A Study of the Pelagic Larval Duration of *Acropora humilis*, Coral Recruitment and Connectivity in the Saudi Arabian Red Sea

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ABSTRACT

Combined knowledge of the pelagic larval duration of coral species and coral recruitment patterns can provide evidence of inter-reef connectivity and indicate a reef's ability to recover. We attempted to determine the maximum pelagic larval duration of *Acropora humilis*. Larvae were reared in a controlled environment unfavorable for settlement. The larvae lived in a pelagic state for a maximum of 29 days, although this is probably an underestimate of actual longevity for this species. Given the information available from the literature with respect to larval dispersal rates, it is not expected that larvae with this longevity will disperse further than 10-20 km from their natal reef, if at all.

A long-term recruitment monitoring project was also set up on Abu Shosha Reef, which suffered nearly complete coral loss due to a bleaching event in summer of 2010. In April 2011, 60 settlement plates were placed on the reef. In July, a total of 102 living scleractinian recruits were counted on the plates. While pocilloporids were the most dominant recruits on the reef (57.8%), about 20.6% of living recruits belonged to Acroporidae, a family whose live cover on the reef is extremely low (0.67%). However, the overall mean density of recruits was very low (1.7 living recruits/100cm^2) compared to similar studies around the world despite the

spawning season having just ended. Fish surveys showed herbivore biomass to be very low compared to other reef systems in the world, but densities were significantly higher than another reef in the Red Sea with about 10 times more live coral cover. Recovery from bleaching for Abu Shosha and similar reefs in the region may be very slow relative to rates observed in other parts of the world if recruitment rates and herbivore communities remain low.

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General Introduction

Many land and marine invertebrates are relatively immobile as adults and rely on wind, currents and other physical processes to disperse their progeny over wide distances (Nathan and Muller-Landau 2000). For marine populations, the overwhelming consensus, at least until recently, is that larvae are very widely dispersed (more so than for terrestrial organisms), and therefore, sub-populations are well-connected (Palumbi 1994). While there is controversy over whether such wide dispersal is advantageous to marine populations or if it is merely a byproduct of more advantageous mechanisms of self-seeding (Strathmann et al. 2002), it is well-recognized that the importance of this connectivity lies mostly in that it is directly related to the resilience of an ecosystem (Hogan et al. 2011). In other words, when natural or anthropogenic disturbances deplete the numbers of adults in a community, it can only hope to recover or return to its original state if it has a sufficient supply of larvae recruiting in from over large distances.

A large percentage of coral reefs around the world is in decline mostly due to human activities; managing them in a way that minimizes negative impacts and maximizes ecosystem resilience is the only way we can ensure that they will continue to play their role in the ecological balance of our world ocean and to provide enormous socio-economic benefits to humankind (Bellwood et al. 2004). Therefore, studying aspects of coral reef connectivity is highly relevant towards understanding how best to manage these ecosystems in a sustainable manner (Bellwood et al. 2004; Almany et al. 2009). Very recent work shows some evidence

that these two scenarios may not be mutually exclusive (e.g., Planes et al. 2009; Berumen et al. in press).

There are two general approaches, among others, to studying connectivity; one is to study the supply of larvae and biological characteristics of the larval phase of marine organisms (e.g., Graham et al. 2008), while the other is to study recruitment to reefs and try to determine how much of it was or was not self-seeded (e.g., using genetic techniques or by comparing with the adult community) (Adjeroud et al. 2007; Saavedra-Sotelo et al. 2011). Some studies have attempted to look at both sides of the problem simultaneously (Hodgson 1985).

Currently, there is considerable controversy as to whether coral reef communities are maintained by their own larvae or by recruits arriving from other reefs (Cowen et al. 2000; Cowen and Sponaugle 2009). While older studies suggested high probabilities of long-distance dispersal (Harrison et al. 1984; Hodgson 1985), recent studies suggest that local retention may be occurring more than originally thought (Fisher and Bellwood 2003; Jones et al. 2005; Almany et al. 2007).

In this work, I attempted to study connectivity and resilience from two points of view. In the first chapter, I discuss some characteristics of the larval phase of the scleractinian coral *Acropora humilis* and their potential for dispersal, while, in the second chapter, I discuss recruitment rates and the herbivore community on a recently-disturbed inshore reef and their implications to the reef's potential for recovery.

Chapter I: Pelagic Larval Duration of *Acropora humilis*

1.1 Introduction

Information regarding larval survivorship, behavior and competency for settlement combined with oceanographic information can be useful in estimating potential dispersal distances of marine species, but there is much discussion and controversy over the extent of the link between dispersal and characteristics of the larval phase (Cowen et al. 2000; Miller and Mundy 2003; Cowen et al. 2006; Almany et al. 2007; Cowen and Sponaugle 2009; Cetina-Heredia and Connolly 2011; Saavedra-Sotelo et al. 2011). Over the past few decades, many studies have attempted in different ways to improve our understanding of the survivorship, longevity and energetics of the pelagic larval stage of reef corals and fishes. Due to the difficulties of observing and following the progress of pelagic larvae in the wild, most studies of larval biology were conducted under laboratory conditions. Some were based on direct observations of larval behavior and settlement rates (Baird 2001; Nozawa and Harrison 2005; Graham et al. 2008), while others measured metabolic rates and estimated the length of settlement competency periods based on assumptions of energetics (Richmond 1988). Others yet studied the effects of different environmental variables such as temperature and salinity on larval survivorship (Edmunds et al. 2001; Vermeij et al. 2006; Bauman et al. 2011). Previous studies have also focused on primary causes of mortality and identified them to include predation (Thorson 1950), starvation (Strathmann 1985), unfavorable

environmental conditions (Edmunds et al. 2001; Vermeij et al. 2006), and genetic defects and disease (Rumrill 1990).

Growing larvae in a controlled environment, where predation, disease, and suboptimal environmental conditions are removed as potential sources of mortality, does not accurately simulate the natural circumstances in which larvae must survive. Thus, larvae may be expected to live longer and have lower mortality rates in a laboratory than they would in the wild, which means that dispersal distances may be overestimated. However, the information gained from growing larvae under laboratory conditions is still useful for understanding energetic constraints on survival and for obtaining estimates of maximum longevity (Graham et al. 2008). Most previous studies on larval survival did not continue until the entire cohort of larvae died (Harii et al. 2002; Nishikawa and Sakai 2005; Nozawa and Harrison 2005) with the notable exception of Graham et al. (2008) who studied the mortality rates and maximum longevity of 5 broadcast spawning corals (including one species of *Acropora*) and reported longevity estimates for these species ranging from195-209 days. Prior to Graham et al.'s study, the longest larval phase reported for a broadcast spawning coral was 130 days (Baird 2001; Graham et al. 2008).

As for larval settlement, most studies have shown that larvae are competent to settle within 2-3 days after spawning and can remain competent for at least up to 3 months (Baird 2001; Harii et al. 2002; Miller and Mundy 2003; Nishikawa et al. 2003; Nishikawa and Sakai 2005). Therefore, in order to determine the maximum possible pelagic larval duration, experimental conditions must be as non-optimal for settlement as possible. Coral larvae have the capacity to settle on a large variety of

natural and artificial surfaces including but not limited to plastic, glazed and unglazed ceramic, and dead coral branches, and it has been shown that plastic is one of the least favorable surfaces for larvae to settle on (Harriott and Fisk 1987).

The focus of this study was to determine the longevity and mortality rates of pelagic larvae of a single scleractinian species in the Red Sea and use this information to make a rough estimate of maximum possible dispersal distance for that species based on information in the literature. We chose *Acropora humilis* for this study, which is a broadcast spawning coral As is the case for most broadcast spawning corals, the larvae of *A. humilis* are azooxanthellate, and so must rely on their own energy stores in a very oligotrophic environment in order to survive their pelagic phase (Baird 2001; Edmunds et al. 2001). To our knowledge, no such studies have been done on corals in the Red Sea. Because of the unique physiochemical characteristics of the Red Sea, namely high average sea surface temperatures, high salinity, and low nutrient input, it is possible that there may be some differences in mortality rates and longevity of planulae between the Red Sea and other locations.

Surveys done continuously since March/April 2011 (spring/early summer season in the Red Sea) revealed that *Acropora humilis* colonies on inshore reefs in the vicinity of Thuwal, Saudi Arabia, had white (presumably immature) eggs since April. *A. humilis* did not spawn along with the other *Acropora* species that spawned synchronously on April 17th, two nights before the full moon (Bouwmeester et al. 2011; Appendix I). There is no information in the current literature on the exact timing of spawning of *A. humilis* in the Red Sea, and an unpublished report claimed that *A. humilis* was seen spawning white gamete bundles in other parts of the world

(A. Baird, personal communication). Thus, we decided to monitor *A. humilis* continuously until spawning occurred and attempt to collect the spawn and rear the larvae in the lab under conditions that are as optimal as possible to minimize causes of mortality.

1.2 Materials and Methods

1.2.1 Sample Collection

Samples of 5 *A. humilis* colonies were taken out of Palace Reef (22°18'19.26''N, 38°57'56.66''E) on May 11th, 2011, and transported in buckets of seawater back to King Abdullah University of Science and Technology (KAUST) where they were placed in one of the basins of a saltwater cascade fountain that circulates openly with KAUST harbor water. The basin area was about 50 m x 20 m and about 1 m deep. To ensure its suitability, the basin water was tested using a Nutrafin aquarium test kit on April 14th for pH, dissolved oxygen (DO), turbidity, salinity, temperature, phosphates, ammonium and nitrates, and it was monitored regularly for changes in nutrient concentrations and temperature throughout the duration of the experiment.

Every evening for 2.5-3.5 hours immediately after sunset (and until midnight on the night of the full moon), the colonies were taken out of the basin and placed in buckets of the same basin water to be observed for setting behavior and spawning. New sample colonies were collected approximately every 10 days, and the surviving colonies of a previous batch of samples were taken back to the reef.

The experiment continued in the basin for 10 days after which it was moved to an artificial canal in KAUST which also had open circulation with the harbor. The move was necessary due to maintenance issues and observed unfavorable changes in ammonium concentrations. The corals were placed at a depth of approximately 1 m in the canal, and the water was monitored for changes in nutrient concentrations and temperature. However, another change in location became necessary as we observed fluctuations in ammonium concentrations toxic to corals. Turbidity was also quite high and mortality of sample colonies was becoming more frequent. Thus, the colonies were moved on June 8th to two 80 L acrylic tanks in the lab connected to a filtration tank with a closed circulation system. However, corals did not survive in this aquarium system, most probably due to a lack of chemical and biological stability in the newly assembled system.

Therefore, in order to bypass the difficulties of keeping coral colonies alive and healthy outside the reef environment, it was decided to attempt to collect gamete bundles from the field while SCUBA diving at night. I built 7 spawning tents (figure 1) using cloth, nylon-coated rope, 0.5 L Nalgene plastic bottles for collection of gametes and plastic bottles to serve as buoys for keeping the collection bottles positioned correctly over the colonies with the openings pointed downward to receive the positively buoyant bundles.

While collecting *A. humilis* samples from the field on June 4th, 2011, we observed that eggs had turned reddish in color, indicating ripeness. Thus, we no longer suspected that *A. humilis* might spawn white gamete bundles, but that it was more likely that it would spawn on the night of the next full moon (June 15th) or sometime a few nights before or after the full moon. Thus, we organized a series of night dives from June 11th-17th. We selected 7 random *A. humilis* colonies that were at 6-10 m depth and checked them for having ripe, reddish eggs by breaking off a maximum of 3 branches to expose oocytes (Harrison et al. 1984; Baird et al. 2002). When a colony with ripe eggs was found, a spawning tent was tied around it and the buoy bottle was filled up to a third with air from an alternate air source. Finally, a light stick was attached to the rope holding the buoy bottle in order to facilitate finding the tents throughout the night. The tents were deployed at the beginning of the first dive of the evening which began just before sunset and lasted around 90 minutes. They were spaced at a distance of at least 7-10 meters away

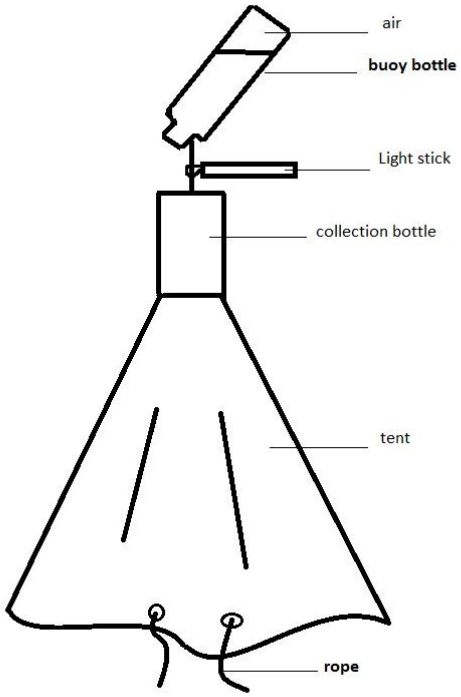


Figure 1: Sketch of spawning tent. The tent was prepared with a hole at the top where a collection bottle was secured. A rope was threaded through the rim of the tent to allow it to be tied around a coral colony such that any spawn produced cannot escape the tent. Another bottle was attached to the top of the collection bottle and used as a float to keep the tent from collapsing so that positively buoyant spawn can rise up into the collection bottle.

from each other. Throughout the dive, the collection bottles and other *A. humilis* colonies on the reef were checked for setting behavior. After a surface interval of around 30-45 minutes, a second dive was done to continue monitoring the tents and observing the reef for any spawning or setting activity. The tents were then collected at the end of the second dive. In this way, we monitored *A. humilis* colonies more-or-less continuously for around 4-5 hours after sunset every night for one week.

When spawning occurred, the collection bottles were closed and 6 out of 7 tents were taken back to the boat. The seventh net was not collected due to technical urgencies to return to the surface. Upon reaching the boat, the spawn from the 6 retrieved collection bottles was pooled together in a bucket for transport back to KAUST at a concentration of about 1 part gamete bundles to 4 parts seawater. This high concentration is essential in the first 1-2 hours to ensure sufficient fertilization (Graham et al. 2008).

1.2.2 Rearing

After about 2 hours of mixing the gamete bundles together at a high bundle-to-water ratio (during which fertilization and cleavage would have occurred), the mixture was diluted twice to prevent polyspermy (Graham et al. 2008); once after 2 hours of mixing, and again 30 minutes later. The embryos were skimmed off the surface and divided over 3 buckets with approximately 20 L of 0.2 μm filtered seawater (FSW) at a ratio of about 1 part embryos to 15 parts water. Over the next 3 days, the water was changed in the buckets on a daily basis, the waste produced was

cleaned constantly using pipettes and plastic film wrap, and the development and motility of embryos was monitored using a dissection microscope (ZEISS, 5 x magnification). Throughout the experiment, the surplus larvae in the buckets were kept as waste-free as possible, and the water was kept at 26-27° C and changed regularly. Embryos and larvae were also kept under a 12-hour photoperiod. There was always an effort to minimize the effects of excessive handling or disturbance to the embryos.

