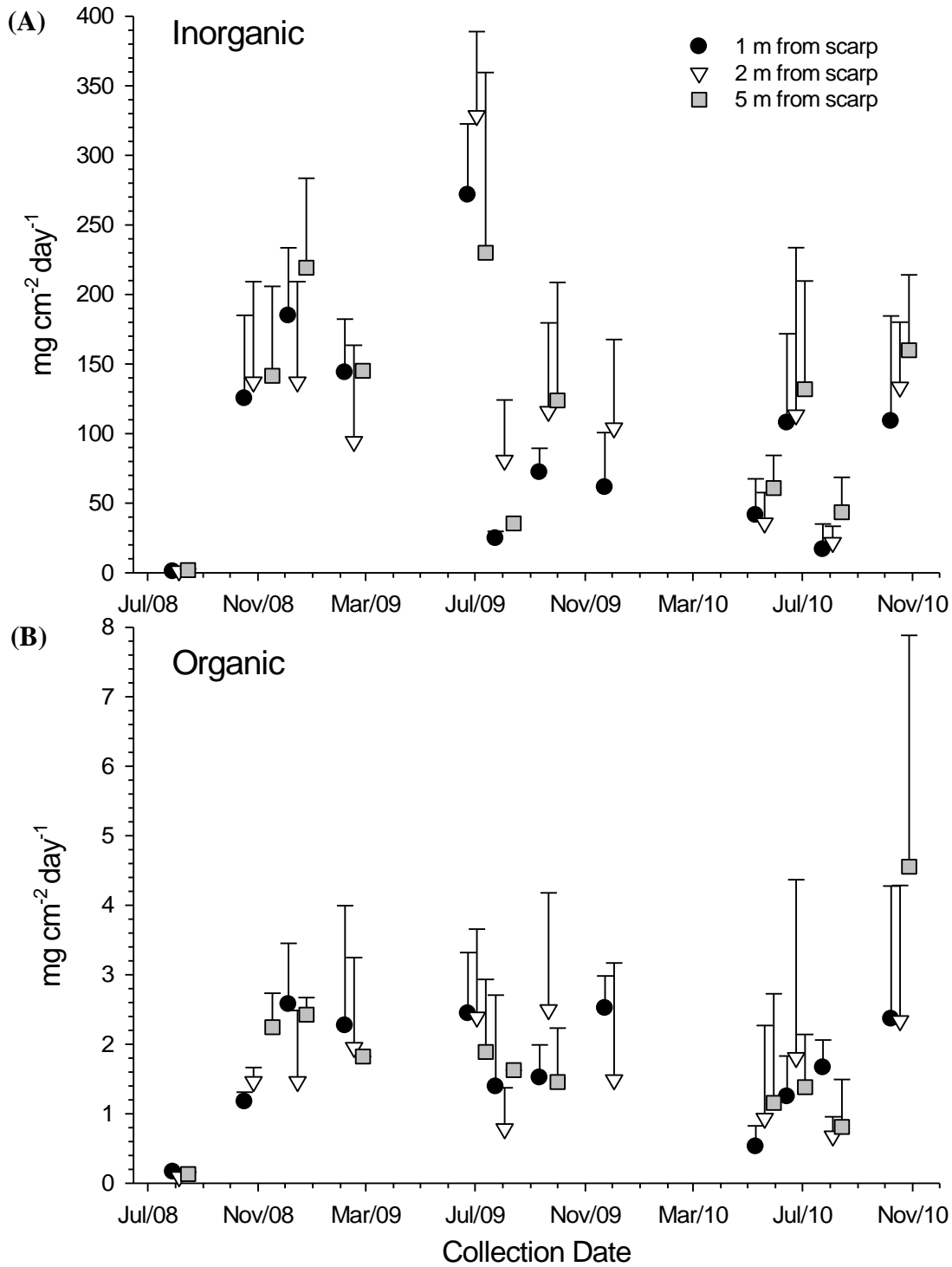
Figure 2. (**A**) Inorganic and (**B**) organic sedimentation rates at 1, 2, and 5 m from the scarp from July 2008-

October 2010 at J-Y Reef. N=4-10 traps per data point and error bars are ± 1 S.D.
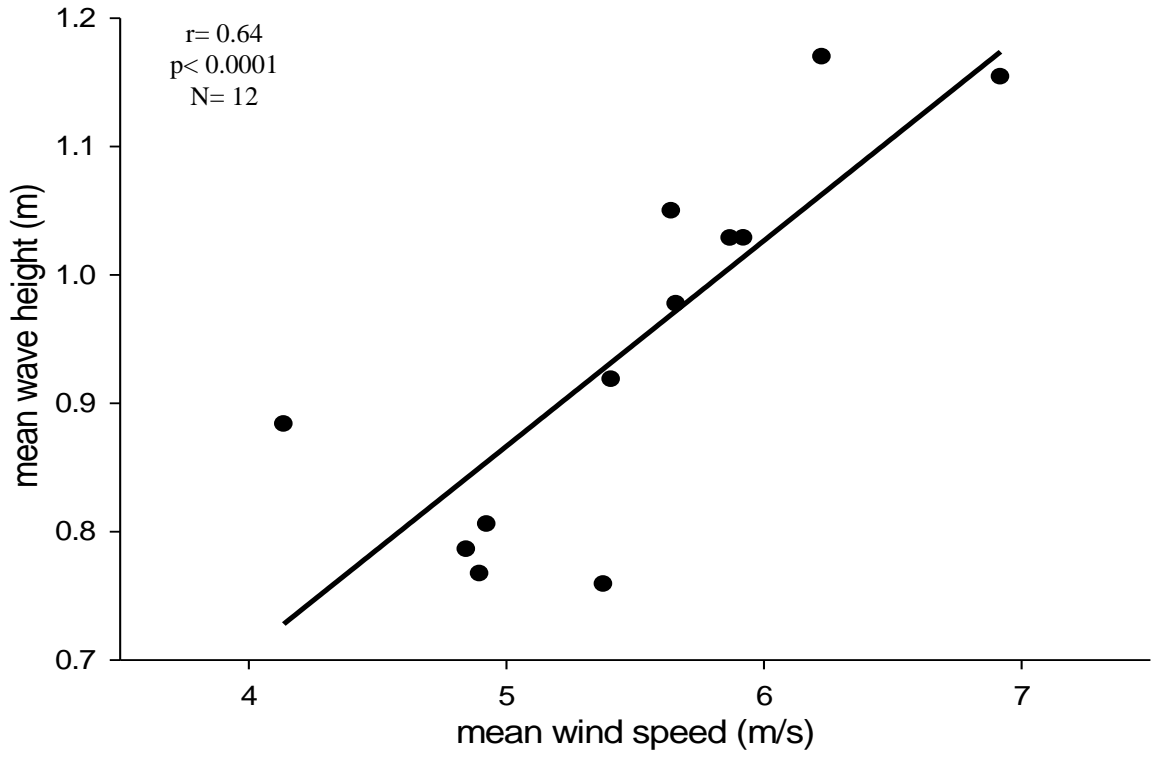
Figure 3. Correlation between mean wind speed (m) and wave height (m/s) collected from Gray's Reef buoy, Georgia, USA, from July 2008-October 2010.
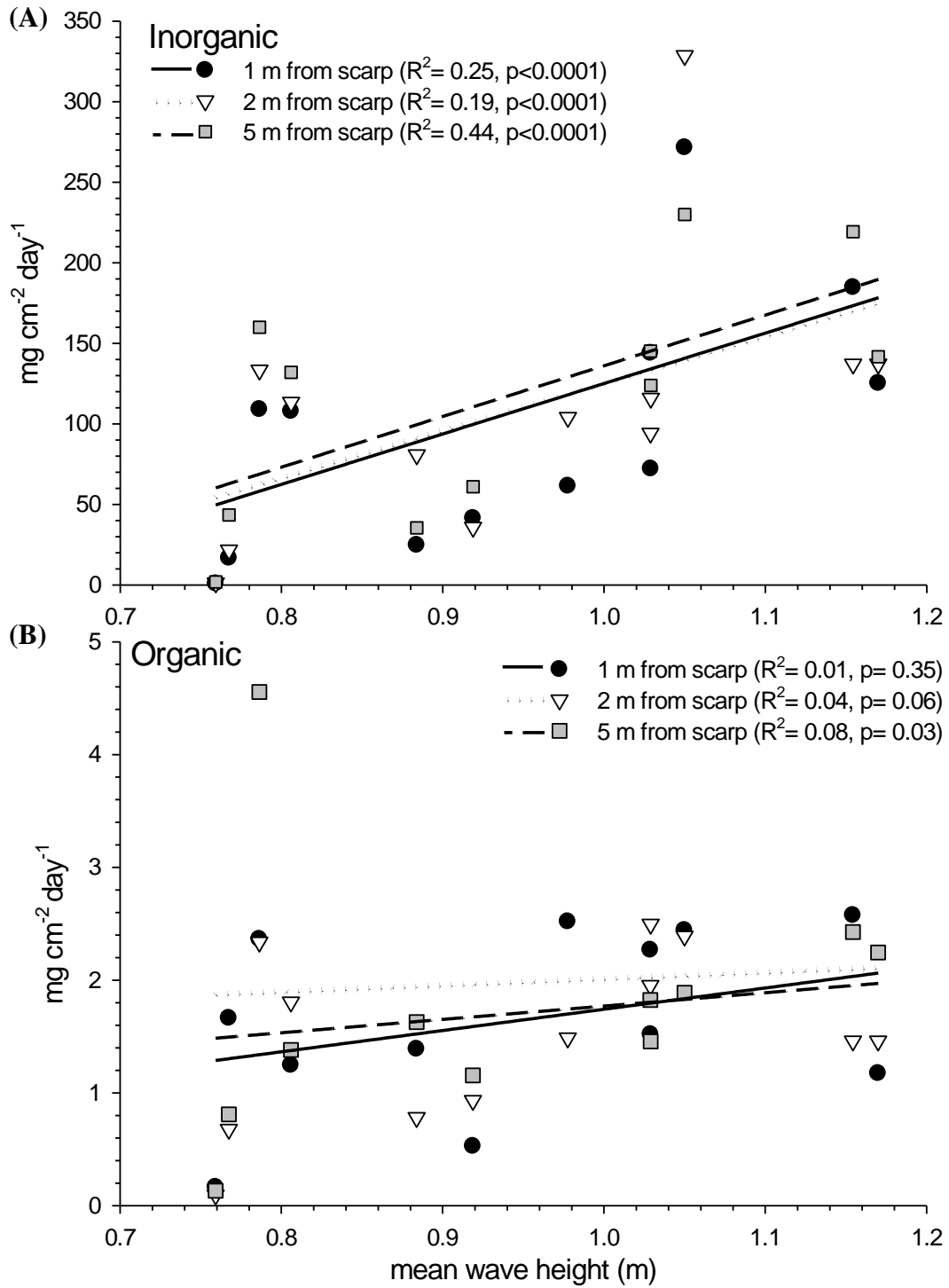
Figure 4. Relationship between mean wave height and sedimentation rates collected from 1, 2, and 5 m from the reef scarp for **(A)** inorganic and **(B)** organic sediments.
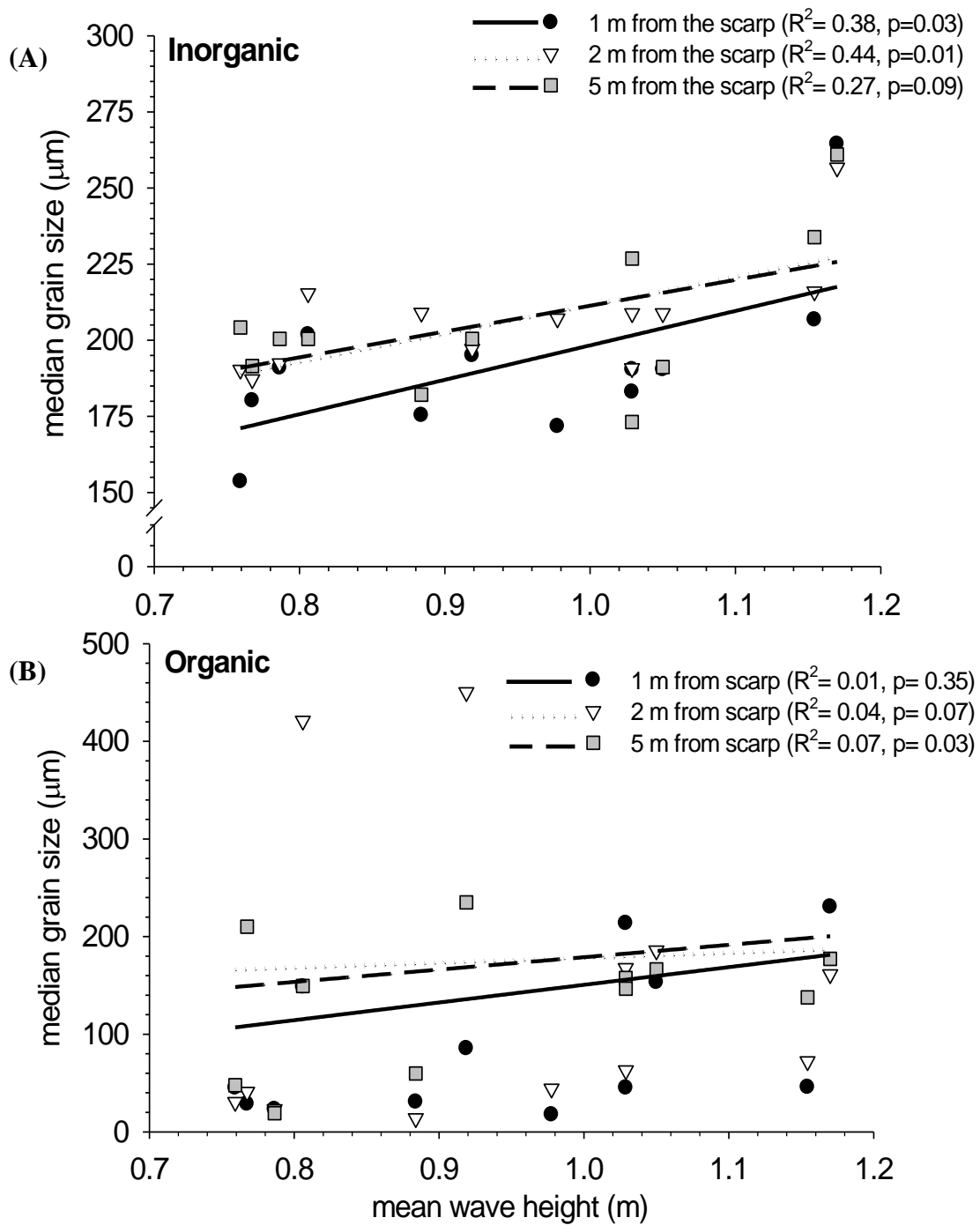
Figure 5. Relationship between mean wave height and median grain sizes collected from 1, 2, and 5 m from the reef scarp for **(A)** inorganic and **(B)** organic sediments.

CHAPTER 2

GROWTH AND SURVIVAL OF VARIOUS JUVENILE MORPHOLOGIES OF THE TEMPERATE CORAL, *OCULINA ARBUSCULA*, IN A HIGH SEDIMENT ENVIRONMENT

INTRODUCTION

Recruitment is broadly defined as the addition of new individuals to a population. In marine organisms this process usually includes a planktonic larval phase combined with either a sessile or demersal adult phase (Caley *et al.* 1996). Marine ecologists agree that both pre-settlement and early post-settlement (i.e., within weeks or months) processes influence adult populations and community structure in benthic marine systems (Thorson 1950; Gaines and Roughgarden 1985; Sammarco 1991; Wittenberg and Hunte 1992), but there is debate about which stage is a better predictor of adult population dynamics (Sammarco 1991).

Development of the larval stage of many marine sessile invertebrates occurs in the water column (Iwasa and Roughgarden 1986; Connelly and Roughgarden 1999). Larvae may remain in or near their area of origin and recruit locally to the population (reviewed in Jones *et al.* 2009) or be transported by currents and waves tens to thousands of kilometers from their natal habitat (Gaines and Roughgarden 1985). Regardless of dispersal distance, larvae are exposed to physical and biological disturbances in the water column such as predation, salinity changes, and unfavorable currents or temperatures. The idea that external biotic and abiotic forces limit the number of larvae in a given area gave rise to the theory of "supply side" ecology (Iwasa and Roughgarden 1986; Miller *et al.* 1989). Supply side ecology states that the larval supply in a marine environment is the major factor controlling adult marine population dynamics (Lewin 1986; Wing *et al.* 1995; Caley *et al.* 1996; Connelly *et al.*

2001). Variability in larval supply has been used as an explanation for patterns in adult populations and community structure in rocky intertidal zones, coral reefs, and temperate subtidal communities (Wing *et al.* 1995; Palma *et al.* 1996; Hughes *et al.* 2000; Connelly *et al.* 2001). However, while most marine populations are dependent upon the supply of larvae in the plankton (Caley *et al.* 1996), areas producing or receiving adequate numbers of larvae are probably structured more by post-settlement processes.

Newly-recruited individuals have a lower threshold than adults for resisting biotic and abiotic pressures because they are smaller and have less energy to expend. A review by Gosselin and Qian (1997) found juvenile mortality in benthic marine invertebrates is highest within the first four weeks of settlement to the benthos (>90 %) and may be >30% in the first day of settlement. As juveniles grow, mortality decreases exponentially (Gosselin and Qian 1997).

One group of benthic marine invertebrates that has been studied extensively in terms of both larval and post-settlement phases is tropical corals. As in many other benthic invertebrates, there is disagreement as to whether coral populations are structured more by pre- or post-settlement processes (Mundy and Babcock 2000). There are two distinct modes of sexual reproduction in corals— brooding and broadcast spawning (Richmond 1997). A majority of corals (about 85%) utilize broadcast spawning in which eggs and sperm are released into the water column and development to the planula stage occurs in the plankton (Richmond and Hunter 1990). Broadcast spawned planulae are vulnerable to predation, pollution, and changes in temperature, salinity, and light availability (Richmond 1997; Edmunds *et al.* 2001) because they are small and may spend weeks to months in the water column.

Once coral larvae are ready to settle, they generally exhibit a negative phototactic response and begin actively searching for suitable substrata. Habitat selection is important in determining subsequent adult distributions (Mundy and Babcock 2000; Baird *et al.* 2003); coral planulae require hard substrata or loose pieces of rubble for settlement and will not settle on soft sediment (Maida *et al.* 1994; Richmond 1997). Once recruited to the benthos, juveniles must tolerate competitive interactions, predation, and disease with lower energy reserves than adult conspecifics (Bak and Meesters 1988; Box and Mumby 2007).

Sedimentation is considered a significant factor influencing post-settlement survival in stony corals (Cnidaria: Scleractinia) (Fabricius *et al.* 2003). Sediment can affect corals directly through abrasion (Aller and Dodge 1974; Loya 1976; Rogers 1983; Miller *et al.* 2000) and partial or total burial (Lasker 1980; Babcock and Davies 1991; Birkeland 1997; Wesseling *et al.* 1999; Babcock and Mundy 2006) and indirectly through reduced food capture (Bak 1978; Stafford-Smith and Ormond 1992), decreased photosynthetic rates (Riegl and Branch 1995; Te 1997), and reduced calcification rates (Goreau 1959). Tolerance to sediment stress is up to 2 orders of magnitude lower in juvenile corals than that of adults (Fabricius *et al.* 2003).

 To deal with the negative effects of sediment, corals have evolved sediment rejection mechanisms that are classified as passive and active. Passive sediment removal is dependent on coral morphology and skeletal architecture (Bak and Elgershuizen 1976; Lasker 1980; Rogers 1983; Rice and Hunter 1992; Stafford-Smith 1993). Arborescent and ramified colony growth forms are generally considered efficient because sediment does not settle on branches easily (Stafford-Smith 1992; Veron 2000). Calice shape, height, and number of septa contribute to passive sediment shedding at the corallite level by creating small vortices or

concentrating sediment in a small area of the polyp for easy removal (Hubbard and Pocock 1972; Riegl 1995; Todd 2008). Vertical or angled orientation of the colony on substratum and water movement may also increase the amount of sediment that is passively removed (Rogers 1990).

Though passive mechanisms are beneficial because they require no energy expenditure from corals, they are only practical for removing limited amounts of sediment (Lasker 1980). During times of chronic or high sediment influx, active mechanisms must be employed to compensate for sediment that cannot be removed solely by passive methods. Active mechanisms are a function of animal behavior and require energy expenditure for the physical transport of particles off the colony surface (Lasker 1980; Stafford-Smith 1993). Riegl and Branch (1995) found scleractinian corals exposed to high levels of sediment allocated up to 65% of their total available energy to mucus production for active sediment removal processes. Active removal is generally initiated within 10 minutes of sediment contacting coral surfaces and occurs through polyp distention, ciliary action, and mucus production (Stafford-Smith and Ormond 1992; Stafford-Smith 1993). Efficiency of sediment removal is species-specific and active mechanisms can vary within species (Stafford-Smith and Ormond 1992; Stafford-Smith 1993). For example, Gleason (1998) found different sediment shedding ability in *Porites astreoides* colonies of differing color, although they had an identical colony shape.