1.2.3 Measuring Survival

When most embryos developed into fully motile larvae, they were pipetted one by one into 13 small plastic jars containing 100 ml of 0.2 μm FSW at a concentration of 1 larva ml^{-1} and checked daily. The jars were stabilized inside a water bath that was kept at 26-27° C. It was planned to count all the larvae every 3 days in order to plot survivorship curves as per Graham et al. (2008) and find out the longest pelagic larval duration. The larvae were to be pipetted into fresh FSW while being counted and their numbers recorded.

However, contrary to expectations, larvae were dying en masse within a maximum of 48 hours after transfer to the small containers. Different kinds of containers were tried in order to rule out the possibility that toxins were leaching out of the plastic jars. We tried rearing the larvae in high quality Nalgene plastic jars, another type of plastic jar and in glass beakers, but larvae continued to die en masse in all our trials. The trials were as follows: 4 days after spawning (DAS), we transferred 1300 larvae into 13 plastic jars; 7 DAS, we transferred 400 larvae into 4

glass beakers and added another 200 in 2 more beakers on the next day; 9 DAS, we transferred 600 larvae to 6 Nalgene plastic jars; from 11-17 DAS, trials continued with Nalgene jars and half the initial concentration of larvae (50 larvae in 100 ml rather than 100 larvae in 100 ml) was used in order to address the possibility that overcrowding was causing death. Every new trial commenced when the larvae of the previous trial had died. The FSW used in the experiment was re-tested using two different Nutrafin water testing kits for the presence of high levels of nutrients and results were negative for any toxic levels of ammonium, nitrates or phosphates, and so, was deemed to be suitable.

Yet, many larvae still remained alive in the original 20 L buckets, and a large proportion was fully motile. The inability to keep the larvae alive in the small jars made it impossible to count them or plot survivorship curves. Thus, after all attempts given our facilities failed to keep a known number of larvae alive in small containers, we decided to focus our attention on simply maintaining good conditions for the living larvae remaining in the buckets and note the time at which the last larva died. Pictures were taken of samples of the larvae and a short video documenting their appearance and movement was filmed (supplementary material).

1.3 Results

Setting behavior of *A. humilis* colonies on Palace Reef was observed at 19:45 on June 17th, 2011, two nights after full moon (figure 2). At 21:20 (about 2 hours, 15 minutes

after sunset), *A. humilis* finally spawned reddish, positively buoyant gamete bundles about 1 mm in diameter (figure 3). Spawning lasted for 20 minutes.

Figure 2: Setting of *Acropora humilis* was observed less than one hour after sunset on June 17th, two nights after the full moon. Gamete bundles become visible at the tips of the polyps (photo by Maha Khalil, June 17, 2011).

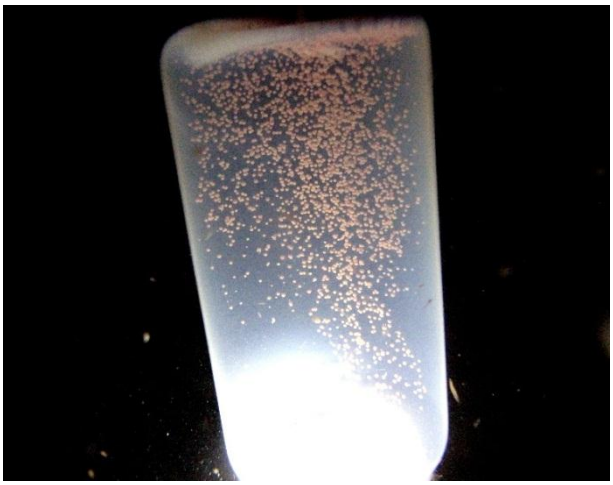


Figure 3: Spawn of *Acropora humilis* rising into collection bottle of a spawning tent (photo by Maha Khalil, June 17, 2011).

Rotational motion of embryos was observed 2 days after spawning (DAS). By 3 DAS, a small proportion of larvae were swimming freely. Full motility was observed in the majority of larvae 4 DAS.

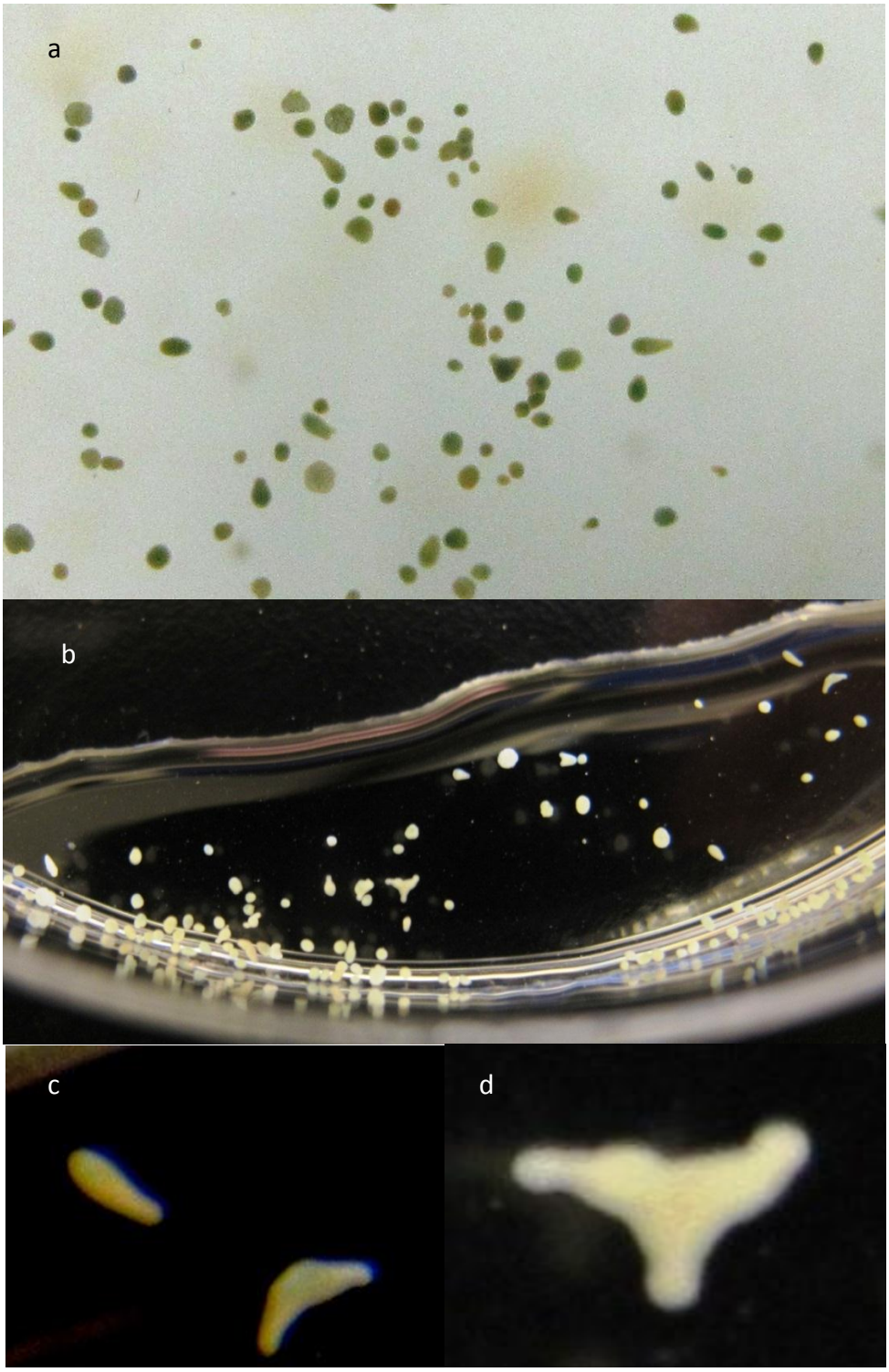


Figure 4: ***A. humilis*** **larvae; a) and b) samples of the batch of larvae, showing the mix of colors, shapes and sizes which atypical of larvae supposedly collected from a single species; c) a larva that appears to be deformed or fused with another larva (right) next to a typical healthy pear-shaped larva (left); d) deformed larva that appears to be composed of three larvae fused together.**

The cohort appeared to be somewhat mixed in appearance, size, color and degree of motility which is unusual for healthy larvae collected from one species. Many larvae also appeared to be deformed or fused with other larvae (figure 4).

When known numbers of larvae were transferred to small containers for the purpose of regular counting, they started to die en masse. Whenever mass death occurred, the larvae were replaced with fresh ones for a new trial. Mass death of larvae occurred repeatedly in all small containers on the following days: 5, 6, 7, 9, 10, 12, 14, 15 and 17 days after spawning. This made calculating mortality rates and plotting survivorship curves impossible for this cohort.

An obvious decrease in motility and positive buoyancy in about 50% of the larvae remaining alive in the large buckets was also noted 19 DAS.

The last group of larvae that remained in the buckets died 29 DAS, thus making 29 days the longest longevity estimate for this cohort of larvae.

1.4 Discussion

1.4.1 Larval Mortality and Longevity

Most of the recent studies on the pelagic larval duration of coral species have reported much longer estimates of longevity than the result of our experiment. Our longevity estimate of 29 days for *Acropora humilis* is almost 7 times shorter than the shortest maximum longevity estimate reported by Graham et al. (2008) for a broadcast spawning coral (*Favia pallida,* 195 days). Even studies focused only on competency period (not maximum longevity) reported much longer competency periods than our longevity estimate. For example, Nishikawa and Sakai (2005)

reported a competency period for *Acropora digitifera* of 54 days and 69 days for *A. tenuis.* Other broadcast spawning corals like *Favites chinensis* and *Goniastrea aspera* were also reported to have similarly long settlement competency periods (Nishikawa and Sakai 2005).

While very short larval longevities (23 days for *Acropora formosa*, 7 days for *A. tenuis* and 5 days for *A. millepora*) were previously reported by Harrison et al. (1984) in the Caribbean, it is not clear whether filtered seawater was used in that study. Not using filtered seawater could greatly reduce survivorship by allowing disease-causing agents (bacteria or protozoa) to be present. Also, as mentioned above, a much longer competency period was later reported for one of the species in that study (*A. tenuis)* by Nishikawa et al. (2003) in southern Japan, suggesting that the results of Harrison et al. (1984) may not be broadly applicable.

Some evidence suggests that high sea surface temperatures are correlated with short larval longevities. For example, Edmunds et al. (2001) have shown that elevated temperatures significantly reduce larval longevity and increase mortality rates in zooxanthellate larvae of brooding *Porites* species by lowering the rate of photosynthesis, and thus, reducing the energy stores of the larvae in their pelagic stage. Nozawa and Harrison (2005) have also shown a similar negative correlation between sea surface temperature and length of settlement competency periods in broadcast spawning corals. While this may suggest that short longevities in the Red Sea may be a natural feature for this environment due to its high average sea surface temperature, we cannot conclude this without gathering further evidence and

replicating the experiment for many species over several seasons and under more stable laboratory conditions. Also, even under the high temperature treatments in Nozawa and Harrison's study (2005), the shortest settlement competency period reported for any of the broadcast spawning corals was almost twice as long as our maximum longevity estimate for *A. humilis*. Bauman et al. (2011) have also shown that fecundity and oocyte size in several broadcast spawning corals in the Persian Gulf is similar to other regions of the world despite mean sea surface temperatures of about 36° C, indicating that the reproductive systems of corals in warm regions such as the Persian Gulf and the Red Sea may be already fully adapted to the environmental conditions. However, larval longevities were not considered in that study.

The above evidence leads us to conclude that our inability to keep *A. humilis* planulae alive in small concentrations, the regular occurrence of mass death, and our short estimate of longevity are more likely to be due to unstable and suboptimal laboratory conditions than to natural causes. Thus, our longevity estimate of 29 days is probably an underestimate of the true value. Future work will need to pay close attention to several of the aforementioned variables to ensure that lab conditions are more suitable for larval rearing (see Section 1.4.3 below).

1.4.2 Potential Implications to Dispersal

Despite the high probability that 29 days is a major underestimate of *A. humilis* larval longevity, it is still interesting to consider implications that a short larval duration would have on the potential dispersal ability of the species.

Many factors besides larval longevity affect dispersal. Some factors may aid long-distance dispersal, such as favorable current velocities, favorable chemical and physical conditions and long pre-competency periods, while other factors work against it, such as larval behavior, mortality, diffusion, rapid settlement, and unfavorable environmental conditions (Cowen and Sponaugle 2009).

Many studies conclude that dispersal potential for marine larvae with pelagic phases of a few weeks to several months is on the order of tens to hundreds of kilometers (Harrison et al. 1984; Kinlan and Gaines 2003; Cowen and Sponaugle 2009). Evidence from plankton tows and longevity estimates suggests that a longevity of 91 days was enough to recruit *Acropora* species from Johnston Atoll all the way to the Hawaiian Islands 720 km away (Harrison et al. 1984). Note that this longevity estimate is less than half the estimate calculated for any of the species in the study done by Graham et al. (2008). Also, studies based on mid-water current speeds in Lizard Island estimate that larvae could be transported away from their natal reefs at a speed ranging from 4 to 47 km $week^{-1}$ (Frith et al. 1986). Such evidence suggests that long-distance larval dispersal is easily achievable by coral reef organisms.

But many of the more recent studies tend to show evidence to the contrary – at least for coral reef fish. Studies on larval behavior show that fish larvae are capable of, and in fact seem to have a preference for, staying near their natal reefs (Jones et al. 2005; Almany et al. 2007; Dixson et al. 2008). Fisher and Bellwood (2003) have shown that the undisturbed swimming speeds of the larvae of some reef fishes can reach up to a maximum of between 16 and 20 cm s^{-1} (for some

species, that is equivalent to about 10-13 body lengths s^{-1}). Together with vertical migration to avoid high speed currents, these swimming speeds were found to be sufficient for larvae to be able to control their position and swim against most subsurface currents that are present during spawning seasons. Not only are fish larvae physically capable of recruiting back to their natal reefs, it seems that a large percentage of them does in fact do so. Hamner et al. (2007) have shown that the majority of buoyant fish eggs spawned on a reef in Palau drift back towards their natal reef by the effect of tidal currents even before they have hatched into motile larvae. Almany et al. (2007) have also used a technique based on maternal transmission of stable isotopes and showed that 60% of settled juvenile fish from two species were locally spawned. The two species studied had different reproductive strategies and pelagic larval durations (<2 weeks and > 1 month). Similarly, Jones et al. (1999) reported a 15-60% rate of retention of a damselfish species using florescent tetracycline to mark the otoliths of large numbers of embryos in the field.

However, the same rates of retention may not be true for coral larvae. Invertebrate larvae which rely mostly on cilia for locomotion (and particularly coral larvae) are significantly slower than fish larvae, and the efficiency of the beating of their cilia decreases significantly if their size exceeds 1 mm (Chia et al. 1984). Most of the swimming speeds reported for scleractinian planulae (though none belonging to the genus *Acropora*) were between 0.04 and 0.5 cm s^{-1} except for one study that reported speeds of 1-3 cm s^{-1} for the coral *Caryophyllia smithii* (Tranter et al. 1982). In addition, most coral larvae do not become competent for settlement until

approximately 2 – 3 days after spawning (Baird 2001; Miller and Mundy 2003; Nishikawa et al. 2003; Nishikawa and Sakai 2005; Nozawa and Harrison 2005) which provides a window of opportunity for dispersal away from the natal reef before larvae become motile and competent.

While this suggests that the potential for long-distance dispersal by ocean currents is much greater for corals than for fish (Connolly and Baird 2010), other studies suggest otherwise. Using elemental fingerprinting to track the origins of newly settled coastal mussels (also invertebrates with relatively slow-moving larvae), Becker et al. (2007) have shown that almost all mussel larvae in their study area were retained within 20-30 km of their geographic natal origin. Moreover, oceanographic models have shown that the residence time of a body of water over a coral reef ranges from 0.48 - 5.6 days, which could mean that a large percentage of a cohort may still be on its natal reef by the time it is competent to settle (Black et al. 1991; Cetina-Heredia and Connolly 2011). Most of the biophysical models which estimated larval dispersal to be on the scale of several hundred kilometers did not take into account the diluting effect of mortality and diffusion, while those models which did take those factors into account have shown that there is a decrease in larval concentrations of 5 to more than 9 orders of magnitude with increasing distance from the source reef due to mortality and diffusion (Cowen et al. 2000) and that, realistically, larval exchange is probably on the scale of only 10 – 100 km for largely passive larvae that survive several weeks to several months (Cowen et al. 2006).

Also, if we take into account the high sea surface temperatures of the Red Sea, which may or may not have an effect (Edmunds et al. 2001; Bauman et al. 2011), it is possible that chances of long-distance dispersal are even lower. Previous studies have shown that, for some scleractinian planulae, raising the water temperature in controlled experiments is positively correlated with motility rates and negatively with settlement rates (Bassim and Sammarco 2003). High temperatures also seem to be correlated with shorter pre-competency periods (Heyward and Negri 2010) – the overall effect being negative for long-distance dispersal. Thus, it seems that the probability of our *A. humilis* larvae being transported far from their reef of origin and reach another reef where they can settle, assuming their longevity really is 29 days, is very small. While we do not have enough local data to give a valid numerical estimate, it is very likely that dispersal distance for these larvae will be in the lower end of the ranges predicted by the more conservative estimates in the literature (maximum of around 10 – 20 km) if they manage to be transported away from the reef at all.

1.4.3 Suggestions for Improving Experimental Procedure

There are many possible reasons that can explain our failure to maintain *A. humilis* larvae in small containers or generally to maintain them for a longer time. For instance, the highly mixed appearance of the planulae and the apparent deformity of many of them suggest two possibilities. First, an error of identification of *A. humilis* in the field could have occurred, and thus the gamete bundles collected in the field may have been from several members of the *A humilis* species group which all

resemble *A. humilis* morphologically, not to mention that there is some morphological variation between different colonies of the same species depending on depth and location on the reef, and differentiating between them in the field may be a challenge (Wallace 1999; Wolstenholme 2004). Current taxonomic studies concerning Red Sea corals are also lacking, and morphological boundaries between these species may be different locally within the Red Sea from what they are in other regions of the world. Thus, we may have unintentionally cross-fertilized closely related species which resulted in poor viability of the resultant larvae.

Another more likely possibility is that the concentration of embryos or the ratio of embryos-to-water in the first 48 hours after spawning may have been higher than we thought, and overcrowding may have lowered the fitness of the larvae by producing too much waste and lowering oxygen levels too quickly. It could have also contributed to some of the observed deformities by fusing embryos together. It is also possible that handling the larvae while changing water and transferring them may have been too disturbing to their development. However, our methodology was similar to previous studies that have achieved success in counting individual larvae and determining mortality rates (Graham et al. 2008). More frequent but gentler techniques for changing water could be used to remove waste more effectively without the disruptive effects of rough handling. For example, instead of buckets and beakers, other kinds of containers could be used where old water can be drained from the bottom rather than skimming the larvae off the surface and transferring them to fresh containers.

Keeping the larvae in a properly aerated and openly circulating system with natural sunlight and moonlight cycles (as in Nishikawa et al. (2003)) could have also helped in keeping the larvae healthy for longer. Unfortunately, such facilities were not available to us throughout the duration of the experiment.

Finally, it is also possible that the larvae we collected this year were simply genetically defective due to poor fitness of the parent colonies. The recent bleaching event that affected many inshore reefs in the area (K. Furby and M. Berumen, unpublished data) may have affected the reproductive process for corals on these reefs. Previous studies have shown that surface temperatures could produce negative effects on reproductive fitness and possibly fecundity of hermatypic corals (Jokiel and Guinther 1978) as well as reef fish (Donelson et al. 2010). However, we do not have sufficient evidence to support this possibility.

Thus, the following suggestions could be taken into account for attempting to repeat this experiment in future seasons:

1- In order to have more confident identification of *A. humilis* in the field, we should use more conservative morphological boundaries while identifying and selecting colonies. If molecular species ID techniques become available, this would be a useful tool.

2- Embryos should be diluted to lower concentrations than used in this study immediately after fertilization and cleavage.

3- In addition to filtering the water used in the experiment, the water could also be subjected to UV light overnight before use to ensure the elimination of potentially harmful microbes.

4- Changing the water in which the larvae are reared should be done daily at least for the first two weeks of life or until mortality rates stabilize, using a gentler technique that minimizes handling and disturbance to larval development. After the first two weeks of life, water can be changed only once a week as per previous studies. The water should also be aerated. An even better approach would be to rear the larvae in a flow-through system that circulates openly with filtered Red Sea water.

5- Once it is possible to rear the larvae in the lab, more detailed information on survivorship will be accessible as it should become possible to count larvae in smaller volumes and plot survivorship curves as well as obtain a more accurate estimate of longevity. Finding out whether the larvae of *A. humilis* have a type I, II, III or other survivorship curve would help us understand at what stage larvae are more vulnerable to causes of mortality and what proportion of a cohort may potentially survive to be transported to reefs beyond their natal reefs (Graham et al. 2008). Such data would be of great importance for incorporating into biophysical models of dispersal.

Chapter II: Coral Recruitment on Abu Shosha Reef in Summer 2011

2.1 Introduction

Recruitment rates and patterns, like many other biological and physical factors (Hughes 1989; Karlson and Hurd 1993), are now widely known to affect coral assemblages on a reef and the dynamics by which populations are maintained (Hughes 1985; Underwood and Fairweather 1989; Caley et al. 1996). They can also provide evidence of inter-reef connectivity (Fisk and Harriott 1990; Bellwood et al. 2004; Cowen et al. 2006) and resilience as corals rely mostly on sexual reproduction to recover from severe disturbances (Smith 1992; Hogan et al. 2011). The larvae of species that spawn their gametes are more relevant to evidence of connectivity as these larvae disperse much further than those of brooding corals, but, unfortunately, individual survivorship is believed to be much lower (Harrison and Wallace 1990).

There are mixed opinions on the relationship between recruitment rates and adult populations of reef organisms. Previous studies have shown that, at least for some spawning coral species, recruitment rates are correlated with variation in fecundity rather than with adult population densities (Hughes 1985; Edmunds 2000; Hughes et al. 2000). And yet, there are other studies which acknowledge a stock-recruitment relationship for corals based on adult coral cover (Hughes and Jason 2000). All studies, however, recognize that recruitment rates and post-settlement mortality are important factors for recovering lost coral cover (Caley et al. 1996; Adjeroud et al. 2007; Ceccarelli et al. 2011) even if recruitment levels are

not consistently correlated with live coral cover (Fisk and Harriott 1990; Adjeroud et al. 2007). More studies that follow the survivorship of newly-settled recruits could help us better understand the relationship between recruitment and the adult stock (Caley et al. 1996).

Much discussion is also available on what cues influence coral settlement patterns and if these patterns are consistent with adult zonation. Mundy and Babcock (1998) showed that coral settlement in any of six species of scleractinians that they selected (including *Goniastrea aspera* and *Acropora tenuis*) is dependent on either light quality or light intensity (as a proxy mostly for depth) but not both together. However, the same authors later conducted an experimental study that showed that settlement is likely to be indiscriminant with regards to depth and that zonation is later determined by post-settlement factors such as predation and wave action (Mundy and Babcock 2000).

Coral recruitment studies have used a number of different methodologies for determining recruitment rates. While some authors have installed single plates bolted to the substrate in different ways (Mundy 2000), others have used plates arranged on metal racks (Abelson et al. 2005), and others yet have used plates stacked on top of each other with a few centimeters of space in between (Maida et al. 1994). Mundy (2000) has shown that recruitment rates do not differ significantly between the individually installed plates and plates on steel racks, but showed that individual installment of plates is much more cost efficient and facilitates statistical analysis as the method does not violate the assumptions of independence required

by many tests. The same author has also shown that the angle at which plates are installed does not affect recruitment rates significantly (Mundy 2000). As for the material of which plates are made, some authors in the past have used branches of coral as settlement plates (e.g. Rogers et al. (1984)) while others used ceramic tiles. Harrison and Fisk (1987) have shown that studies that use different types of plates are not comparable, and that ceramic (or terracotta) tiles are the most cost-efficient and the best at attracting recruits. Most of the recent studies now use terracotta tiles (e.g. Fisk and Harriott (1990) and Adjeroud et al. (2007)).

Coral recruitment is also strongly related to the health of the herbivore community on a reef, and thus, a healthy herbivorous community is critical for the resilience of a coral reef and its ability to regain lost coral cover. Depending on the spatial scale considered, algal cover decreases with high herbivorous fish densities (Newman et al. 2006; Burkepile and Hay 2011), and coral cover was observed to increase after disturbance up to 13 times faster in the presence of a healthy herbivore community (particularly parrotfishes and surgeonfishes) (Hughes et al. 2007). This is because when herbivorous fish remove excess macroalgae, they give corals a competitive advantage over algae in the struggle to find space to grow, and they provide bare rock space for new coral recruits to settle on (Rogers et al. 1984; Hughes et al. 2007). Bellwood et al. (2006) have also shown that some groups of fish which may not be the more dominant herbivores under natural circumstances can be surprisingly important in removing macroalgae after major disturbances increase algal cover, which indicates that the protection of all herbivores as a functional group is important. Others have also shown evidence that an optimal

level of grazing by echinoids (e.g. *Diadema* and *Echinometra* urchins), although abrasive and potentially lethal to individual coral recruits, actually increases levels of coral recruitment and helps structure coral communities; turchin grazing appears to maintain a balance between competition with algae for space and intermediate biological disturbance (Sammarco 1980,1982).

With this information considered, we designed this project with the aim of studying coral recruitment rates and patterns and assess the health of the herbivorous fish community on Abu Shosha Reef, a reef recently disturbed by bleaching, in order to assess the reef's potential for recovery.

2.2 Materials and Methods

2.2.1 The Study Site

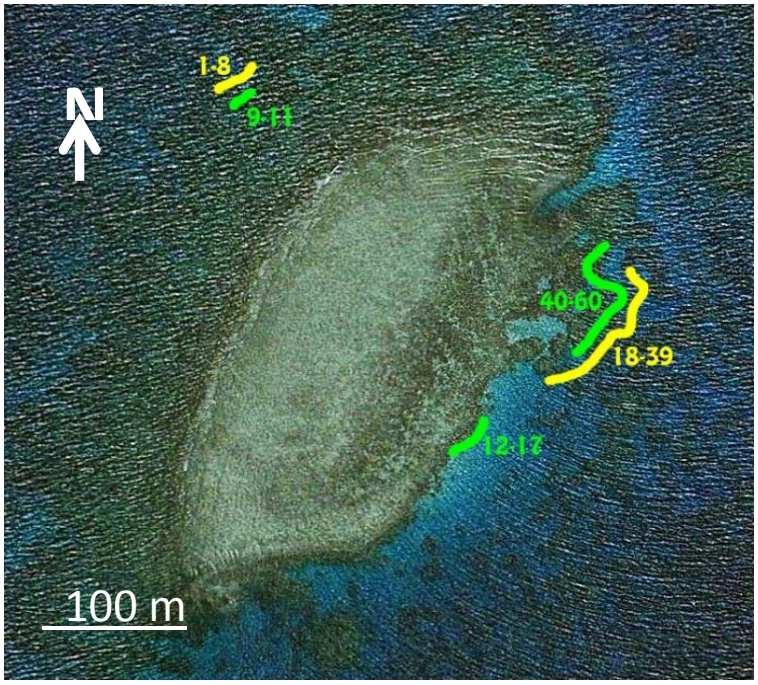


Figure 5: The location of 60 settlement plates on Abu Shosha Reef. The plates are placed along the green and yellow lines with green representing the reef edge (plates 9-17 and 40-60) and yellow representing a depth of 5 m (plates 1-8 and 18-39). The north-west facing side of the reef is the exposed side while the south-east facing side is the sheltered side (Google Earth. August 3rd, 2009. August 30th, 2011).

Abu Shosha Reef (22°18'13.03''N, 39°02'51.91''E) is a more-or-less oval-shaped (150 m x 360 m) inshore reef about 5 km north-west of the harbor of Thuwal, Saudi Arabia (figure 5). The northern and western side of the reef is exposed to wave action and currents while the southern and eastern side is relatively sheltered. Most of the hard substrate available for scleractinian corals is within the top 5 – 7 meters of depth, below which corals grow on patches on a sandy slope.

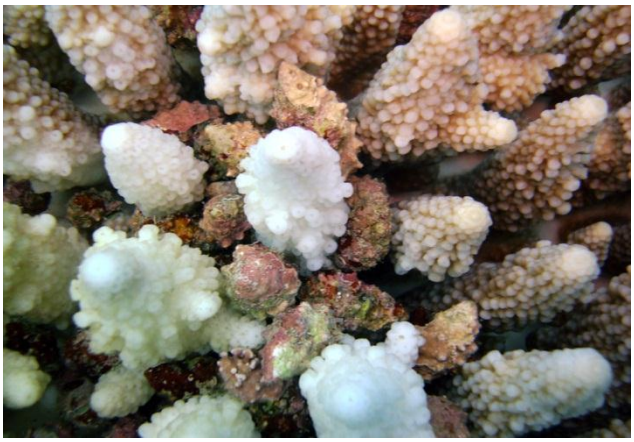


Figure 6: Heavy predation by *Drupella* snails on a colony of *Acropora samoensis.* Most *Acropora* colonies which remained alive on Abu Shosha shallower than 10 m were in poor health either due to disease or predation (photo by Jessica Bouwmeester 2011).

A bleaching event affected many inshore reefs in Saudi Arabia in summer 2010 (K. Furby and M. Berumen, unpublished data) including Abu Shosha. The live coral cover of the reef (surveyed a few months after the bleaching event) is about 6.84% of which around 0.67% is acroporid corals (J. Bouwmeester unpublished data). Dead coral colonies overgrown with algae are prevalent and finding a healthy acroporid colony is difficult, especially shallower than 10 meters. Throughout the period of April-June 2011, only one living acroporid colony encountered at 5 meters or shallower was found to have eggs. Many of them were also heavily preyed upon by *Drupella* snails (figure 6) (J. Bouwmeester unpublished data). Most of the living coral remaining on the reef at the time of this study were pocilloporids and massive poritids.