Though there is much known concerning passive and active sediment rejection in stony corals (Cnidaria: Scleractinia), studies have focused on adult colonies (e.g. Hubbard and Pocock 1972; Stafford-Smith and Ormond 1992; Stafford-Smith 1993; Riegl and Branch 1995; Gleason 1998; Nugues and Roberts 2003). Previous studies comparing adult colonies

have found that certain morphologies are better suited to tolerate high sedimentation (Hubbard and Pocock 1972; Riegl 1995; Todd 2008). However, disparate evidence exists between laboratory and field conditions and among experimental studies concerning passive and active sediment shedding efficiencies in corals (see Stafford-Smith and Ormond 1992). For example, a significant correlation between calice size and active sediment rejection was reported in Hubbard and Pocock (1972) and Stafford-Smith (1993). These studies contradict results from Bak and Elgershuizen (1976), who noted sediment rejection efficiency was independent of calice size. Additionally, the role sediment plays in the survival of juvenile corals remains relatively unexplored (Ritson-Williams *et al.* 2009). It is generally accepted that juvenile corals are more susceptible to increased sedimentation than adult conspecifics due to their small size and lack of morphological complexity (Bak and Engel 1979; Lirman *et al.* 2003; Babcock and Smith 2000; Edmunds and Gates 2004). However, no studies to date have quantified the tolerance of sedimentation with relation to intraspecific variation in juvenile morphology. There may be a benefit to investing energy into upward growth soon after settlement to the benthos to "escape" the negative effects of environmental stressors such as sediment.

For the present study, I investigated the effects of sedimentation on growth and survival of various juvenile morphologies of *Oculina arbuscula*, a stony coral that inhabits rocky ledge reefs within the SAB. Previous studies investigating effects of sediment on other species of scleractinian corals suggests that a branching morphology is more efficient for sediment rejection than a more encrusting morphology, thus I predicted juveniles with greater branching would exhibit enhanced passive and active sediment shedding ability. Additionally, I predicted that more highly branched *O. arbuscula* juveniles would have

higher growth rates and increased chances for survival than encrusting or dome shaped individuals in a high-sediment environment.

METHODS

Study site

The study was conducted at J-Y Reef (31° 24.340 N, 80° 47.431 W), a temperate hard bottom reef at 18-20 m depth approximately 32 km off the coast of Sapelo Island, Georgia, USA , in the South Atlantic Bight (SAB) (Figure. 1). J-Y Reef hosts high abundances of the scleractinian coral *Oculina arbuscula*, as well as many other invertebrate species such as sponges, bryozoans, cnidarians, decapods, mollusks, echinoderms, and tunicates. Sessile benthic invertebrates are densely packed within the first 2 m of scattered vertical ledges of moderate relief (1-2 m) that plateau into sandy expanses approximately 5 m from the scarp edge. Sedimentation rates in this area are consistently >50 mg cm^{-2} day^{-1}, creating a very high-sediment environment (Chapter 1). Erosion and deposition of sediments can expose or cover irregularly occurring hard-bottom ledge habitats, suggesting that sediment may be an important factor shaping the benthic sessile communities that form a conspicuous part of these ledges (Wenner *et al.* 1983; Hopkinson *et al.* 1991).

Study Organism

Oculina arbuscula is a branching scleractinian coral found in the temperate waters of the SAB that forms colonies of tangled branches up to 1 m in height and is a broadcast spawning species (Ruppert and Fox 1988). *Oculina arbuscula* occurs on vertical and cryptic surfaces as well as exposed horizontal surfaces throughout its range (Miller 1995). Adult colonies commonly occur within the first 2 m of rocky ledges (Figure 6). Juvenile morphologies at J-Y Reef range from flat or encrusting colonies to branching colonies. The

adult morphology of this species facilitates sediment removal by minimizing flat surfaces and allowing water flow through branches (Todd 2008); however, intraspecific variation in juvenile sediment shedding ability among morphologies has not been previously investigated.

Passive and active sediment shedding assays

Juvenile *O. arbuscula* <40 mm in diameter representing a range of colony morphologies (Figure 7) were collected by prying them off substrata with a dive knife from an artificial reef (the Liberty Ship Daniels) and the J-Y Reef ledge. Colonies were placed in an aerated cooler with 35 ppt sea water for transport (approximately 4 h). Passive and active sediment rejection abilities were investigated in the laboratory with these colonies by adding inorganic sediments to the surfaces of dead and live juveniles, respectively. Each colony was super glued to a rubber stopper (base diameter of 15 mm) that served as a pedestal to keep the coral above the bottom of the container and avoid burial by sediment during experiments (Figure 7). The amount of sediment shed by juvenile *O. arbuscula* as a sole function of morphology (i.e., passive sediment shedding rate) was estimated using skeletons devoid of animal tissue. Colonies were put in plastic bags containing deionized water for 2 weeks so that all living tissue rotted off and could be washed from the skeleton easily under running water. Bare skeleton is more porous than live tissue and sediment can get lodged in the septa and coenosteum causing retention of inorganic particles that would not occur with live tissue present (Lasker 1980). To reduce overestimation, bare skeletons were coated with a thin layer of paraffin wax to mimic tissue.

Live colonies used in active sediment shedding assays were kept in a 38 l glass aquarium containing artificial seawater (Instant Ocean; 35 ppt) and housed in a climate

controlled room 20.5 ($\pm$ 0.5 S.D.) °C. An overhead light bank of 8, 27-Watt daylight

fluorescent lights (Sylvania Co, Sylvania, GA) suspended 1 m from the water surface

provided light intensity equal to that reaching horizontal surfaces at J-Y Reef ($\approx$ 47.7 µmol s^{-1}

m^{-2}) (K.O. Matterson, pers. communication.).

Colonies were removed from the glass aquarium and placed individually in the center

of a 1 l plastic container prior to each experiment (14 cm L x 10 cm W x 6 cm H). Containers

were filled with 34 ($\pm$ 1.2 S.D.) ppt seawater and kept at 23 ($\pm$ 1.1 S.D.) °C. A small air stone

was placed in each container to prevent a reduction in oxygen concentration. Air stones

provided a single stream of bubbles on the periphery of the container so minimal movement

of water occurred in the container.

Inorganic sediments gathered at J-Y Reef were combusted in a muffle furnace at

500°C for at least 1 h to remove organic content. A treatment of either low (30 mg cm^{-2}) or

high (100 mg cm^{-2}) inorganic sediment was applied using a flour sifter with a rotating handle.

Levels of sediment application were chosen based on sediment trap data collected from J-Y

Reef from July 2008- October 2010 (see methods in Chapter 1, Figure 2). The percent

composition of various grain sizes (>500µm: $\approx$5%, 250-500µm: $\approx$5.5%, 125-250µm: $\approx$82%,

63-125µm: $\approx$5.5%, and <63µm: $\approx$2%) of sediments used in treatments was also chosen to

reflect natural field conditions at J-Y Reef (see Chapter 1, pp 23). Approximately one-third of

the total mass of sediment was applied at each of three 1 min intervals spaced approximately

20 min apart. This application process ensured that sediment runoff resulting from heavy

amounts of sediment accumulating on the coral at once was minimized.

Three plastic bottle caps were placed around the coral and served as sediment traps

(surface area = 19.6 cm^2) to determine if sediment added to the container fell uniformly over

the container surface (Figure 8A). Sediments that remained on the coral and in each bottle cap were collected 24 h after final application (Figure 8B) and filtered separately on pre-weighed filters with a pore size of 0.45 μm (Type HAWP, Millipore). Sediments on filter papers were rinsed with deionized water to remove dissolved salts (Gleason 1998). Each filter with collected sediments was placed in a preweighed aluminum weigh boat, dried for 24 h at 60°C, and reweighed to the nearest 0.1 mg. This procedure provided an estimate, in still water, of how much sediment juvenile *O. arbuscula* colonies shed.

Passive and active assays were run simultaneously and photos taken at 0 min and 24 h after sediment application (Figure 9). Passive experiments were replicated three times for each of 25 colonies. Active shedding experiments were completed once for each treatment (low and high) per live colony to reduce the effects of stress. Low and high sediment treatments were conducted haphazardly. Corals were placed in an indoor laboratory aquarium for at least 24 hours between experimental trials and fed Zooplex® marine invertebrate food (Kent Marine Science, Franklin, WI).

At the conclusion of sediment shedding assays, planar and total surface areas were determined for each colony. Planar surface area was quantified using ImageJ software on photographs taken at a standard distance of 30 cm above the colony (Abramoff *et al.* 2004). Total surface area was estimated with the aluminum foil method (Marsh 1970). The surface of each colony was covered with aluminum foil, ensuring foil did not crumple or overlap and cause overestimation of surface area. The foil was removed and weighed to the nearest 0.1 mg. Foil mass was converted to total surface area by scaling to the mean mass of 50 pre-cut 2 cm^2 rectangles of foil (Marsh 1970). The ratio of total surface area to projected surface area was used as a measure of colony complexity. Colonies with a higher ratio were considered

more morphologically complex (i.e., exhibit upward growth or branching) and colonies with a ratio close to one were relatively flat or dome shaped.

The amount of sediment retained on each coral in passive and active sediment shedding experiments met normality and homogeneity of variance assumptions after $\log_{10}$ transformation. Linear regressions were performed with the morphological complexity ratio as the independent variable and amount of sediment retained on the colony surface as the dependent variable.

In situ monitoring of growth and survival rates for juvenile *Oculina arbuscula*

Concrete recruitment tiles measuring 15 cm L x 15 cm W were monitored by digital photography for one year to investigate juvenile growth and survival in the field. Photographs provide a permanent record of the location, size and shape of sessile organisms that can be analyzed digitally (Gosselin and Qian 1997). A total of 20 recruitment tiles were placed haphazardly between rods used for sediment trap collection. Ten tiles were placed between rods at 1 m from the scarp and 10 tiles were placed between rods at 2 m from the scarp. These distances were chosen because three 1 x 10 m belt transects conducted haphazardly at 1, 2, and 5 m from the scarp showed adult *Oculina arbuscula* are most abundant within the first 2 m of the reef scarp (Figure 6). The recruitment tiles used for this study were originally placed north of the sediment trap transect lines on J-Y Reef in July 2004 by a previous graduate student (Wagner 2006). They were moved to the vicinity of the sediment traps in August 2009. Each tile had two large *O. arbuscula* adult colonies epoxied to the upper surface when they were originally placed at J-Y Reef. These colonies, if present, were excluded from analyses. Over time the tiles have been conditioned and additional *O. arbuscula* recruited to the upper surfaces. All tiles had at least one juvenile *O. arbuscula* on

the surface at the onset of the experiment.