2.2.2 Coral Recruitment

In late March/early April, 2011 – around 7 months after the bleaching event, 60 settlement plates (10 cm x 10 cm) made with terracotta tiles were placed around

Abu Shosha Reef. The settlement plates were divided between 2 depths: reef edge and 5 m (figure 5). Plates 1-11 were placed on the north-west-facing side of the reef exposed to stronger currents and wave action, and plates 12-60 were placed on the south-east-facing side of the reef which is more sheltered. It was not possible to split the plates evenly between the sheltered and exposed sides due to technical difficulties, prevalent weather conditions, and strong currents. The tiles were glazed on one side, and so, two tiles were superimposed on each other to form one settlement plate. The glazed sides, which are not ideal for coral settlement, were pressed against each other and the unglazed sides were exposed and available for settling recruits. The plates were mounted on bolts that were screwed into the reef in a way such that the plates were parallel to the substrate (thus at more-or-less random angles) and distanced from it by about 1 cm.

About 4 months after placement, the plates were removed from the reef and replaced by new ones. The recovered plates were taken back to the lab for analysis. A dissecting microscope was used to examine the plates and find scleractinian recruits. Recruits on each plate were counted, roughly sized, photographed in high resolution (at least 2 pictures per recruit at different zoom levels) and their location on the plate was noted as “top” or “bottom” surface.

The high resolution images collected were then used to identify the recruits to family level as per Babcock et al. (2003). Recruits that could not be identified or were too eroded were grouped in the category "Other". The percentage abundance and the density of each category (recruits/plate = recruits/100cm^2) were calculated. The overall average density per plate was also calculated.

Mann-Whitney tests were done using SPSS Statistics 19 to determine whether there is any significant difference between recruit densities from Acroporidae, Pocilloporidae, and "Other" categories based on depth or the presence/absence of shelter from currents and wave action.

2.2.3 Fish Surveys

In March and August 2011,we surveyed the abundance and total lengths (TL) of some species of parrotfishes (Scaridae), groupers (Serranidae), and surgeonfishes (Acanthuridae) on Abu Shosha. A list of the species we surveyed is shown in table 1. Note that we grouped all fish from the genus *Scarus* together. For each transect, we recorded the counts of each fish group under size categories that had a range of 10 cm (e.g. 0-10 cm, 10-20 cm, 20-30 cm, etc.).

In each month, we covered 15 transects which were 50 m x 5 m. Five transects were at 10 m, five were at 5 m and the remaining five were on the reef edge. Transects covered both the sheltered and exposed sides of the reef. One diver swam ahead at a constant speed about 2 m over the reef and recorded the numbers of fish found within 2.5 m on either side under the different length categories. A second diver followed about 2 m behind the first while unreeling a transect tape.

Once the divers had covered 50 meters, the diver handling the tape signaled the end of the transect using a noisemaker. Transects were at least 7 – 10 meters apart and went around the contour of the reef. The same diver was always responsible for data recording. His error in visually estimating a distance of 2.5 m was calculated repeatedly at the beginning of each day using standards of known length and found to be, on average, within 0.39 m (± 0.07 S.E).

Table 1: List of fish species surveyed in March and August 2011 on Abu Shosha Reef. Corresponding "*a*" and "*b*" values are shown only for the species that were encountered.

Fish Species	***a***	***b***
SCARIDAE		
Bolbometapon m.		
Cetoscarus bicolor	0.020	3.000
Hipposcarus harid		
Chlorurus gibbus	0.021	3.096
Chlorurus sordidus	0.021	3.096
Scarus sp.	0.032	3.060
SERRANIDAE		
Plectropomus pessuliferus		
Plectropomus areolatus		
Variola louti		
Cephalopholis argus	0.013	3.114
Cephalopholis miniata	0.018	2.989
Cephalopholis hemistiktos	0.023	3.000
Epinephelus summana	0.021	3.000
ACANTHURIDAE		
Acanthurus sohal	0.019	3.055
Acanthurus nigrofuscus	0.041	2.867
Ctenochaetus striatus	0.025	3.056
Zebrasoma xanthurum		
Zebrasoma desjardinii	0.034	2.861

Counts of individuals in each length category were converted into biomass following Friedlander and DeMartini (2002) using the following equation:

$$W = a \times L^b$$

where *W* is the weight of the fish in grams, *L* is its total length in cm and *a* and *b* are species-specific constants that relate the length of a fish to its biomass. For the *L* value, we used the average value of the range of each of our size categories (e.g. for the 10 – 20 cm category, we calculated L = (10 + 20)/2 = 15 cm). The *a* and *b* values for each species were obtained from FishBase (2010) (see table 1). Wherever several values of for *a* and *b* were presented in the database, we used an average of the available values. For species whose *a* and *b* values were not available, we used the corresponding values of the closest related species or sister species according to the World Atlas of Marine Fishes (Kuiter and Debelius 2006): for *Zebrasoma desjardinii* we used *Z. velifer* and for *Chlorurus gibbus* we used *C. sordidus*.

The biomass data obtained was then used to evaluate the health of the fish community on Abu Shosha. Using the statistical software R (R Development Core Team 2011), Non-parametric PERMANOVA (Anderson 2001; Anderson 2005) was used to compare the biomass estimates at different depths for the different fish groups, and multi-dimensional scaling plots (Izenman 2008) were created. The counts of fish recorded were also compared using Mann Whitney tests to the counts of the same fish collected in June 2011 from another inshore reef in Saudi Arabia (Coastguard 1 Reef 20° 08' 58.16"N, 40° 14' 28.53"E) that has about 10 times more live coral cover than Abu Shisha (66.4% ± 6.32 SE). Mann-Whitney comparisons were done using the software SPSS, version19. The coral cover and fish count data from Coastguard Reef 1 was supplied by M. Berumen (unpublished data 2011).

2.3 Results

2.3.1 Coral Recruitment

A total of 102 (28.7 %) living scleractinian recruits, 23 (6.7 %) dead coral recruits and 230 (64.8 %) bryozoan recruits were found on the 60 settlement plates, exclusively on the bottom surfaces. Six groups of scleractinians were identified: Acroporidae, Pocilloporidae, Poritidae, Faviidae, Mussidae, and Other. There was also a notable abundance of algae on most plates, particularly the plates that did not have many coral or bryozoan recruits. However, we did not measure algal cover on the plates. Top-facing plates had zero coral recruits.

The overall average density of living scleractinian recruits was 1.7 recruits/plate (1 plate = 100cm^2), and the maximum number found on any plate was 11 recruits (tables 2 and 3). The average number of recruits on 5-meter versus reef edge plates and sheltered versus non-sheltered plates are also shown in tables 2 and 3, respectively. The percentage of living recruits found on settlement plates was higher at the reef edge (59.8%) than at 5 meters (40.2%), and on the sheltered side of the reef (87.3%) than on the exposed side (12.7%) (figures 7 and 8, respectively). Twenty-six plates (43.3 % of the total) had zero scleractinian recruits.

The majority of scleractinian recruits belonged to the family Pocilloporidae (57.84 %). Acroporidae was the second most abundant family (20.59 %) followed by the category “other” (table 4 and figure 9). Poritidae made up 2.94% of coral recruits and Faviidae and Mussidae made up 1.96% each (table 4).

Table 2: Descriptive statistics of living scleractinian recruits found on settlement plates split by depth.

Depth	Number of Plates	Mean	Std. Error	Median	Minimum	Maximum
5 meters	29	1.41	0.316	1	0	6
reef edge	31	1.97	0.509	1	0	11
Total	60	1.7	0.304	1	0	11

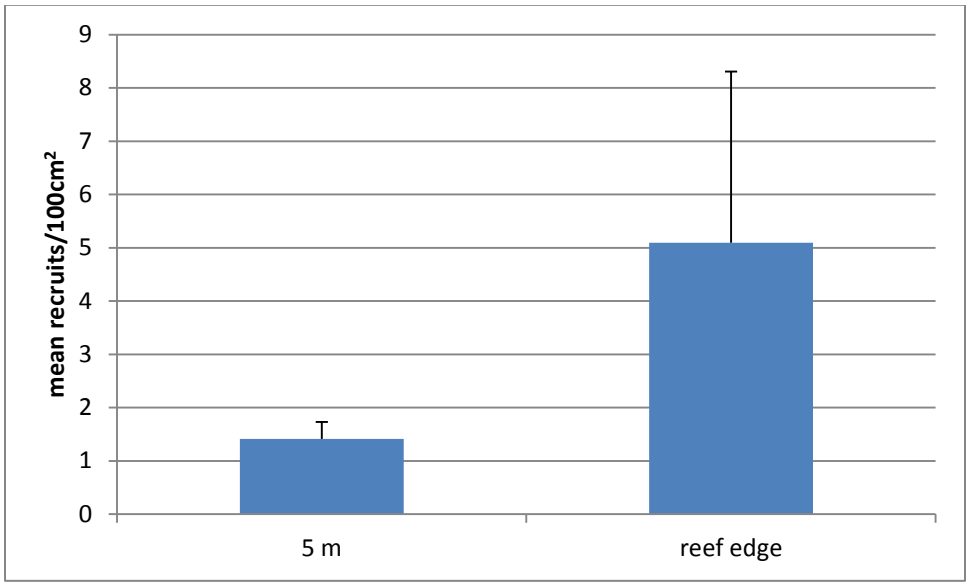


Figure 7: Mean density of living coral recruits found per plate at 5 meters vs. plates on the reef edge. Error bars represent standard error of the mean. Corals recruited more on average at the reef edge.

Table 3: Descriptive statistics of living scleractinian recruits found on settlement plates split by shelter.

Habitat	Number of	Mean	Std.	Median	Minimum	Maximum
Exposed	11	1.18	0.55	1	0	6
Sheltered	49	1.82	0.35	1	0	11
Total	60	1.70	0.30	1	0	11

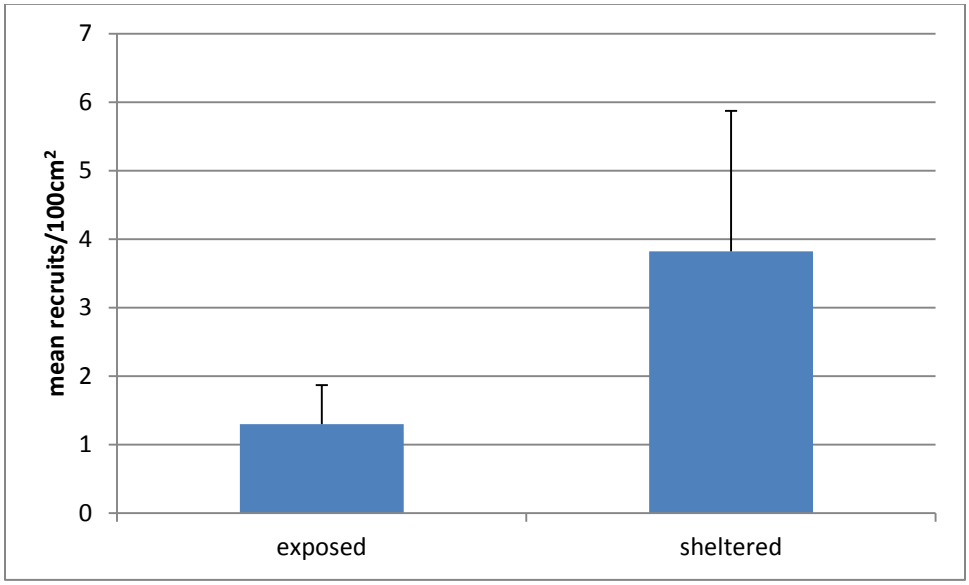
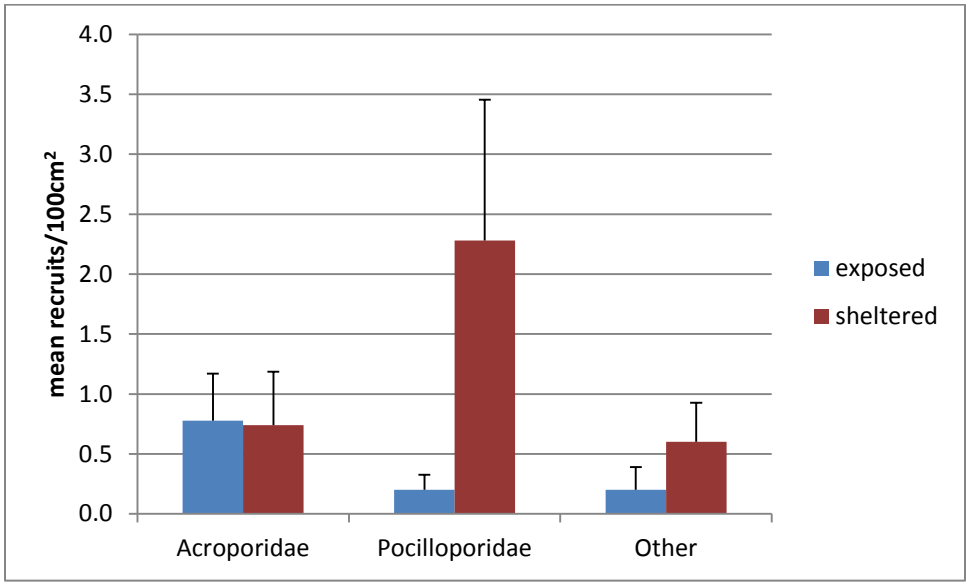


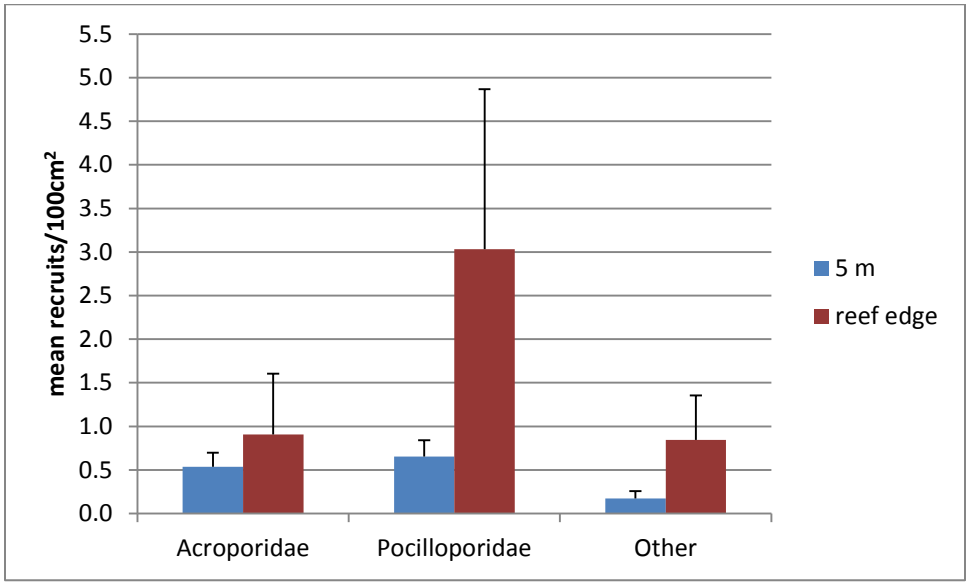
Figure 8: Mean density of living coral recruits per plate found on exposed vs. sheltered plates. Error bars represent standard error of the mean. Corals recruited more on average on the sheltered side of the reef.

Table 4: Counts, densities and percentages of coral families identified on settlement plates: Acro = Acroporidae; Poc = Pocilloporidae; Por = Poritidae; Fav = Faviidae; Mus = Mussidae.

Location and Depth	Number of plates	Acro	Poc	Por	Fav	Mus	Other
Sheltered side							
5m	21	8	17	0	0	0	3
reef edge	28	6	40	2	1	2	10
percentage of total		13.73	55.88	1.96	0.98	1.96	12.75
average desnsity (recruits/100cm2)		0.29	1.16	0.04	0.02	0.04	0.27
Exposed side							
5m	8	7	2	1	1	0	2
reef edge	3	0	0	0	0	0	0
percentage of total		6.86	1.96	0.98	0.98	0.00	1.96
average desnsity (recruits/100cm2)		0.64	0.18	0.09	0.09	0.00	0.18
Total percentages		20.59	57.84	2.94	1.96	1.96	14.71
Overall average density (recruits/100cm2)		0.37	0.97	0.03	0.03	0.03	0.27



(a)



(b)

Figure 9: Mean density per plate of the three major categories of recruits on the (a) sheltered versus exposed plates, and (b) 5 meter versus reef edge plates. Error bars represent standard error of the mean. In general, all categories recruited more at the shallower depth and the more sheltered side of the reef. Only acroprid recruits showed no preference by habitat shelter.

The number of living recruits was also found to correlate negatively with the number of bryozoans found on the plates (figure 10). However, the correlation was insignificant (R^2= 0.037).

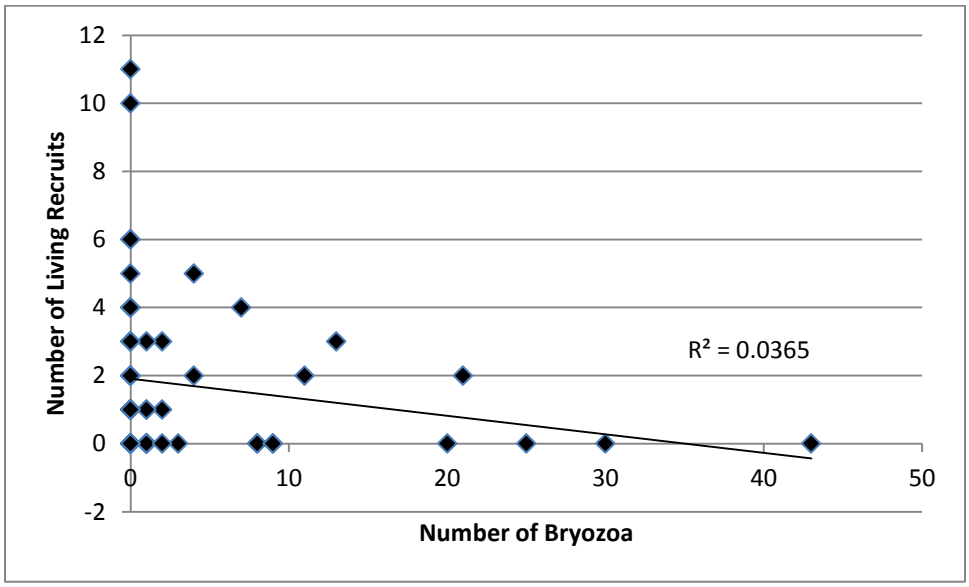


Figure 10: Scatter plot of the number of living recruits against the number of bryozoa on settlement plates. The plot shows an insignificant negative correlation between the two variables.

Mann-Whitney tests were done for the three major categories of recruits (Acroporidae, Pocilloporidae, and Other) to see if there are significant differences in medians of counts grouped by shelter or depth. All test results were insignificant except for acroporid counts grouped by depth (U = 356.5, z = -1.78, one-tailed significance p = 0.038), showing that acroporids recruited more to deeper plates, and pocilloporid counts grouped by habitat (U = 178, z = -1.96, one-tailed significance p = 0.025) (tables 5 and 6). There was also no significant difference between the numbers of all coral recruits pooled together grouped by depth or by shelter (two-tailed significance p = 0.816 and 0.483, respectively) (tables 7 and 8).

Table 5: Significant result of Mann-Whitney test for acroporid recruit counts grouped by depth.

	Acroporidae
Mann-Whitney U	356.5
Wilcoxon W	852.5
Z	-1.78
Exact Sig. (1 tailed)	0.038

Table 6: Significant result of Mann-Whitney test for pocilloporid counts grouped by habitat.

	Pocilloporidae
Mann-Whitney U	178
Wilcoxon W	244
Z	-1.962
Exact Sig. (1 tailed)	0.025

Table 7: Insignificant Mann-Whitney result for all living coral recruit counts grouped by depth.

	Living Recruits
Mann-Whitney U	434.5
Wilcoxon W	869.5
Z	-0.233
Asymp. Sig. (2-tailed)	0.816

Table 8: Insignificant Mann-Whitney result for all living coral recruit counts grouped by shelter.

	Living Recruits
Mann-Whitney U	234.5
Wilcoxon W	300.5
Z	-0.701
Asymp. Sig. (2-tailed)	0.483

2.3.2 Fish Surveys

In March, an overall average of 9.15 g/m^2 of fish biomass (± 2.54 SE) was calculated from our observations (all depths and fish families pooled). In August, we calculated an average of 8.22 g/m^2 (± 2.41 SE). Scarids contributed the highest amount of

biomass in both surveys and at all depths (table 10 and figure 8). In March, they contributed most at 5 meters (average 40.01 g/m^2 ± 15.77 SE), while in August, they contributed more at the reef edge (47.39 g/m^2 ± 8.59 SE). Acanthurids contributed generally more than the serranids but always markedly less than the scarids (in March, grand mean of 4.54 g serranids/m^2 ± 1.68 g SE; August 0.89 g serranids/m^2 ± 0.43 g SE).

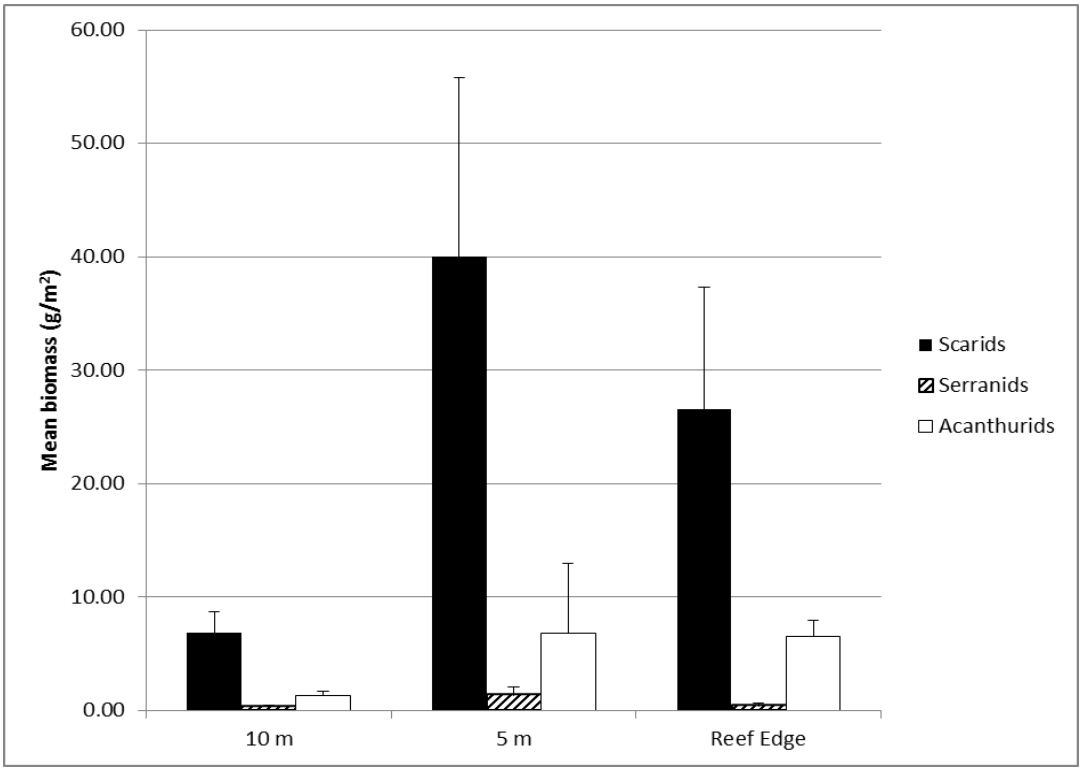
Table 9: Mean biomass (g/m^2) and standard errors of the mean for scarids, acanthurids and serranids at 10 m, 5 m and reef edge in (a) March, (b) August.

(a)

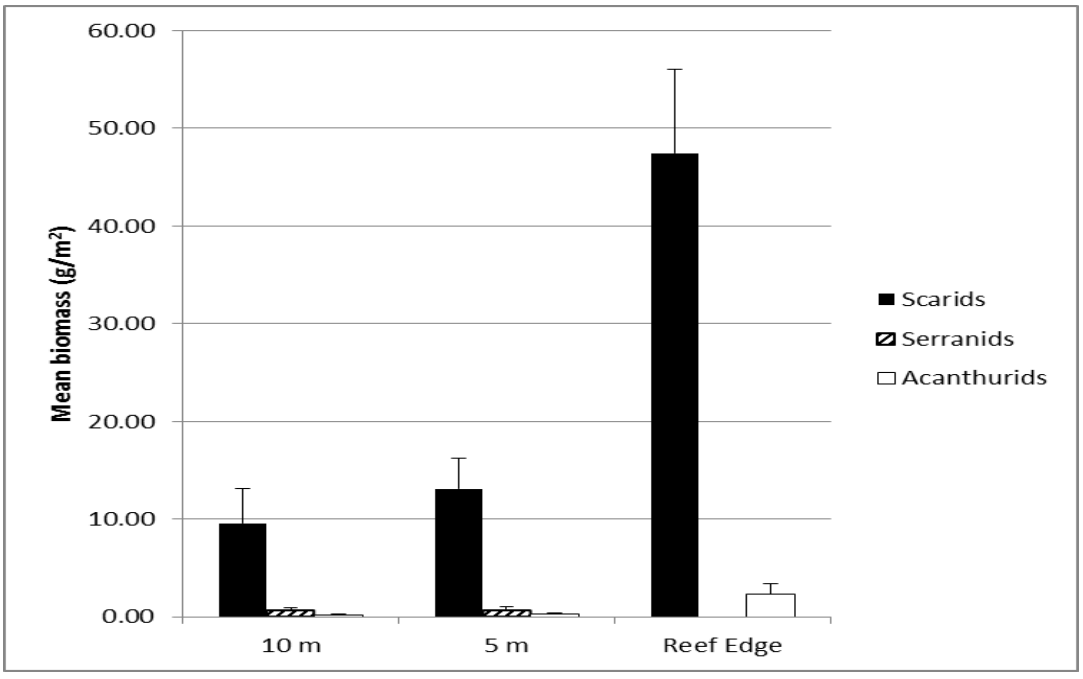
	March Biomass (g/m^2)							
Family	**10 m**		**5 m**		**Reef Edge**		**overall mean**	**SE**
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**		
Scarids	6.83	1.89	40.01	15.77	26.57	10.72	22.26	6.24
Serranids	0.37	0.13	1.32	0.74	0.42	0.24	0.64	0.23
Acanthurids	1.31	0.36	6.85	6.11	6.56	1.38	4.54	1.68

(b)

	August Biomass (g/m^2)							
Family	**10 m**		**5 m**		**Reef Edge**		**overall mean**	**SE**
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**		
Scarids	9.56	3.60	13.09	3.14	47.39	8.59	23.35	5.48
Serranids	0.68	0.26	0.61	0.46	0.00	0.00	0.43	0.18
Acanthurids	0.16	0.08	0.24	0.15	2.28	1.08	0.89	0.43



(a)



(b)

Figure 7: Average biomass per transect on Abu Shosha for Scarids (shaded), Serranids (solid) and Acanthurids (open) at each depth in (a) March, (b) August. Bars represent standard error of the mean. Scarids consistently contributed the most biomass at each depth for both months but were most abundant on the reef edge in August and most abundant at 5 m in March. Serranid biomass was consistently very low throughout. Acanthurid biomass was considerably lower in August than March.

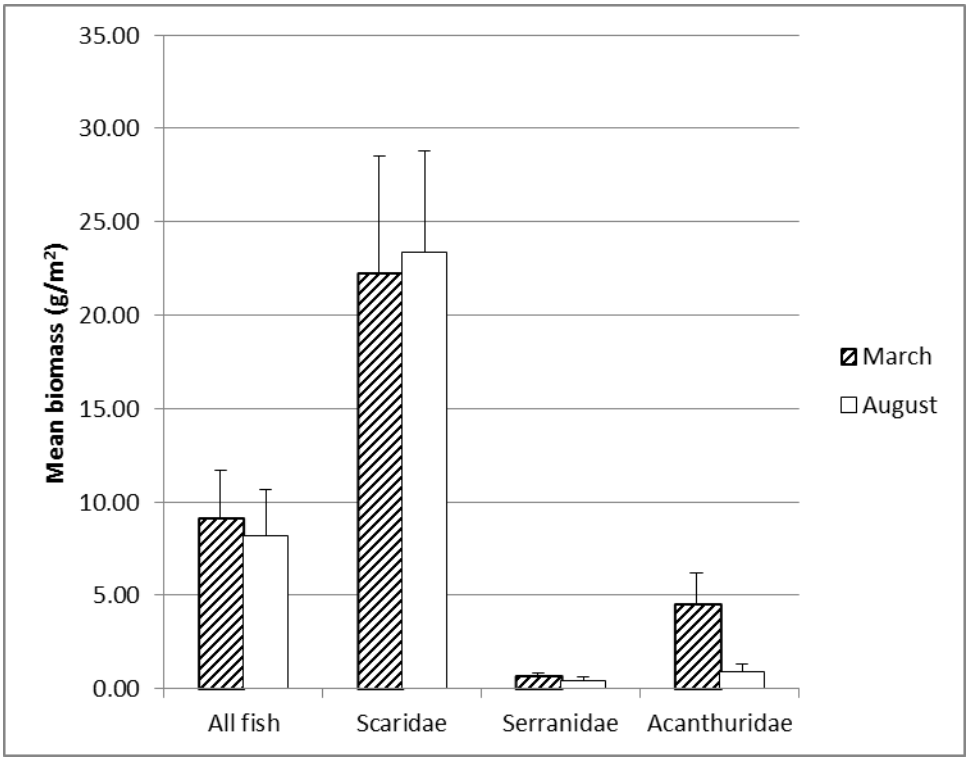


Figure 11: Comparison between March (open) and August (shaded) mean biomass (g/m²) for each family with all depths pooled together. Bars represent standard error of the mean. Scaridae was the dominant family in both months. Serranidae biomass was very low compared to the other two groups in both months. Acanthurid biomass was considerably higher than serranids biomass in March but very low in August.

Table 10: Insignificant Mann-Whitney results for comparison of all fish biomass calculated in March vs. August.

	Biomass
Mann-Whitney U	830.000
Wilcoxon W	1865.000
Z	-1.475
Asymp. Sig. (2-tailed)	.140

Preliminary comparisons using Mann Whitney showed no significant difference between fish biomass (all families pooled) in March and August ($p>0.05$)

(table 10). However, the biomass of acanthurids was significantly lower in August than in March ($U=42.5$, z -2.9, $p<0.05$) (table 11).

Table 11: Significant Mann-Whitney results for comparison of acanthurid biomass calculated in March vs. August.