A 5 megapixel Olympus C-5050 digital camera with an internal strobe enclosed in an underwater housing and secured to a PVC framer was used for all photos. Photographs were taken from the top and profile view of each tile for ease in measuring lateral diameter and area (projected surface area) and height of branches (upward growth). Tiles were centered in the PVC framer for each top view photograph and aligned against the side of the PVC framer for the profile view to ensure replication. Two to three photographs were taken from the sides of each tile to ensure accurate identification of colonies. Adobe Photoshop CS2 was used to identify colonies on each tile and monitor them in subsequent photos. Every colony was outlined with the 'magic wand' tool and a separate layer was created with all outlined colonies appearing against a black background (Figure 10). Each layer created in Adobe Photoshop CS2 was exported as a JPEG image into ImageJ software. ImageJ estimated total growth of juveniles from the top and profile views of each photograph (Abramoff *et al.* 2004). ImageJ measured the maximum diameter as the longest distance between any two points within the colony boundary edges. Colonies with an initial diameter >40 mm did not meet the definition of juvenile size and were excluded in analyses. Total growth for colonies without upward growth or branches (planar area) was estimated from the outline of the colony taken from the top view. Total growth for colonies with an upright or branching morphology was estimated as a combination of planar area and branch area. The linear lengths (cm) of all branches were digitally estimated from the profile views and converted to total surface area (cm^2) using the aluminum foil technique (Marsh 1970). A standard for the relationship between linear length and branch surface area and diameter was created using branches from dead colonies. Twenty branches were cut at the base with a Dremel hand tool

fitted with a diamond saw bit. All branches were measured linearly by placing a ruler at the base of the branch and measuring the distance to the tip of the branch. Each branch was then covered with a layer of aluminum foil and weighed in a preweighed and precombusted aluminum weighing pan. The weight of foil used to cover the branch was converted to total surface area using a conversion equation. Total surface area was then scaled to the linear length of each branch for a ratio of surface area per unit linear length (2.35 cm^2 per 1 cm linear length, ± 0.39 cm S.D.). Mean diameter was calibrated with the same branches used to calculate total surface area. The linear distance across the base of each branch was measured three times and averaged (mean diameter $= 0.46$ cm ± 0.019 cm S.D.). Thus total surface area of a colony was calculated as:

$TA_i = p + 2.35 * bl - 0.46 * bn,$

where TA_i is the total area of the ith colony, p is the planar surface area, bl is the branch length, and bn is the number of branches on the colony. Branch lengths were added to the planar area and the diameter of branch bases subtracted from the total area to compensate for redundancy of digital measurements using these methods. The equation was tested on 20 juvenile *O. arbuscula* with a known *TA* calculated from the aluminum foil technique. The equation estimated *TA* within $0.22\text{ cm}^2 \pm 0.15\text{ cm}^2$ S.D. of the actual total surface area of juveniles. These conversions were necessary because total surface area of small colonies cannot be accurately measured from photographs; however, planar area, linear length and diameter of branches were obtainable from profile view photographs of recruitment tiles. The growth rate for each time interval was scaled as a mean daily growth rate by dividing total growth by the number of days between photographs and computing the mean of these rates. Partial mortality is commonly seen in modular colonial organisms, thus growth rates could be

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either positive or negative for each date. Mortality rates were also recorded and were defined as any colony that was absent in a photograph after being present in a previous date's photograph (Figure 10).

Stage-based transition matrix model development

A transition matrix model was created from juvenile growth and survival data collected in the field. Variations on standard "stage class" Lefkovitch (1965) projection matrices have been widely used in population dynamics studies and to elucidate a variety of short and long term changes in invertebrate population structures (Caswell 1983). Stage-based models are best used for parameters that are not age-specific (Caswell 1989), such as survival and growth rates in corals (van Moorsel 1985; Edmunds 2000). The poor correlation between age and size in corals results from partial mortality, fission and fusion in colonies (Rylaarsdam 1983; Hughes and Jackson 1985). A study by Barbeau and Caswell (1999) modeled size-based short-term changes in sea scallop larvae in relation to predation and dispersal. Transitional probabilities resulting from survival, growth, and movement within and among size classes were used to conceptualize short-term growth and survival patterns in the field (Barbeau and Caswell 1999). Similarly, a short-term model was created for the present study in this fashion to estimate juvenile *O. arbuscula* population dynamics over one year at J-Y Reef.

Juvenile *O. arbuscula* were divided into 5 size classes: <10 mm, 10-19 mm, 20-29 mm, 30-39 mm, >40 mm. Juveniles were also divided into branched and unbranched categories. Transition probabilities were calculated as the number of individuals that transitioned from size class *j* to size class *i* divided by the total individuals in size class *j* from

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the previous date: $N_{i\,t+1} = \dfrac{N_{j\to i}}{N_{it}}$

Individuals exhibited transitions during each monitoring interval that included any of the following: mortality, partial mortality, persisted in the same size class, growth, branched and suffered partial mortality, branched and persisted, or branched and grew. The probabilities of transitioning to any of these states were averaged across all time intervals and combined into a matrix model with elements representing all state fate transitions for juveniles based on photographic monitoring (Ruesink 1997). Transition probabilities are represented by the equation: $p_{avg} = \dfrac{\Sigma p_{ti}}{5}$

where p_{avg} is the average transition probability, Σp_{ti} is the sum of all probabilities for a specific transition, and 5 is the number of total time intervals during monitoring (Table 2). All transitions observed within unbranched and branched size classes and from unbranched to branched morphology are represented in Figure 11. Transition probabilities were used in conjunction with corresponding sedimentation rates for inorganic particles occurring at J-Y Reef to determine if sedimentation influenced variation in survival and growth with relation to morphological complexity.

The transition probabilities for total and partial mortality, persistence, growth and branching for each time interval were paired with the mean inorganic sedimentation rates for the corresponding interval. Partial mortality was calculated as a mean of all transition probabilities from size i to all smaller size categories (i.e., $3 \to 2$ and $3 \to 1$). Growth and branching were calculated as means of all transition probabilities from size i to all larger size or branched categories, respectively. For statistical analysis, all probabilities were arcsine

square root transformed to meet parametric assumptions. ANCOVAs (analysis of covariance) determined if mean inorganic sedimentation rate was a correlated variable that explained variation in transition probabilities for various size classes and morphologies of juvenile *O. arbuscula* defined in the above section.

RESULTS

Passive and active sediment shedding assays

Grain size distribution for inorganic sediments used in laboratory sediment shedding experiments were similar to those accumulating in sediment traps at J-Y Reef (Kolmolgorov-Smirnov Goodness-of-Fit test, D= 0.96, N= 35, p= 0.18) (Figure 11). The silt fraction in laboratory sediments was lower than field observations because concentrating enough silt in the laboratory to contribute adequate mass for experiments was difficult; however, overall distribution of grain sizes used in laboratory experiments generally reflected natural composition of sediments. Inorganic particles fell uniformly across the surface of experimental containers and were not significantly different from the desired application levels of 30 and 100 g cm-2 in low and high sediment treatments, respectively (two-tailed t-test, t= 1.83, p= 0.07 for low treatment, t= 0.89, p= 0.37 for high treatment). Thus, methods of applying sediment were appropriate and were correctly scaled for the surface area of experimental containers.

When considering passive mechanisms alone, juveniles with a greater branching morphology retained significantly less sediment on their surfaces after 24 hours. Greater branching complexity accounted for 44% of the variance in passive sediment shedding ability in juvenile *O. arbuscula* under low sediment application compared to 21% of sediment shedding ability in the high sediment treatment (linear regressions, R^2= 0.44, p= 0.0003 for

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low and R^2= 0.21, p= 0.02 for high) (Figure 12 A and B).

The effect of morphology on sediment shedding ability that was observed in passive assays disappeared when live colonies were tested (linear regressions, R^2= 0.05, p= 0.22 for low and R^2= 0.09 and p= 0.13 for high) (Fig. 13 A and B). Active mechanisms employed by live tissues were able to compensate for initial differences in morphology and even in high sediment treatments all colonies were able to clear 65 mg cm^{-2} or more of inorganic particles in 24 hours.

In situ monitoring of growth and survival rates for juvenile *Oculina arbuscula*

The probabilities for all transitions (growth, mortality, partial mortality, persistence in a size class, and becoming a branching morphology) obtained from the field were compiled into a transition matrix model (Figure 14). This model showed that the impact of sedimentation rates on mortality differed among juvenile size classes and between colony morphologies for the largest size class of >40 mm (ANCOVA, $F_{4,4}$ = 6.36, p= 0.02) (Figure 15). Except for the 20-29 mm size class, a significant positive association between sedimentation rate and mortality was observed in the smallest and intermediate juvenile size classes of *O. arbuscula*. Partial mortality was observed in all size classes and morphologies; however, juveniles >20 mm in diameter did not revert to <10 mm in diameter during the study. Probabilities of mortality for juveniles that successfully grew into a branched morphology with a diameter >40 mm during the study were not affected by levels of inorganic sedimentation.

Except for the unbranched 30-39 mm size class, growth rates were negatively impacted by increasing sedimentation rates in all size classes and morphologies (ANCOVA, $F_{4,4}$= 1.73, p= 0.2) (Figure 16). The lack of a significant relationship may be attributed to

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small sample size in several size classes (i.e. 5 colonies in the 30-39 mm branched size class). Growth from one size class to the next larger size class was common (i.e., from 11-19 to 20-29 mm size class). However, growth in juveniles <10 mm in diameter was highly variable and colonies of this size were equally likely to transition to any larger size class in one monitoring interval during the study. The probability of juveniles >20 mm in diameter transitioning to a branching or upright morphology was greater for colonies <20 mm in diameter.

Partial mortality that resulted in a colony diameter loss equal to one size class was also common in unbranched colonies during the study. In contrast, colonies that reached >40 mm with a branching morphology were not likely to experience partial mortality (Figure 14). Mortality was not observed in branching colonies 30-39 mm in diameter, but this may be due to a low sample size observed during the study (N= 5).

DISCUSSION

Sediments raining down on the surface of a coral colony will be rejected passively via polyp and colony morphology, and actively through energy expenditure by live tissues (Lasker 1980). Passive mechanisms such as colony morphology are important to corals because they can greatly reduce the amount of energy used for clearing processes, an activity that is more metabolically expensive for juveniles (Stafford-Smith and Ormond 1992). The present study examined the contribution of colony morphology in passive and active sediment rejection efficiencies in juvenile *O. arbuscula* inhabiting hard-bottom reefs of the SAB. Juvenile *O. arbuscula* with a greater branching or upright morphology passively shed more sediment than those with a more encrusting morphology. In high-sediment environments such as the SAB, a more complex morphology may be advantageous by

passively reducing the amount of sediment that ultimately will require active rejection by juveniles that have smaller energy reserves than adults (Lasker 1980; Stafford-Smith 1993; Riegl 1995).