	Biomass
Mann-Whitney U	42.500
Wilcoxon W	162.500
Z	-2.905
Asymp. Sig. (2-tailed)	.004
Exact Sig. (1-tailed]	.003

The results of PERMANOVA show that depth alone and depth together with month had a significant effect on fish biomass, but that month alone had no significant effect (table 12). The non-metric multidimensional scale (NMDS) model in figure12 displays some patterns found in the biomass data. Each of the numbers on the plot refers to the biomass observations from one transect. Numbers 1 – 15

Table 12: Results of non-parametric PERMANOVA showing a significant effect of depth alone and depth-with-month on fish biomass, and no significant effect for month alone.

	Df	Sums of Squares	Mean Squares	F. Model	R2	p
Depth	2	4518.2	2259.09	6.908	0.297	0.003
Month	1	109.6	109.65	0.335	0.007	0.618
Depth:Month	2	2753.7	1376.84	4.210	0.181	0.026
Residuals	24	7848.8	327.03		0.515	
Total	29	15230.3			1	

refer to transects done in March, and 16 – 30 refer to transects done in August. The plot shows that at reef edge and 5 meters, most of the biomass, especially in August was contributed by scarids and acanthurids. Points 22, 24 and 26 – 30, which seem to cluster more closely together, correspond to 5 meter and reef edge transects in August where the biomass of serranids was zero. The plot also shows that most of the biomass contributed by serranids was at 5 meters and 10 meters. Points 4 and 18 refer to transects where scarid biomass was zero. The plot may also be showing trends of habitat preference based on food availability and shelter for the different families. Serranids may be more abundant deeper due to the presence of more sheltered crevices while the herbivores may have more food available to them at shallower depths and particularly at the reef edge.

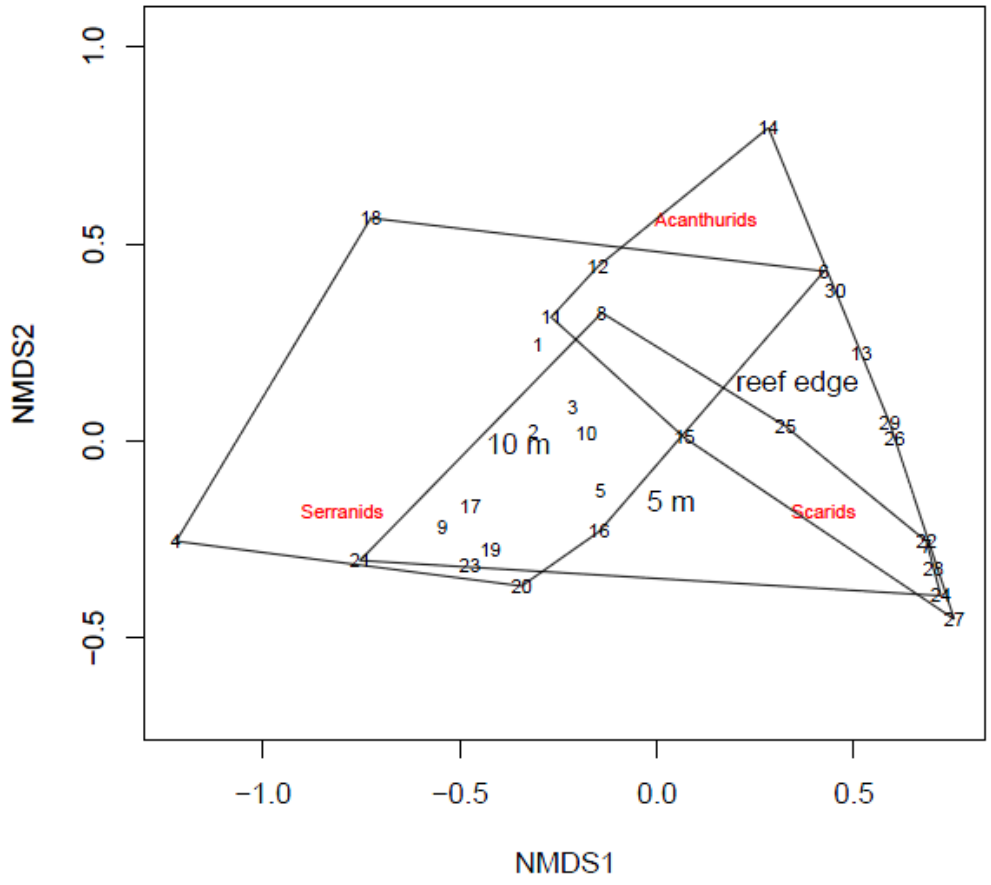


Figure 12: Non-metric multidimensional scale plot of fish biomass data. Each number on the plot refers to biomass observations from one transect. Points 1 – 15 refer to transects done in March, and 16 – 30 refer to August transects. The figure visually represents the distribution of biomass from the different families at different depths. For example, points 22, 24 and 26 – 30 cluster together close to Scarids and correspond to transects where serranid biomass was zero and scarid biomass was high at the reef edge and 5 m depths. Similarly, points 4 and 18 stand out as they correspond to transects where scarid biomass was zero and serranid biomass was relatively high at 10 m. Points that fall more towards the center of the plot correspond to transects where there was a more even mix of biomass contribution from the three families.

If we pool together all herbivore biomass (scarids and acanthurids together), we find that the biomass of herbivores in March ranged from 0.02-79.6 g/m^2 (mean 26.8 g/m^2 ±7.04 g S.E.), while in August it ranged from 0.09-66.31 g/m^2 (mean 24.24 g/m^2 ± 5.59 g S.E.).

The results of the comparison between fish counts in Abu Shosha and those from Coastguard Reef are shown in table 13 and figure 13. Scarids were more abundant in Abu Shosha (0.081 fish/m^2 ±0.02 SE) than in Coastguard Reef (0.018 fish/m^2 ±0.006 SE), and Mann-Whitney tests showed the difference is significant ($U=8$, $z=-3.57$, $p<0.001$) (table 14). There were also more acanthurids in Abu Shosha on average, but the difference was not found to be statistically significant ($p>0.05$). Serranids were on average more abundant in Coastguard Reef, but again the difference was not found to be statistically significant ($p>0.05$).

Table 13: Average number of fish per square meter at 0-6 meters in Coastguard Reef versus Abu Shosha Reef in summer 2011.

	Fish counts m^{-2}			
	Coastguard 1		Abu Shosha	
Family	**average**	**SE**	**average**	**SE**
Scaridae	0.018	0.006	0.081	0.020
Acanthuridae	0.070	0.012	0.081	0.020
Serranidae	0.008	0.002	0.003	0.002

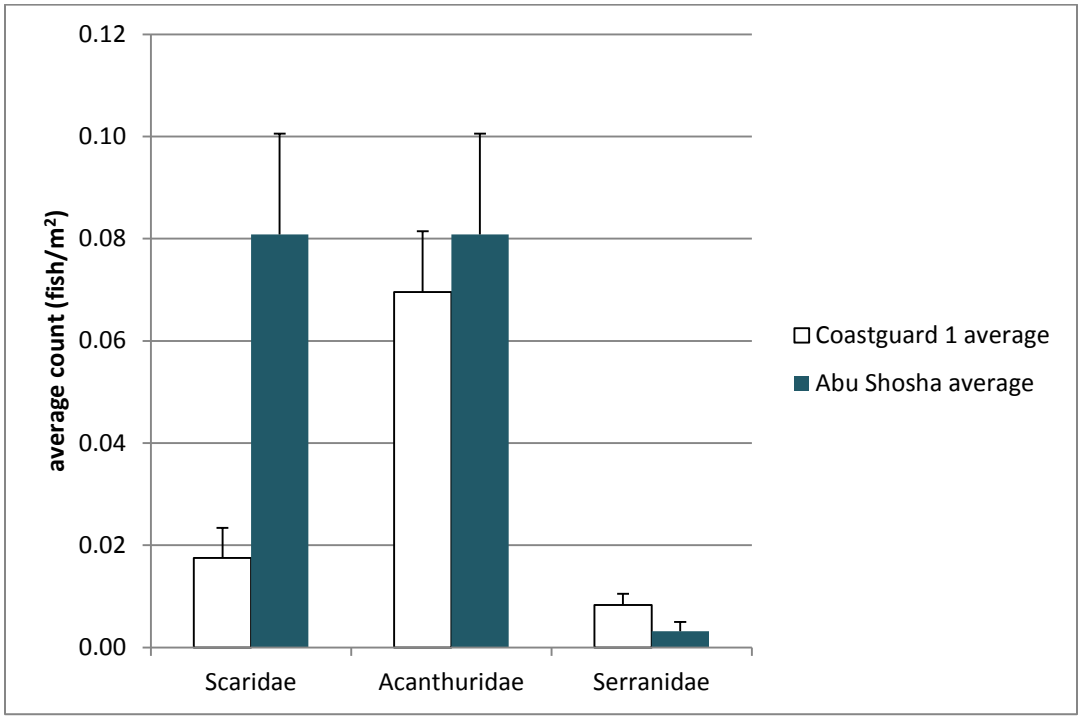


Figure 13: Mean fish counts per square meter in Coastguard 1 Reef (open) versus Abu Shosha Reef (solid) from depths of 0-6 meters in summer 2011. Error bars represent standard error of the mean. Herbivorous fish counts were higher in Abu Shosha than in Coastguard 1, particularly scarid counts. Serranids were more abundant in Coastguard 1.

Table 14: Mann-Whitney test results for comparisons of fish counts between Coastguard Reef and Abu Shosha.

	Scarids	Acanthurids	Serranids
Mann-Whitney U	6.000	57.000	37.000
Z	-3.573	-.198	-1.627
Asymp. Sig. (2-tailed)	0.000	0.843	0.104
Exact Sig. (1-tailed)	0.000	0.872	0.140

2.4 Discussion

2.4.1 Recruitment Rates

The first notable observation in this dataset is that no coral recruits grew on the upper surfaces of the plates. The lack of recruits on upper surfaces is consistent with previous studies which usually found significantly more recruits on lower, more

sheltered surfaces, and most authors have attributed this pattern to sedimentation and the effect of grazing by fish (Wallace 1985; Maida et al. 1994; Mundy 2000; Mundy and Babcock 2000; Adjeroud et al. 2007). However, the studies we reviewed rarely reported 0% recruitment on top surfaces of settlement plates, which may indicate particularly intense grazing by fish on Abu Shosha Reef and/or particularly low recruitment rates in general. Some more detailed studies of coral recruitment suggest that scleractinians in fact recruit faster on upper surfaces that are more exposed to light but that post-settlement survivorship on these surfaces is poor (Birkeland 1977).

Another more striking observation is the overwhelming abundance of bryozoans (64.8% of all recruits on plates). Previous studies claim that bryozoans and other benthic organisms (e.g. oysters) appear to decrease post-settlement survivorship of scleractinians (Dunstan and Johnson 1998). Glassom et al. (2004) found a similar negative correlation between percent cover of bryozoa (and other sessile organisms) and the number of coral recruits. However, the pattern was not consistent and was even reversed for one of the seasons of Glassom's study. Many studies have also found significant negative correlations between scleractinian recruitment and turf algal densities (Rogers et al. 1984; Connell et al. 1997; Vermeij and Sandin 2008). While we did not measure the percent cover of algae on our plates, we can anecdotally report markedly high densities of it on plates that had few or no coral recruits. There is also evidence of positive correlation between crustose coralline algae and coral recruit densities in other studies, and it is suggested that crustose coralline algae may be providing settlement cues for corals

(Morse et al. 1988; Vermeij and Sandin 2008). Gathering more data on non-coral benthic recruits on the settlement plates can allow us to study more interactions between these organisms and scleractinians as well as among the organisms themselves.

The overall average density of scleractinian recruits in our study (1.7 recruits/100cm^2) is extremely low compared to most studies done in other regions (Harriott and Fisk 1988; Fisk and Harriott 1990; Adjeroud et al. 2007). Fisk and Harriott (1990) reported the highest coral recruitment rates so far from a large-scale study on the Great Barrier Reef (up to 488 recruits/100 cm^2, two orders of magnitude higher than our maximum density per plate). Also, Adjeroud et al. (2007) reported mean densities per plate in French Polynesia that are about 5.3 times higher than our value. Both of these studies, however, were conducted at lower latitudes than the Red Sea, and it is thought that recruitment rates naturally decrease with increasing latitudes (Glassom et al. 2004; Abelson et al. 2005; Adjeroud et al. 2007). Nonetheless, Adjeroud et al. concluded that the rates they reported are too low for their area of study and more similar to sub-tropical recruitment rates (2007), and yet, their recruitment rates are considerably higher than ours. We also compared our values to those reported by studies done in the Gulf of Aqaba and found that they reported average recruitment rates per 100cm^2 that varied from about half our mean value to about 6 times higher over two summer seasons and across a large number of sites (Glassom et al. 2004). Moreover, Abelson et al. (2005) conducted a larger scale study on the reefs of Eilat and reported generally lower recruitment rates than ours. However, their methodology

was different and comparing results is, unfortunately, probably not valid. Similarly, Rogers et al. (1984) report recruitment rates that appear to be possibly lower than ours, but their settlement plates were made of cross sections of *Acropora palmata* branches rather than terracotta tiles, making their results incomparable to ours (Harriott and Fisk 1987). As previously suggested (Abelson et al. 2005), we believe that standardization of methods (type of settlement plate, method and pattern of installment, etc.) used in coral recruitment studies is much needed so that results can be more easily comparable. In any case, it is important to note that most of the studies that are mentioned here were done over much longer time-scales and mostly larger spatial scales, and they all report very high variability in recruitment rates across seasons, years and for different sites. The small scale of our study (being limited to one reef and, so far, one season) means that we cannot claim to have an accurate picture of recruitment rates on Abu Shosha yet.

2.4.2 Relative Abundances and Differences by Depth and Shelter

Regarding the relative abundances of recruits, we find that our data is consistent with many other studies in that pocilloporids and acroporids were the most dominant groups, and that the percentage of the former (mostly brooders) far exceeds that of the latter (mostly spawners) (Abelson et al. 2005; Adjeroud et al. 2007). However, some studies report much higher percentages of acroporids than pocilloporids in the summer season, consistent with the timing of spawning (Wallace 1985; Fisk and Harriott 1990), and this was not the case in Abu Shosha even though multi-specific spawning of acroporids near our study area occurred in

April (Bouwmeester et al. 2011; Appendix I), May and June (J. Bouwmeester unpublished data), and our plates were taken out of the reef and examined in July. The relative abundance of acroporids in our study is much lower than most studies we reviewed for the summer season (Wallace 1985; Fisk and Harriott 1990; Adjeroud et al. 2007).

Nonetheless, it is interesting that that 22 (20.59%) of the 102 recruits belonged to the family Acroporidae when only 0.67% of the adult living coral cover on Abu Shosha is attributed to this family. The vast majority of adults from this family down to 5 meters also appeared to be in very poor health and only one had eggs during the reproduction season (J. Bouwmeester unpublished data). It is still, however, difficult to hypothesize the natal origin of these acroporid recruits for several reasons. First, we did not carry out a comprehensive survey of the reproductive status of adult acroporids on the reef, and colonies at 10 meters or deeper, while still very few in general, appeared to be in substantially better health than colonies at shallower depths (J. Bouwmeester personal observation). Likewise, corals at 15 and 10m were least affected by the 2010 summer bleaching event (K Furby and M Berumen, unpublished data). Second, studies that were previously done on reefs with disturbed or depauperated adult communities and found high recruitment rates have concluded that inter-reef connectivity is important on these reefs (Harriott and Fisk 1988). However, there is no standard that determines how low the cover of an adult population should be in relation to the number of recruits of that same population in order to be able to claim that recruits were not self-seeded. Third, the relationship between recruit densities and adult populations is

generally unclear. Rogers et al. (1984) found that settlement rates increased as adult cover increased but quickly saturated at 10% cover. In fact, studies in various parts of the world that explored the possibility of correlation between recruit densities and adult populations found the two variables to be independent of each other (Rogers et al. 1984; Dunstan and Johnson 1998; Edmunds 2000; Vermeij and Sandin 2008). However, it seems that at least in some studies the densities of surviving *juveniles* (< 5 cm in diameter) eventually become similar to adult populations (Bak and Engel 1979). The low density and reproductive condition of adult acroporids on Abu Shosha down to 5 meters makes it seem more likely that the acroporid recruits settled on our plates arrived from a reef other than Abu Shosha. However, we cannot be certain of this as we did not consider the reproductive health of adult colonies below 10 meters. Knowing that a single pair of healthy colonies from the same species can produce hundreds of gamete bundles depending on its size and fecundity, it is still possible that our 22 acroporid recruits may have come from Abu Shosha. The return of acroporid cover to Abu Shosha would be a very good sign of recovery as these corals tend to be more vulnerable to bleaching, die faster and recover slower than other families such as pocilloporids (Baird and Marshall 2002). Continuous and more comprehensive monitoring of recruits and adults on Abu Shosha and perhaps genetic analyses of the new recruits arriving in Abu Shosha may provide a better idea of the natal origin of the recruits of spawning species on Abu Shosha (*sensu* Saenz-Agudelo et al. 2009).

As for spatial variability, our results showed a significantly higher number of acroporid recruits at 5 meters than at the reef edge and significantly more

pocilloporid recruits on the sheltered as opposed to the exposed part of the reef. Most of the studies we have reviewed that compare spatial variability of recruits in the field did not install settlement plates at a depth of 0 – 1 meters, but tended to install plates at 5 meters or deeper. Studies always found very large variability and no consistent patterns over their study periods with regards to depth for different families or overall recruitment rates, but found that recruits generally tended to have better survivorship in sheltered locations (Wallace 1985; Dunstan and Johnson 1998; Adjeroud et al. 2007). The number of plates we installed on the sheltered side of the reef was much more than the number of plates on the exposed side (49 versus 11 plates respectively), and with such unequal sample sizes, we cannot be certain that shelter has a significant effect on recruit densities. The higher number of acroporid recruits at 5 meters is most likely due to post-settlement mortality caused by predation or physical forces rather than settlement preference by planulae (Mundy and Babcock 2000). Birkeland (1977) has shown that even though corals may recruit faster to shallower depths, they tend to have much higher survivorship at greater depths. However, our data is merely a snapshot of recruitment patterns on Abu Shosha, and continuing to gather information over a longer period of time will give us more information on the degree of variability of recruitment both spatially and temporally.

2.4.3 Potential Implications to Recovery

The effect of disturbances on recruitment rates is generally poorly understood, and some of the evidence gathered from previous studies done on recently-disturbed

reefs is contradictory. For example, Fisk and Harriott reported extremely high recruitment rates on the Great Barrier Reef, and their highest record (4.88 recruits/cm^2) came from a reef whose adult live cover had just been decimated by an outbreak of *Acanthaster planci* (1990). Ceccarelli et al. (2011) also observed a 300% increase in coral cover in only 4 years after a bleaching event in north Western Australia. On the other hand, Adjeroud et al. (2007) attribute the drop in recruitment rates they observed in the middle of their 5-year study period to a bleaching event that may have affected the fecundity of corals in their study area. Yet again, even a highly vulnerable species (but a fast-growing one) of *Acropora* was observed to recover within 6 years from a bleaching event due to rapid recruitment (Linares et al. 2011). Therefore, it is not entirely clear how such disturbances affect recruitment rates, but it is accepted that, in general, corals recover faster from acute disturbances that cause them physical damage than they do from disturbances that change the chemistry of the environment, and that they tend to recover faster on wave-exposed sides of reefs (Connell et al. 1997).

As mentioned before, recovery after massive loss of adult coral cover will undoubtedly depend on the degree of inter-reef connectivity (Hogan et al. 2011) and the health of the herbivorous community (Hughes et al. 2007). At least for this recruitment season, we do not see enough evidence of how well-connected Abu Shosha Reef is. Abu Shosha may in fact be a well-connected reef as it is in close proximity to many other inshore reefs in the area, but its recruitment rates may be low because all of these reefs are more-or-less similarly affected by the bleaching event and have lost most of their coral cover. Another possible explanation is that

Abu Shosha never was a good receiver of larvae and had always been more reliant on self-seeding, but due to the loss of its adult population, it is no longer able to produce enough quantities of larvae to maintain itself.

Regardless of how well-connected Abu Shosha is, the current evidence suggests that the rate of recovery for Abu Shosha and similarly-affected reefs in the region may be rather slow unless recruitment rates increase and survivorship of recruits is high. Due to the highly variable nature of connectivity and of recruitment rates both spatially and temporally (Wallace 1985; Hogan et al. 2011), we must continue to monitor the reef for several seasons before drawing any major conclusions.

2.4.4 Fish Community

Our fish counts and biomass calculations are generally very low compared to most studies we have reviewed. For example, on the Great Barrier Reef, following the major bleaching event of 1998, it was found that in experimental areas where herbivorous fishes were not excluded by cages, fish biomass were about 2 – 3 orders of magnitude higher than even our maximum values, and this allowed coral cover to increase about 13 times faster (6.0% to 20.2% cover in 2.5 years) than areas where fish were excluded (Hughes et al. 2007). Similarly, Friedlander and DeMartini (2002) and Wismer et al. (2009) also found 2 – 3 orders of magnitude more herbivore biomass than our results in Hawaii (even on unprotected reefs) and on the Great Barrier Reef, respectively. Only one of the studies reviewed (carried out on Caribbean reefs) reported mean herbivore biomass values similar to our study

(Williams and Polunin 2001). Table 16 summarizes comparisons with other studies. However, note that these studies were carried out on a much larger spatial and/or temporal scale than our study and some of them included more comprehensive herbivore surveys; Wismer et al. (2009) included the families Siganidae, Labridae, Kyphosidae and Ephippidae in their herbivore counts in addition to Scaridae and Acanthuridae, while others did not make clear which families they included (e.g., Hughes et al. 2007). However, all report that parrotfish and surgeonfish were generally the most important herbivores in their study areas. Therefore, the comparison with this study is still meaningful.

Table 15: Mean herbivore biomass comparisons with other studies in theCaribbean, Hawaian Islands and Great Barrier Reef (GBR). All units were scaled to g/m².

Study	mean herbivore biomass (g/m2)	negative correlation with algal cover
This study (2011) - Saudi Arabian Red Sea	0.02 - 79.61 (grand mean 26.8)	not tested
Williams & Polunin (2001) - Caribbean	2.5 - 17.1	no
Wismer et al. (2009) - GBR	8 - 317	yes
Friedlander & DeMartini (2002) - Hawaii	41 - 464	not tested
Hughes et al. (2007) - GBR	450 - 4290	yes

A report on herbivore abundance in the Gulf of Aqaba also reported fish counts that are generally about one order of magnitude higher (up to 0.234 herbivores/m$^{2)}$ than our grand mean of fish per square meter in both Abu Shosha and Coastguard 1 Reef (Bouchon-Navaro and Harmelin-Vivien 1981). However, this study was undertaken in 1981 and so, may not be comparable to our study. Also, although the Gulf of Aqaba is part of the Red Sea, it is a very different environment in terms of productivity levels and local management and protection laws.

These very low fish densities on both Abu Shosha as well as Coastguard Reef may be due to several reasons. First, it is possible that the reefs of the central Saudi Arabian Red Sea naturally do not support high densities of fish due to low productivity. However, in the absence of data from this region over the past few decades, we cannot be certain of this. Another possibility is that these low densities may be the result of intense overfishing in Saudi Arabia of which there is evidence (Jin et al. In press).

Despite herbivore densities in both Abu Shosha and Coastguard being very low compared to other regions, the fact that the mean density of scarids in Abu Shosha is significantly higher than Coastguard Reef may provide some hope of recovery. The lower densities of serranids and the general absence of large piscivorous predators on Abu Shosha may explain the higher abundance of scarids and acanthurids compared to Coastguard Reef, and while the absence of these groups in itself may be indicator of poor reef health or overfishing, it may at this stage be beneficial by allowing for more grazing of algae on Abu Shosha, and thus encouraging coral recruitment.

While the difference in fish densities (all three families pooled together) on Abu Shosha between March and August is not significant, the density of acanthurids alone was significantly lower in August. Longer-term monitoring is needed to evaluate whether Abu Shosha's herbivore densities are stable, increasing or in decline, and whether they are sufficient to allow recovery of coral cover and how fast recovery would be.

2.4.5 Improvements to Study Design

Some measures can be taken to improve the experimental design and allow for better analysis of the data.

First, the number of settlement plates on the reef should be divided more-or-less equally between the exposed and sheltered part of the reef and between the different depths to avoid bias and facilitate statistical analysis. For example, we cannot conclude from this dataset that recruitment rates are higher on the sheltered side of the reef because the experimental design is very biased towards the sheltered side with 49 plates on that side and only 11 on the exposed side.

At least doubling the number of settlement plates and adding an array of plates at 10 meters deep (and possibly deeper depths) would also help improve the study by providing a larger dataset, which would be particularly useful due to the fact that variability in coral recruitment usually tends to be particularly high (Wallace 1985). Installing plates at 10 meters will be useful for getting more information about recruits which tend to survive better at deeper levels of a reef slope. It would also facilitate comparisons with other studies which often have data from as deep as 18 meters and less often from reef edge (or 0-2 meters). However, since the bathymetry around Abu Shosha will probably not allow the installation of plates deeper than 10-12 meters, having an array of plates at reef edge, 5 meters and 10 meters should suffice in giving a complete picture of recruitment patterns.

Also, in order to have a better understanding of the reasons for low recruitment and the reef's potential for recovery, we can look more closely at herbivory on the reef. For example, we can survey turf algal cover and urchin

densities. The former could be studied along with herbivore densities over time (Wismer et al. 2009), and the latter has been shown to positively correlate with recruitment rates up to a certain extent (Sammarco 1980). Also, rather than limiting fish surveys to certain species within certain families, a more comprehensive survey of all herbivores, corallivores and piscivores could provide a more accurate picture of the reef's fish community and functional groups over time. Previous studies have shown that there is more redundancy than complementarity between the feeding preferences of scarids and acanthurids (Burkepile and Hay 2011), and so, looking at the densities of other herbivores as well as types of algae on the reef may be useful. Together with continued monitoring of algal cover, adult coral cover, recruit densities and juvenile coral densities, this would give a better picture of the reef's recovery patterns.

Conclusions

Using information about the early life stages of organisms to predict future ecological impacts is complicated by uncertainty in many aspects. However, this study provides the first glimpse into the biological characteristics of coral larvae from the Red Sea. The benefit of knowing the maximum longevity of planulae or recruitment rates as they relate to dispersal and connectivity is limited by the uncertainty of whether or not the planulae will in fact live so long, travel so far, reach another reef, still be competent to settle when they do and/or survive after settlement long enough to reproduce sexually (Cowen and Sponaugle 2009). Connectivity patterns are highly variable both spatially and temporally (at the scale of seasons (Hepburn et al. 2009) and years (Hogan et al. 2011)) as well as among species (Berumen et al. in press), which also adds to the complications and makes it necessary to study aspects of connectivity over as large a temporal scale as possible and with as many replicates as possible (Hogan et al. 2011).

Our data for both projects presented in this thesis provides little evidence of inter-reef connectivity for the scale at which it was designed. Even though our dataset is small and our evidence is limited, we can derive a few general conclusions.

It is possible that our observations in both projects (short longevity of larvae and low coral recruitment) are directly related and are both due to the bleaching event of summer 2010 lowering the fecundity of adult corals and/or the fitness of

larvae. It is difficult to ascertain whether this is truly the case with our current evidence, but future work might make this possible.

If maximum pelagic larval durations of corals in the Red Sea are indeed as short as we found *Acropora humilis'* to be, and if recruitment rates are generally as low on disturbed reefs as we found them to be on Abu Shosha, this paints a bleak picture for the resilience of Saudi Arabian Red Sea reefs (at least inshore reefs) to disturbances that cause high mortality of corals. To improve reef resilience, protection from overfishing is essential in order to boost herbivore communities and generally preserve a more balanced, productive reef ecosystem (McClanahan and Muthiga 1988; Polunin and Roberts 1993; Friedlander and DeMartini 2002; Mumby et al. 2007).

This work presents some preliminary information on aspects of the early life stages of corals and the resilience of a reef to bleaching in the Red Sea which can be built upon and expanded to provide a larger and more accurate picture.

Appendix I: Synchronous Spawning of *Acropora* in the Red Sea

Reef sites

Synchronous spawning of *Acropora* in the Red Sea

Fig. 1 **a** Setting of gamete bundles in *Acropora gemmifera*, **b** *Chaetodon austriacus* feeding on egg-sperm bundles released from *Acropora lamarcki*

Multi-specific synchronous spawning is a reproductive strategy used by scleractinian corals that has now been described from coral reefs in 23 locations globally (Baird et al. 2009). While high multi-specific synchrony in the reproductive condition of *Acropora* colonies has been documented in the Red Sea in April and/or May (Hanafy et al. 2010), multi-specific synchronous spawning has not been directly observed. In April 2011, mature oocytes were found in a high proportion of colonies in numerous species of *Acropora* on reefs near Thuwal, Saudi Arabia (22°18′19.26″N, 38°57′56.66″E). On the night of April 16 2011, two nights before the full moon, egg-sperm bundles were first observed in *Acropora* polyps at 20:30 h (Fig. 1a). Between 22:30 and 23:45 h, 43 colonies from 10 out of 13 surveyed *Acropora* species released egg/sperm bundles (Fig. 1b), including three species that had not been observed to spawn previously (*A. plantaginea*, *A. parapharaonis*, and *A. lamarcki*). This is the first documented multi-specific synchronous spawning event in the Red Sea, demonstrating that the asynchronous spawning pattern at Eilat in the Gulf of Aqaba (Shlesinger and Loya 1985) is not representative of the Red Sea, and providing further support for the prediction that these events are characteristic of all speciose coral assemblages (Guest et al. 2005).