Interestingly, when sediment rejection experiments were replicated with live colonies, the relationship between morphology and sediment retained on the colony was nullified. These results agree with field studies that demonstrate morphology is not as important as the contribution of living polyp behavior to the sediment clearing process (Lasker 1980). The present results show that live tissues of a range of juvenile *O. arbuscula* morphologies are sufficient to clear at least 65 mg cm^{-2} of sediment in stagnant conditions. Sedimentation rates on J-Y Reef where these juvenile corals were collected often exceed these levels (Chapter 1, Figure 2) so it is likely that they spend a significant amount of energy dealing with this abiotic stress.

Experimental conditions in the laboratory were such that little to no water flow was present in containers. This parameter has been shown in laboratory and field studies to aid sediment shedding so passive and active clearing efficiencies observed in this study should be viewed as conservative estimates (Lasker 1980). Adequate water flow can passively remove sediments and mucus sheets with entrapped sediments from coral surfaces (Lasker 1980) and in extreme cases allows species inefficient at sediment rejection to thrive in sediment laden environments (Riegl 1995). However, passive mechanisms do not always keep juvenile colonies free from sediment, especially under chronically elevated sedimentation such as observed in the SAB (Chapter 1). Small colonies are more easily buried under sediment in these conditions even when water flow is present, thus the efficiency of active mechanisms is also important (Lirman *et al.* 2003).

The advantages of possessing a branching morphology in high sediment environments was confirmed by monitoring survivorship of juvenile *O. arbuscula* for one year on J-Y Reef. Branched juveniles were less likely to suffer mortality than encrusting colonies under all sediment loads during the study. Size was also important to survival in juvenile *O. arbuscula* colonies. In all but one instance, juveniles 20-29 mm in diameter, smaller size classes exhibited an increase in the probability of mortality as sedimentation rates increased. In fact, mortality rates for juveniles 11-19 mm in diameter were as high as 60% at sedimentation rates of 120 mg cm^{-2} day^{-1}. Comparable results were observed in the tropical Pacific coral *Acropora millepora*, where juvenile survivorship in a high-sediment environment (~0.88-11.70 mg cm^{-2} day^{-1}) was only 39% of that observed on control tiles (Babcock and Smith 2000).

Growth rates decreased in the smallest size classes of less complex colonies and morphology did not seem to provide an advantage for growth under high sedimentation. Though no direct measures of juvenile energy budgets were taken in this study, the inverse trend observed in all size classes except 30-39 mm suggests that a trade-off between energy allocated for growth versus sediment rejection may occur in juvenile *O. arbuscula* inhabiting Georgia offshore reefs. More encrusting juveniles may be less equipped to grow and survive in a chronically high-sediment environment if energy requirements for sediment rejection exceed the total energy juveniles are able to obtain. Riegl and Branch (1995) found sediment severely affected coral metabolism in several scleractinian species by decreasing photosynthetic production, increasing relative respiration and increasing carbon-loss through greater mucus output. Mucus production in adult corals can account for up to 65% of energy allocation in corals during sediment stress (Riegl and Branch 1995) and may be higher for

smaller, less complex juveniles. Lower juvenile growth and survival rates are likely to translate into reductions in recruitment to the adult life history phase (Hughes and Tanner 2000) and, over time, may have significant effects on the structure of adult populations. Mortality rates of all juvenile size classes combined reached 66% during the present study. Only 1.7 recruits m^{-2} survived during the study, which mirrors the adult densities of *O. arbuscula* occurring 5 m from the scarp, but is lower than adult densities at 1 m from the scarp (Figure 6). Approximately 30 settlers per m^2 would be needed to result in the number of adults at 1 m from the scarp, indicating that sedimentation may have a significant impact on adult abundances through high juvenile mortality.

Sub-lethal responses to sediment stress that can reduce overall growth and survival of scleractinian coral species include expulsion of zooxanthellae, shrinkage of soft tissue, and exposure of underlying skeletal features (Stafford-Smith and Ormond 1992). These indirect effects of sedimentation can negatively impact heterotrophic feeding ability and reduce fitness through delayed transition to the adult phase or lowered reproductive success (Stafford-Smith and Ormond 1992; Ritson-Williams *et al.* 2009). The reallocation of energy from growth to the production of copious amounts of mucus to actively remove sediment for an extended period of time may also reduce lifetime fitness.

While the negative impacts of sediment on corals are well documented (e.g. Bak and Elgershuizen 1976; Loya 1976; Lasker 1980; Rogers 1983, 1990; Reigl and Branch 1995; Maughan 2001), it should be noted that sediment may also exhibit positive effects. Shelton (1980) found that if sediment contains a high percentage of organic material, corals may ingest the organic fraction for energy acquisition. Though suspended sediment is poor in nutrient quality, it can be the most abundant food source available to tropical corals in turbid

environments (Anthony 1999, 2000; Anthony and Fabricius 2000). Several turbid-adapted tropical species can obtain up to 50% of tissue growth via feeding on fine suspended particles (Pastorok and Bilyard 1985; Anthony 1999). The sedimentation rates present at J-Y Reef act to significantly reduce the amount of incident light available for photosynthesis in juvenile *O. arbuscula*. However, the organic material present in suspended sediments can compensate for reduced photosynthesis in *O. arbuscula* through heterotrophy to maintain zooxanthellae and chlorophyll concentrations (K.O. Matterson unpublished data). Organic particle rates recorded at J-Y Reef (Chapter 1, Figure 2) were high, suggesting that organic material may be a viable food source for *O. arbuscula*. However, ingestion efficiencies were not evaluated in the present study as an active mechanism because only inorganic sediment was used.

In conclusion, I provide evidence in the temperate coral *O. arbuscula* that developing a branched morphology early in life provides a selective advantage for countering the negative impacts imposed by the high sediment loads present on Georgia offshore reefs. This study suggests that sedimentation sets controls on the population structure of *O. arbuscula* in the SAB by causing significant mortality and suppressing growth during the critical early life history stages. These results also indicate that initiating an upright or branching morphology is key for continued growth and survival of juvenile *O. arbuscula* settling to horizontal surfaces in this high-sediment environment.

Table 4. State-fate transition matrix model for juvenile *Oculina arbuscula* monitored at J-Y Reef from September 2009 to October 2010 (corresponds to Figure 11). Movement within the unbranched morphology class is presented in the top left box, movement from an unbranched to a branched morphology is presented in the bottom left box, and movement within the branched morphology class is presented in the bottom right box.

From:

To:	1	2	3	4	5
Mortality	0.37	0.53	0.32	0.46	0.26
1	0.15	0.07	0	0	0
2	0.30	0.17	0.11	0.02	0.04
3	0.04	0.11	0.24	0.21	0.05
4	0	0	0.14	0.04	0.06
5	0.06	0.06	0.07	0.11	0.41
B_1	0	0	0	0	0
B_2	0	0	0	0	0
B_3	0	0	0	0	0
B_4	0	0.01	0	0	0
B_5	0.08	0.05	0.11	0.15	0.18

From:

To:	B_4	B_5
Mortality	0	0.26
B_1	0	0
B_2	0	0
B_3	0	0
B_4	0.5	0.05
B_5	0.5	0.69

Figure 6. Distribution of adult *Oculina arbuscula* colonies at various distances from the reef scarp on J-Y Reef. The scarp is defined as the vertical side of the ledge where it first projects out of the sandy substrata (sensu Ruzicka and Gleason 2009). These data were obtained from three 1 x 10 m belt transects conducted haphazardly at 1, 2, and 5 m from the scarp.

Figure 7. Oculina arbuscula colony morphologies range from **(A)** flat to **(F)** branching and include **(B-E)** various intermediate stages between these two extremes. All morphologies are found interspersed at J-Y Reef. Rubber stopper in each photo is 15 mm at base diameter.
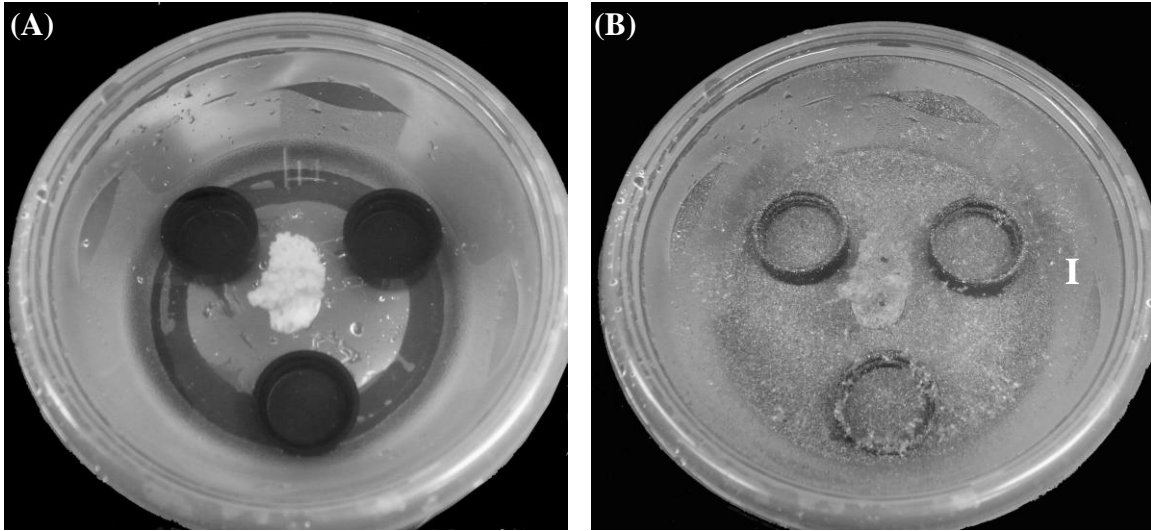
Figure 8. **(A)** Sediment shedding experimental setup prior to sediment application showing the coral colony in the middle with three plastic bottle caps around the container. **(B)** After sediment application. Sediment was collected from each of the bottle caps and from the surface of the coral after all particles settled.
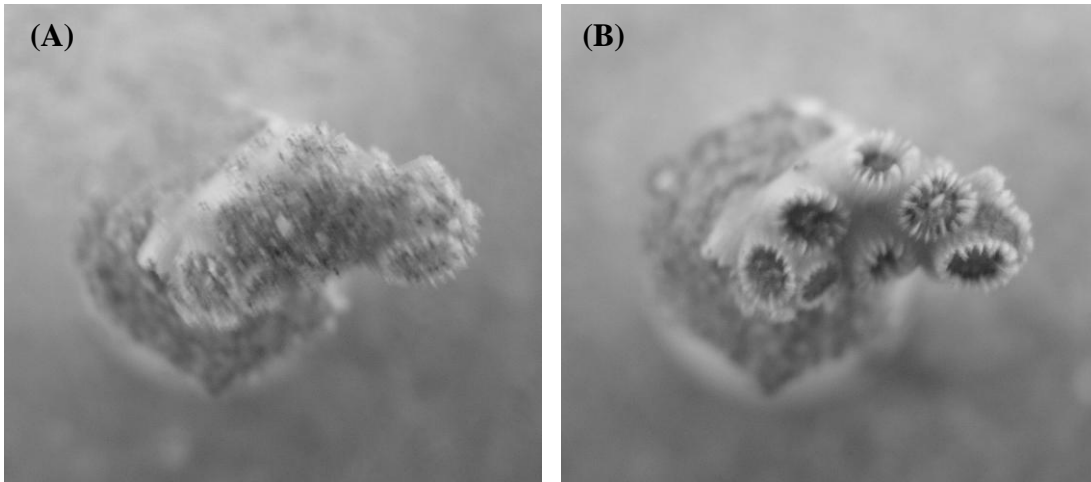
Figure 9. Live juvenile *O. arbuscula* colony at **(A)** 0 min after application and **(B)** 24 hr after application.

Sediment grains are covering most of the colony in **(A)**. The colony surface is visibly clear in **(B)**.
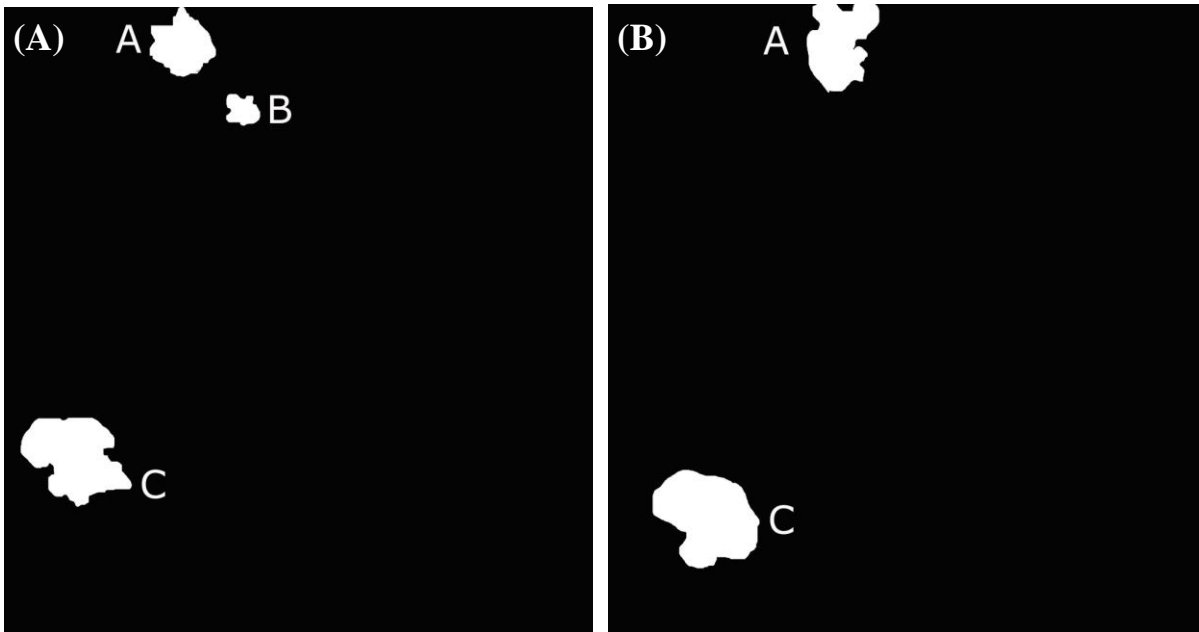
Figure 10. Artificial recruitment tile 1 m from the scarp at two dates: **(A)** September 11, 2009 and **(B)** October 17, 2009. Colonies A and C show increased growth from photo **(A)** to **(B)**. Colony b has experienced mortality (does not appear in **B**).
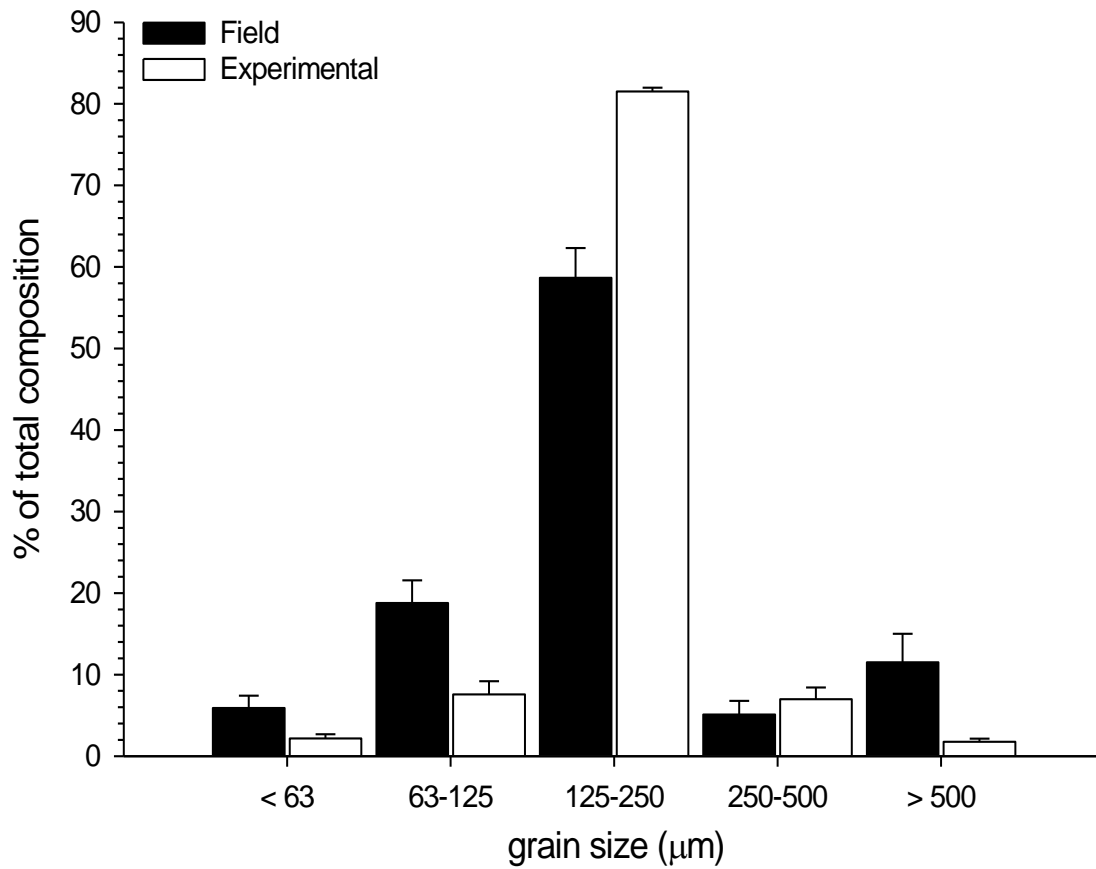
Figure 11. Grain size distributions of inorganic sediments collected from J-Y Reef. The field composition was determined by sieving samples collected in sediment traps at J-Y Reef and the laboratory composition was calculated from sediments combined into a container after combustion. There was no significant difference in the distribution of grain sizes between field and laboratory. Error bars are ± 1 S.E. N= 5 for lab and N= 11 for field.
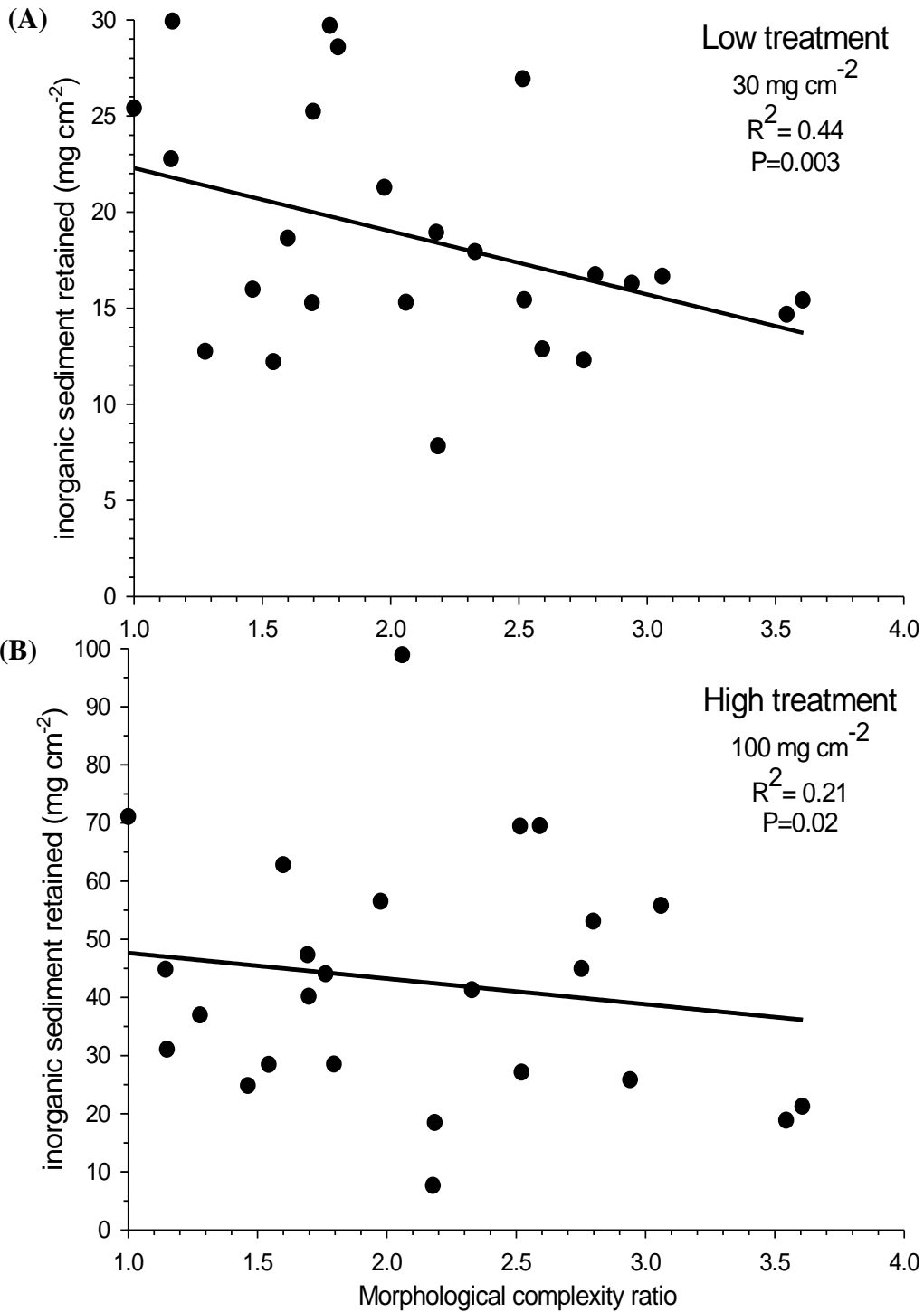
Figure 12. Passive sediment shedding ability of juvenile *O. arbuscula* under (**A**) low and (**B**) high sediment

loads. Each data point represents the sum of three trials per individual (N=25). Data were back transformed for

ease in interpretation.