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References

Baird AH, Guest JR, Willis BL (2009) Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. Ann Rev Ecol Evol Sys 40:551–571
Guest JR, Baird AH, Goh BPL, Chou LM (2005) Seasonal reproduction in equatorial reef corals. Invertebr Reprod Dev 48:207–218
Hanafy MH, Aamer MA, Habib AB, Baird AH (2010) Synchronous reproduction of corals in the Red Sea. Coral Reefs 29:119–124
Shlesinger Y, Loya Y (1985) Coral community reproductive patterns: Red Sea versus the Great Barrier Reef. Science 228:1333–1335

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REFERENCES

Abelson A, Olinky R, Gaines S (2005) Coral recruitment to the reefs of Eilat, Red Sea: temporal and spatial variation, and possible effects of anthropogenic disturbances. Marine Pollution Bulletin 50:576-582

Adjeroud M, Penin L, Carroll A (2007) Spatio-temporal heterogeneity in coral recruitment around Moorea, French Polynesia: Implications for population maintenance. Journal of Experimental Marine Biology and Ecology 341:204-218

Almany G, Connolly S, Heath D, Hogan J, Jones G, McCook L, Mills M, Pressey R, Williamson D (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs 28:339-351

Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local Replenishment of Coral Reef Fish Populations in a Marine Reserve. Science 316:742-744

Anderson M (2001) A New Method for Non-Parametric Multivariate Analysis of Variance. Austral Ecology 26:32-46

Anderson MJ (2005) PERMANOVA: Permutational Multivariate Analysis of Variance. University of Auckland, Aukland

Babcock RC, Baird AH, Piromvaragorn S, Thomson DP, Willis BL (2003) Identification of scleractinian coral recruits from Indo-Pacific reefs. Zool Stud 42:211-226

Baird A, Marshall P, Wolstenholme J (2002) Latitudinal variation in the reproduction of Acropora in the Coral Sea. Proceedings 9th International Coral Reef Symposium 1:385-389

Baird AH (2001) The ecology of coral larvae: settlement patterns, habitat selection and the length of the larval phase. James Cook University, Townsville, p181

Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Marine Ecology Progress Series 237:133-141

Bak RPM, Engel MS (1979) Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Marine Biology 54:341-352

Bassim K, Sammarco P (2003) Effects of temperature and ammonium on larval development and survivorship in a scleractinian coral (Diploria strigosa). Marine Biology 142:241-252

Bauman A, Baird A, Cavalcante G (2011) Coral reproduction in the world's warmest reefs: southern Persian Gulf (Dubai, United Arab Emirates). Coral Reefs 30:405-413

Becker BJ, Levin LA, Fodrie FJ, McMillan PA (2007) Complex larval connectivity patterns among marine invertebrate populations. Proceedings of the National Academy of Sciences 104:3267-3272

Bellwood DR, Hughes TP, Hoey AS (2006) Sleeping Functional Group Drives Coral-Reef Recovery. Current Biology 16:2434-2439

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827-833

Berumen M, Almany G, Planes S, Jones G, Thorrold S (in press) Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network. Ecology and Evolution

Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Third International Coral Reef Symposium 1:15–21

Black K, Moran P, Hammond L (1991) Numerical Models Show Coral Reefs Can Be Self Seeding. Marine Ecology Progress Series 74:1-11

Bouchon-Navaro Y, Harmelin-Vivien ML (1981) Quantitative distribution of herbivorous reef fishes in the Gulf of Aqaba (Red Sea). Marine Biology 63:79-86

Bouwmeester J, Khalil MT, De La Torre P, Berumen ML (2011) Synchronous spawning of Acropora in the Red Sea. Coral Reefs 30:1011-1011

Burkepile D, Hay M (2011) Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. Coral Reefs 30:351-362

Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the Local Dynamics of Open Marine Populations. Annual Review of Ecology and Systematics 27:477-500

Ceccarelli DM, Richards ZT, Pratchett MS, Cvitanovic C (2011) Rapid increase in coral cover on an isolated coral reef, the Ashmore Reef National Nature Reserve, north-western Australia. Marine and Freshwater Research 62:1214-1220

Cetina-Heredia P, Connolly S (2011) A simple approximation for larval retention around reefs. Coral Reefs 30:593-605

Chia F-S, Buckland-Nicks J, Young CM (1984) Locomotion of marine invertebrate larvae: a review. Canadian Journal of Zoology 62:1205-1222

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs 67:461-488

Connolly SR, Baird AH (2010) Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals. Ecology 91:3572-3583

Cowen RK, Sponaugle S (2009) Larval Dispersal and Marine Population Connectivity. Annual Review of Marine Science 1:443-466

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of Connectivity in Marine Populations. Science 311:522-527

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of Marine Populations: Open or Closed? Science 287:857-859

Dixson DL, Jones GP, Munday PL, Planes S, Pratchett MS, Srinivasan M, Syms C, Thorrold SR (2008) Coral reef fish smell leaves to find island homes. Proceedings of the Royal Society B: Biological Sciences 275:2831-2839

Donelson J, Munday P, McCormick M, Pankhurst N, Pankhurst P (2010) Effects of elevated water temperature and food availability on the reproductive performance of a coral reef fish. Marine Ecology Progress Series 401:233-243

Dunstan PK, Johnson CR (1998) Spatio-temporal variation in coral recruitment at different scales on Heron Reef, southern Great Barrier Reef. Coral Reefs 17:71-81

Edmunds PE, Gates RG, Gleason DG (2001) The biology of larvae from the reef coral Porites astreoides, and their response to temperature disturbances. Marine Biology 139:981-989

Edmunds PJ (2000) Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. Marine Ecology Progress Series 202:113-124

FishBase (2010) www.fishbase.org

Fisher R, Bellwood DR (2003) Undisturbed swimming behaviour and nocturnal activity of coral reef fish larvae. Marine Ecology Progress Series 263:177-188

Fisk DA, Harriott VJ (1990) Spatial and temporal variation in coral recruitment on the Great Barrier Reef: Implications for dispersal hypotheses. Marine Biology 107:485-490

Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. Marine Ecology Progress Series 230:253-264

Frith CA, Leis JM, Goldman B (1986) Currents in the Lizard Island region of the Great Barrier Reef Lagoon and their relevance to potential movements of larvae. Coral Reefs 5:81-92

Glassom D, Zakai D, Chadwick-Furman NE (2004) Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. Marine Biology 144:641-651

Graham E, Baird A, Connolly S (2008) Survival dynamics of scleractinian coral larvae and implications for dispersal. Coral Reefs 27:529-539

Hamner WM, Colin PL, Hamner PP (2007) Export–import dynamics of zooplankton on a coral reef in Palau. Marine Ecology Progress Series 334:83–92

Harii SH, Kayanne HK, Takigawa HT, Hayashibara TH, Yamamoto MY (2002) Larval survivorship, competency periods and settlement of two brooding corals, Heliopora coerulea and Pocillopora damicornis. Marine Biology 141:39-46

Harriott V, Fisk D (1987) A comparison of settlement plate types for experiments on the recruitment of scleractinian corals. Marine Ecology Progress Series 37:201-208

Harriott V, Fisk D (1988) Recruitment patterns of scleractinian corals: a study of three reefs. Australian Journal of Marine and Freshwater Research 39 409-416

Harrison P, Wallace CC (1990) Reproduction, dispersal, and recruitment of scleractinian corals. Elsevier, Amsterdam, The Netherlands

Harrison PL, Babcock RC, Bill GD, Oliver JK, Wallace CC, Willis BL (1984) Mass Spawning in Tropical Reef Corals. Science 223:1186-1189

Heyward A, Negri A (2010) Plasticity of larval pre-competency in response to temperature: observations on multiple broadcast spawning coral species. Coral Reefs 29:631-636

Hodgson G (1985) Abundance and distribution of planktonic coral larvae in Kaneohe Bay, Oahu, Hawaii. Marine Ecology Progress Series 26:61-71

Hogan J, Thiessen R, Sale P, Heath D (2011) Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. Oecologia:1-11

Hughes TP (1985) Life histories and population dynamics of early successional corals. Fifth International Coral Reef Congress 5:101-106

Hughes TP (1989) Community Structure and Diversity of Coral Reefs: The Role of History. Ecology 70:275-279

Hughes TP, Jason ET (2000) Recruitment Failure, Life Histories, and Long-Term Decline of Caribbean Corals. Ecology 81:2250-2263

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply-Side Ecology Works Both Ways: The Link between Benthic Adults, Fecundity, and Larval Recruits. Ecology 81:2241-2249

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. Current Biology 17:360-365

Izenman AJ (2008) Multidimensional Scaling and Distance Geometry Modern Multivariate Statistical Techniques. Springer Science+Business Media, LLC, pp463-504

Jin D, Kite-Powell HL, Hoagland P, Solow AR (In press) A bioeconomic analysis of traditional fisheries in the Red Sea off the coast of the Kingdom of Saudi Arabia. Marine Resource Economics

Jokiel PL, Guinther EB (1978) Effects of Temperature on Reproduction in the Hermatypic Coral Pocillopora Damicornis. Bulletin of Marine Science 28:786-789

Jones GP, Planes S, Thorrold SR (2005) Coral Reef Fish Larvae Settle Close to Home. Current biology : CB 15:1314-1318

Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. Nature 402:802-804

Karlson RH, Hurd LE (1993) Disturbance, coral reef communities, and changing ecological paradigms. Coral Reefs 12:117-125

Kinlan BP, Gaines SD (2003) Propagule Dispersal in Marine and Terrestrial Environments: A Community Perspective. Ecology 84:2007-2020

Kuiter RH, Debelius H (2006) World Atlas of Marine Fishes. IKAN-Unterwasserarchiv, Frankfurt

Linares C, Pratchett M, Coker D (2011) Recolonisation of Acropora hyacinthus following climate-induced coral bleaching on the Great Barrier Reef. Marine Ecology Progress Series 438:97-104

Maida M, Coll JC, Sammarco PW (1994) Shedding new light on scleractinian coral recruitment. Journal of Experimental Marine Biology and Ecology 180:189-202

McClanahan TR, Muthiga NA (1988) Changes in Kenyan coral reef community structure and function due to exploitation. Hydrobiologia 166:269-276

Miller K, Mundy C (2003) Rapid settlement in broadcast spawning corals: implications for larval dispersal. Coral Reefs 22:99-106

Morse, Hooker N, Jensen (1988) Control of larval metamorphosis and recruitment in sympatric agariciid corals. Journal of Experimental Marine Biology and Ecology 116:193-217

Mumby PJ, Harborne AR, Williams J, Kappel CV, Brumbaugh DR, Micheli F, Holmes KE, Dahlgren CP, Paris CB, Blackwell PG (2007) Trophic cascade facilitates coral recruitment in a marine reserve. Proceedings of the National Academy of Sciences 104:8362-8367

Mundy C, Babcock R (2000) Are vertical distribution patterns of scleractinian corals maintained by pre- or post-settlement processes? A case study of three contrasting species. Marine Ecology Progress Series 198:109-119

Mundy CN (2000) An appraisal of methods used in coral recruitment studies. Coral Reefs 19:124-131

Mundy CN, Babcock RC (1998) Role of light intensity and spectral quality in coral settlement: Implications for depth-dependent settlement? Journal of Experimental Marine Biology and Ecology 223:235-255

Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in ecology & evolution (Personal edition) 15:278-285

Newman MJH, Paredes GA, Sala E, Jackson JBC (2006) Structure of Caribbean coral reef communities across a large gradient of fish biomass. Ecology Letters 9:1216-1227

Nishikawa A, Sakai K (2005) Settlement-competency Period of Planulae and Genetic Differentiation of the Scleractinian Coral Acropora digitifera. Zoological Science 22:391-399

Nishikawa A, Katoh M, Sakai K (2003) Larval settlement rates and gene flow of broadcast-spawning (Acropora tenuis) and planula-brooding (Stylophora pistillata) corals. Marine Ecology Progress Series 256:87-97

Nozawa Y, Harrison PL (2005) Temporal settlement patterns of larvae of the broadcast spawning reef coral Favites chinensis and the broadcast spawning and brooding reef coral Goniastrea aspera from Okinawa, Japan. Coral Reefs 24:274-282

Palumbi SR (1994) Genetic Divergence, Reproductive Isolation, and Marine Speciation. Annual Review of Ecology and Systematics 25:547-572

Planes S, Jones GP, Thorrold SR (2009) Larval dispersal connects fish populations in a network of marine protected areas. Proceedings of the National Academy of Sciences 106:5693-5697

Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series 100:167-176

Richmond RH (1988) Competency and dispersal potential of planula larvae of a spawning versus a brooding coral. 6th Int Coral Reef Symp 2:827-831

Rogers CS, Fitz HC, Gilnack M, Beets J, Hardin J (1984) Scleractinian coral recruitment patterns at Salt River submarine canyon, St. Croix, U.S. Virgin Islands. Coral Reefs 3:69-76

Rumrill SS (1990) Natural Mortality in Marine Invertebrate Larvae. Ophelia 32

Saavedra-Sotelo NC, Calderon-Aguilera LE, Reyes-Bonilla H, Lopez-Perez RA, Medina-Rosas P, Rocha-Olivares A (2011) Limited genetic connectivity of Pavona gigantea in the Mexican Pacific. Coral Reefs 30:677-686

Saenz-Agudelo P, Jones GP, Thorrold SR, Planes S (2009) Estimating connectivity in marine populations: an empirical evaluation of assignment tests and parentage analysis under different gene flow scenarios. Molecular Ecology 18:1765-1776

Sammarco PW (1980) Diadema and its relationship to coral spat mortality: grazing, competition, and biological disturbance. Journal of Experimental Marine Biology and Ecology 45:245-272

Sammarco PW (1982) Echinoid grazing as a structuring force in coral communities: Whole reef manipulations. Journal of Experimental Marine Biology and Ecology 61:31-55

Smith SR (1992) Patterns of Coral Recruitment and Post-settlement Mortality on Bermuda's Reefs: Comparisons to Caribbean and Pacific Reefs. American Zoologist 32:663-673

Strathmann RR (1985) Feeding and Nonfeeding Larval Development and Life-History Evolution in Marine Invertebrates. Annual Review of Ecology and Systematics 16:339-361

Strathmann RR, Hughes TP, Kuris AM, Lindeman KC, Morgan SG, Pandolfi JM, Warner RR (2002) Evolution of local recruitment and its consequences for marine populations. Bulletin of Marine Science 70:377-396

Team RDC (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Thorson G (1950) Reproductive and Larval Ecology of Marine Bottom Invertebrates. Biological Reviews 25:1-45

Tranter PRG, Nicholson DN, Kinchington D (1982) A Description of Spawning and Post-Gastrula Development of the Cool Temperate Coral, Caryophyllia Smithi. Journal of the Marine Biological Association of the United Kingdom 62:845-854

Underwood AJ, Fairweather PG (1989) Supply-side ecology and benthic marine assemblages. Trends in ecology & evolution (Personal edition) 4:16-20

Vermeij MJA, Sandin SA (2008) Density-Dependent Settlement and Mortality Structure the Earliest Life Phases of a Coral Population. Ecology 89:1994-2004

Vermeij MJA, Fogarty ND, Miller MW (2006) Pelagic conditions affect larval behavior, survival, and settlement patterns in the Caribbean coral Montastraea faveolata. Marine Ecology Progress Series 310:119-128

Wallace CC (1985) Seasonal peaks and annual fluctuations in recruitment of juvenile scleractinian corals. Marine Ecology Progress Series 21:289-298

Wallace CC (1999) Staghorn corals of the world: a revision of the coral genus Acropora (Scleractinia; Astrocoeniina; Acroporidae) worldwide, with emphasis on morphology, phylogeny and biogeography. CSIRO

Williams IW, Polunin NP (2001) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs 19:358-366

Wismer S, Hoey A, Bellwood D (2009) Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. Marine Ecology Progress Series 376:45-54

Wolstenholme J (2004) Temporal reproductive isolation and gametic compatibility are evolutionary mechanisms in the Acropora humilis species group (Cnidaria; Scleractinia). Marine Biology 144:567-582