(A)

(B)
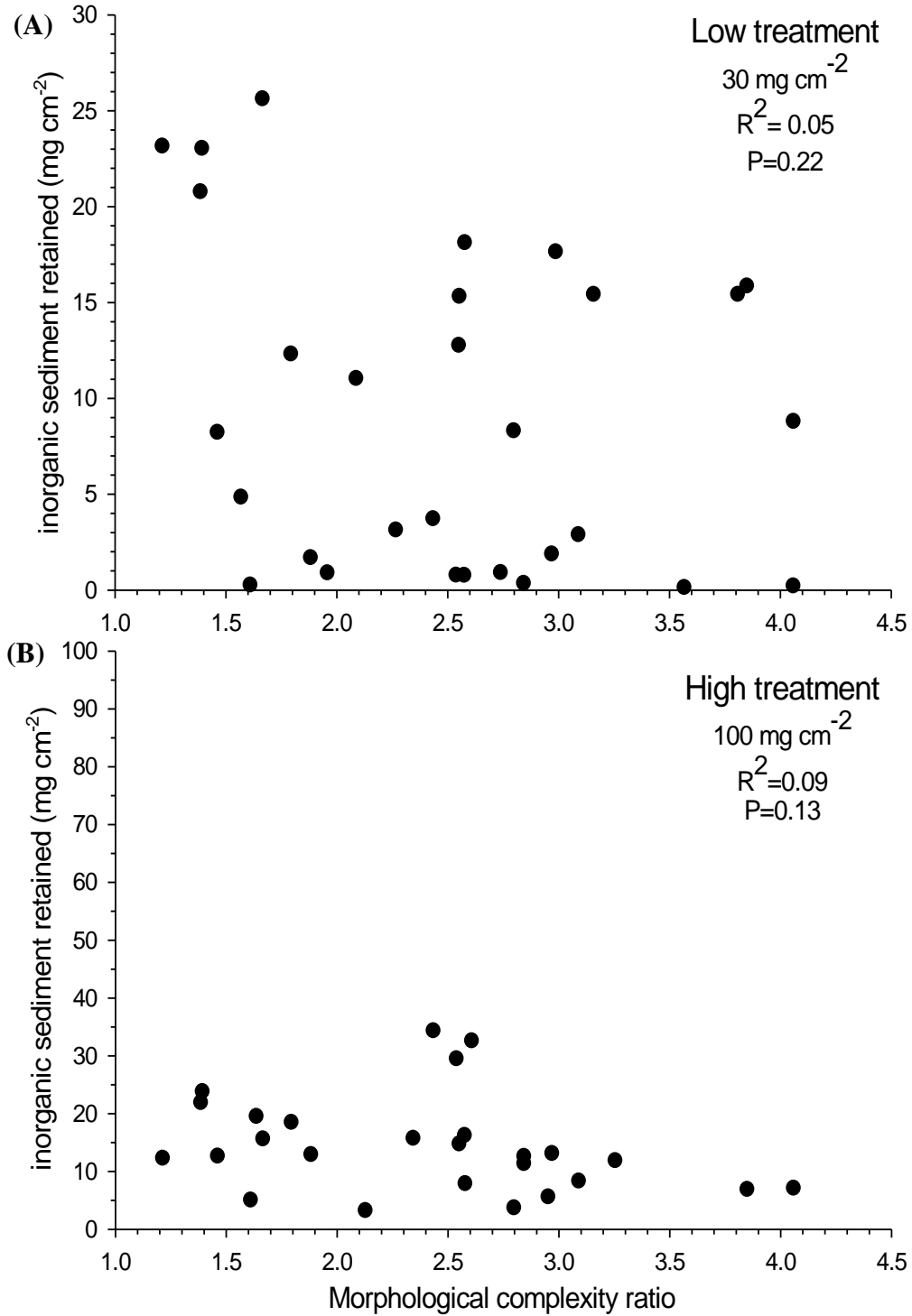
Figure 13. Active sediment shedding ability of juvenile *O. arbuscula* under **(A)** low and **(B)** high sediment loads. N= 30 for low sediment treatment and 26 for high sediment treatment. Data were back $\log_{10}$ transformed for ease in interpretation.
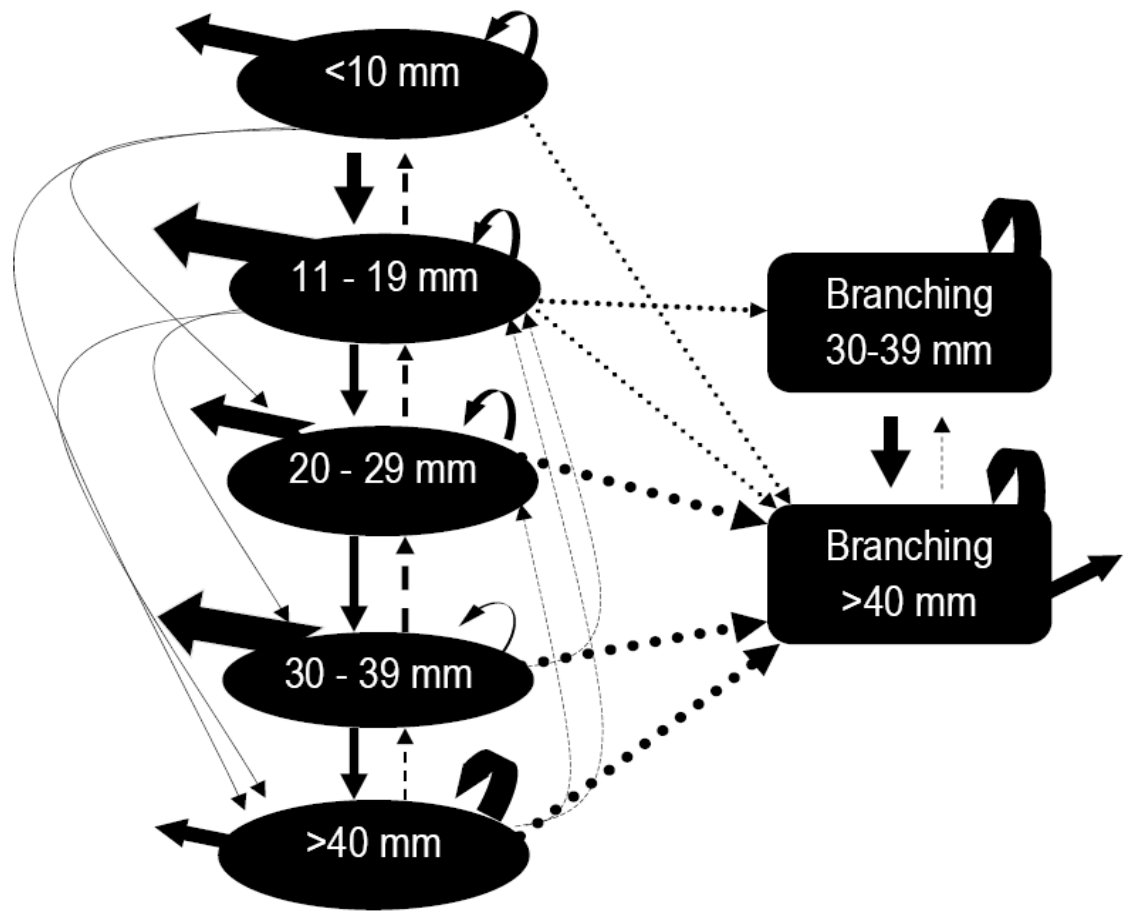
Figure 14. Short-term stage transition model of juvenile *O. arbuscula* at J-Y Reef. Arrow thickness indicates relative probability. Block arrows directed away from the colony into space represent mortality, circular solid arrows denote persistence in a size class, dashed arrows represent partial mortality to a smaller size class, solid arrows represent growth to a larger size class and dotted arrows are movement from unbranched to branched morphlolgy.
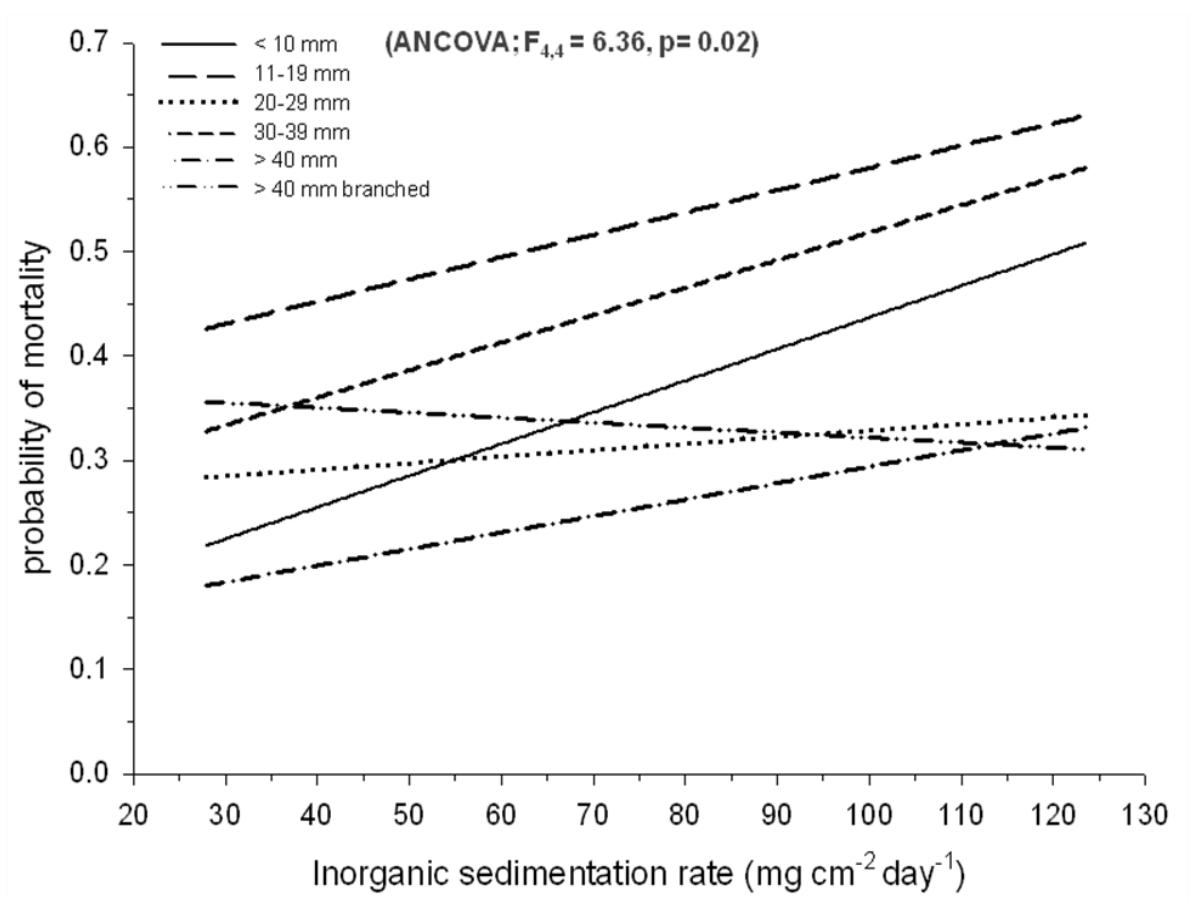
Figure 15. Mean inorganic sedimentation rates plotted with mortality probabilities in all juvenile size classes for

O. arbuscula.
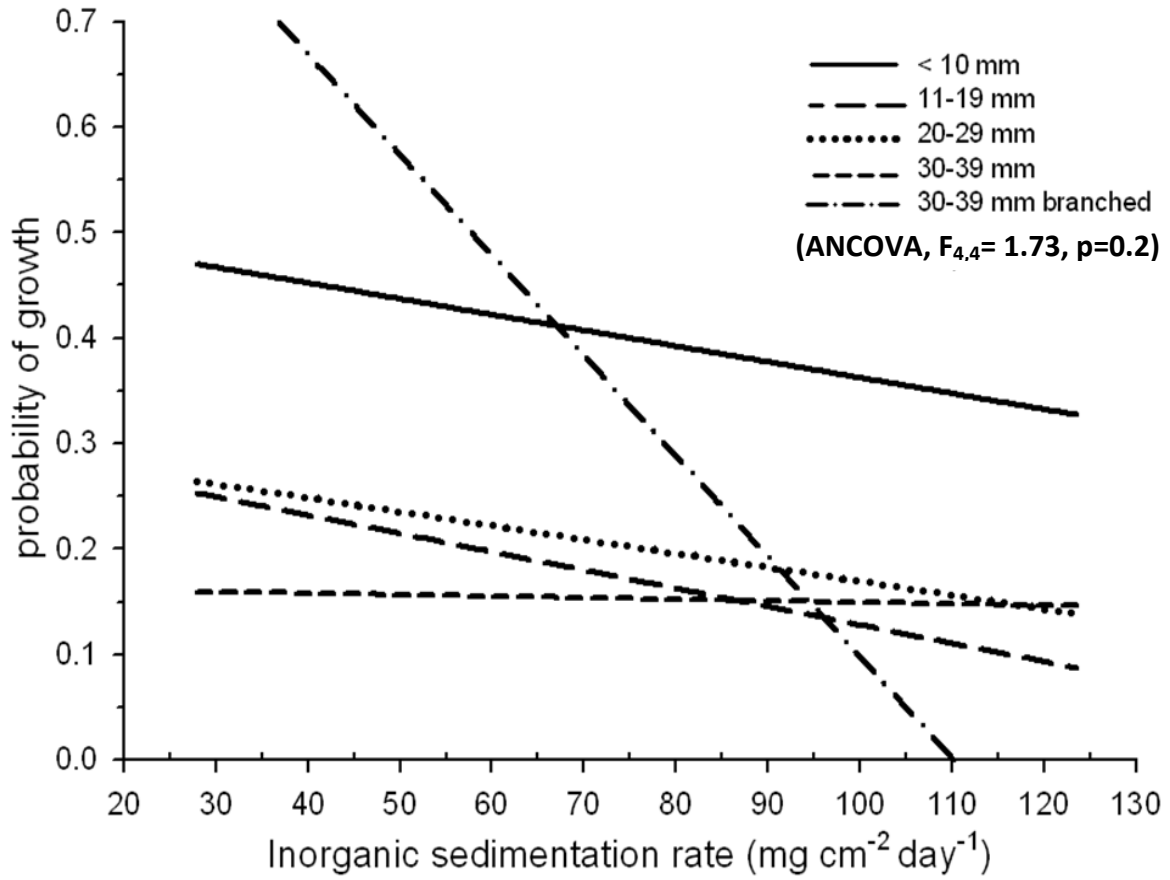
Figure 16. Relationships between inorganic sedimentation rates and growth probabilities in all juvenile size classes of *O. arbuscula*.

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APPENDIX A: INFORMATION CONCERNING TOTAL, INORGANIC, AND ORGANIC SEDIMENTATION RATES FROM JULY 2008 TO OCTOBER 2010.

Table A1. Total, inorganic, and organic sedimentation rates for J-Y Reef from 2008- 2010. Rates are presented as mg cm^{-2} day^{-1} ± 1 S.D.

Collection Date	Total Mass	Organic Mass	Inorganic Mass
7/29/2008	1.17 ± 0.59	0.13 ± 0.02	1.04 ± 0.53
10/17/2008	132.48 ± 66.63	1.32 ± 0.17	131.17 ± 65.93
12/5/2008	162.93 ± 61.20	2.02 ± 0.95	160.91 ± 60.48
2/6/2009	121.16 ± 54.91	2.11 ± 1.51	119.05 ± 53.84
6/23/2009	302.44 ± 104.98	2.42 ± 1.07	300.02 ± 104.25
7/24/2009	56.76 ± 26.96	4.01 ± 3.62	52.76 ± 24.17
9/11/2009	96.04 ± 40.92	2.01 ± 1.08	94.03 ± 40.44
11/23/2009	91.15 ± 53.28	2.51 ± 3.15	88.64 ± 51.51
5/10/2010	39.29 ± 24.14	0.73 ± 0.82	38.56 ± 24.03
6/14/2010	112.12 ± 93.61	1.53 ± 1.57	110.60 ± 92.12
7/24/2010	27.86 ± 34.42	0.66 ± 0.42	19.20 ± 14.98
10/8/2010	123.54 ± 62.06	2.35 ± 1.93	121.19 ± 61.15

Table A2. Percent of total inorganic sedimentation rates ± 1S.D.for each grain size collected from July 2008

through October 2010.

Percent of Total Inorganic Content					
Collection Date	**>500 μm**	**500-250 μm**	**250-125 μm**	**125-63 μm**	**<63 μm**
7/29/08	8.27 ± 0.02	10.12 ± 0.03	58.81 ± 0.07	6.13 ± 0.01	16.67 ± 0.05
10/17/08	9.92 ± 3.71	41.1 ± 10.22	44.25 ± 8.81	2.04 ± 2.14	2.69 ±0.69
12/05/08	7.18 ± 3.45	28.34 ± 6.81	56.12 ± 8.89	2.87 ± 0.33	5.39 ± 1.40
2/06/09	3.33 ± 1.10	21.09 ± 12.05	66.51 ± 11.79	4.24 ± 0.89	4.82 ± 1.77
6/23/09	8.04 ± 7.64	19.68 ± 12.79	66.77 ± 13.53	3.12 ± 0.72	2.39 ± 0.76
7/24/09	5.55 ± 1.08	10.34 ± 1.33	69.44 ± 2.88	8.33 ± 0.21	6.35 ± 0.44
9/11/09	3.68 ± 0.66	29.12 ± 5.04	54.07 ± 4.01	5.61 ± 0.31	7.52 ± 0.93
11/23/09	3.94 ± 1.53	20.47 ± 5.22	59.4 ± 9.12	6.69 ± 0.40	9.5 ± 0.74
5/10/10	5.55 ± 0.66	23.24 ± 2.21	62.49 ± 4.95	3.8 ± 0.16	4.91 ± 0.66
6/14/10	8.49 ± 5.33	24.54 ± 10.65	59.9 ± 15.78	4.04 ± 0.62	3.04 ± 0.97
7/24/10	4.98 ± 0.38	16.79 ± 1.59	66.33 ± 3.25	6.41 ± 0.23	5.49 ± 0.33
10/18/10	5.18 ± 1.63	18.38 ± 3.81	66.6 ± 13.21	4.2 ± 0.22	5.65 ± 0.96

Table A3. Percent of total organic sedimentation rates for each grain size collected from July 2008 to October 2010.

Percent of Total Organic Content					
Collection Date	>500 μm	500-250 μm	250-125 μm	125-63 μm	<63 μm
7/29/08	7.92 ± 0.01	5.71 ± 0.001	19.47 ± 0.03	14.49 ± 0.02	52.41 ± 0.02
10/17/08	16.01 ± 0.04	27.54 ± 0.06	26.54 ± 0.07	4.41 ± 0.01	25.50 ± 0.09
12/05/08	12.03 ± 0.04	13.30 ± 0.02	19.09 ± 0.03	6.25 ± 0.08	49.33 ± 0.30
2/06/09	16.47 ± 0.21	27.69 ± 0.29	28.60 ± 0.18	5.98 ± 0.01	21.26 ± 0.21
6/23/09	15.28 ± 0.03	18.27 ± 0.04	39.91 ± 0.08	5.69 ± 0.01	20.85 ± 0.13
7/24/09	7.05 ± 0.02	7.00 ± 0.01	20.35 ± 0.03	8.95 ± 0.02	56.65 ± 0.83
9/11/09	12.40 ± 0.01	18.41 ± 0.02	27.39 ± 0.02	10.38 ± 0.01	31.42 ± 0.77
11/23/09	6.02 ± 0.01	9.55 ± 0.01	8.23 ± 0.03	4.62 ± 0.01	71.59 ± 0.80
5/10/10	11.48 ± 0.01	7.88 ± 0.01	50.94 ± 0.02	4.12 ± 0.01	25.57 ± 0.06
6/14/10	30.98 ± 0.04	13.55 ± 0.03	18.95 ± 0.05	5.96 ± 0.01	30.56 ± 0.10
7/24/10	4.98 ± 0.02	4.00 ± 0.02	9.35 ± 0.03	3.92 ± 0.02	77.74 ± 8.07
10/18/10	6.67 ± 0.03	7.33 ± 0.04	12.25 ± 0.05	3.39 ± 0.02	70.36 ± 0.49