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By

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Turf Algal/Sediment (TAS) Mats: A Chronic Stressor on Scleractinian Corals
in Akumal, México

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Turf Algal/Sediment (TAS) Mats: A Chronic Stressor on Scleractinian Corals
in Akumal, México

by

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This is dedicated to:

Roy Thomas and Isha Roy,

for giving me the world, through your love,

support, wisdom and sacrifice.

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Turf Algal/Sediment (TAS) Mats: A Chronic Stressor on Scleractinian Corals in
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Turf algal/sediment (TAS) mats are currently prevalent on reefs near Akumal, México. In contrast to turf algae that lack bound sediments, TAS mats outcompete scleractinians by employing one or more of three encroachment methods identified during this investigation. In 2000, all colonies of *Diploria strigosa* and most *Montastraea faveolata* were 100% surrounded by well-developed TAS mats, as were about two thirds of the *Siderastrea siderea*. Given that these species are locally important reef framework-builders and flourished here in recent decades, encroachment by TAS mats is probably a recent phenomenon.

Results indicate that *D. strigosa* is the most vulnerable of the three, losing, on average, $70 \pm 13.2 \text{ cm}^2$ area of tissue/coral/year. Three of the 42 studied colonies suffered complete mortality and another one-third regressed below their estimated

puberty size. *M. faveolata* is similarly vulnerable but survives longer due to its far larger mean colony sizes. *S. siderea*, however, not only loses tissues at a significantly lower rate, but also seems able to outcompete TAS mats with low sediment loads.

Sixty-one species of algae and cyanobacteria (more than two thirds of which were Rhodophyta) were identified in TAS mats that recruited to settling plates and rubble. Manipulations of sediment load in recruited TAS mats indicate that it can affect mat composition at the genus level. Entrapped sediment weight/cm² is positively related to the average turf algal filament height and averages 14.4 times the algal dry weight/cm² in which it is embedded.

The prevalence of TAS mats and their encroachment over scleractinians is likely related to high sediment loading and low rates of herbivory (due to heavy, historical fishing efforts, relatively high territorial pomacentrid populations, and the continued absence of the key Caribbean herbivore, *Diadema antillarum*). The current decline in *D. strigosa* and *M. faveolata* is unsustainable over the long-term with serious impending consequences for local habitat heterogeneity and diversity. Wherever present in abundance, TAS mats should be included as a chronic stressor in future assessments of reef health, and programs to enhance herbivore populations, especially of *D. antillarum* which can effectively remove these mats (*pers. obs.*), should be developed.

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Chapter 1: Introduction to Coral Reefs

TYPES OF CORAL REEFS

Coral reefs have been referred to as the crown jewels of the earth. Contributing to the high diversity of life forms and species found on most reefs are the calcareous cnidarians (stony corals) that create much of the structure and shelter for the residents they harbor. Well-developed reefs are generally found in relatively shallow, tropical waters with low turbidity, and are among the most productive natural ecosystems on earth. The three major types of reefs recognized by Darwin (1842) are fringing reefs, barrier reefs and atolls. Fringing reefs are considered the youngest type of reef geologically. Once it reaches the surface, a reef usually grows oceanward so long as the sea-level remains stable. Fringing reefs typically follow the shoreline closely, sometimes forming the outer border for a narrow, shallow lagoon located between the land and the reef. Atolls develop in a ring or horseshoe shape when the reef around a subsiding island continues to grow upward to compensate for the subsidence (which also results in a deeper and larger lagoon). Barrier reefs are similar to fringing reefs but grow as far as 100 km from shore, allowing the waters between the reef and land to be much deeper. By definition these reefs are located at the edge of the continental or insular shelf (as are fringing reefs if the shelf is very narrow). Barrier reefs have likely developed from fringing reefs through a combination of substratum subsidence and growth towards the open ocean. These are the largest reef

structures, e.g. Australia's Great Barrier Reef which is over 2000 km long and up to 1000 m wide (Achituv and Dubinsky 1990, Birkeland 1997).

MAJOR REEF ZONES

Fringing reefs typically can be divided into three primary zones: lagoon, reef crest and fore reef (Figure 1.1), although there are places where the lagoon is absent because the crest runs into the shore. Each of these zones is dominated by certain kinds of stony corals (hereafter corals) that are best adapted to the local environmental conditions. Coral larvae need hard surfaces on which to settle and this can lead to clumped distributions. Resulting clusters of corals may form patch reefs that are typically found in calm waters like those of a lagoon. Solitary, relatively slowly growing, boulder-shaped coral heads and fragile, branching corals among a mosaic of seagrass beds with intermixed calcareous algae are also characteristic of the lagoon. Towards the reef crest, the seagrass beds become smaller and more sparsely distributed. The rear zone (landward side of the reef crest) is a narrow, linear field of isolated, small massive (boulder) and branching corals interspersed with sand, leading to the reef flat. Corals are closest to the sea surface on the reef flat and may even be exposed at low tide. The seaward side of the reef crest is subject to breaking waves, heavy surge and turbulent waters, making it a high-energy zone. Unlike the rear zone, the reef flat and seaward

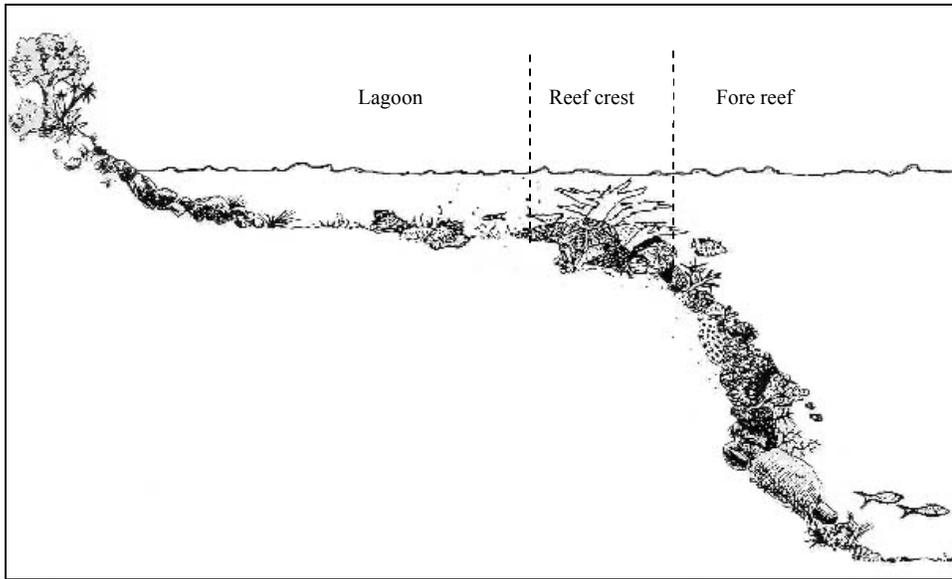


Figure 1.1 The three primary zones of a fringing reef (after Rogers *et al.* 2001).



Figure 1.2. Spur-and-groove formation on a Caribbean reef. The spurs on either side of the photo have developed as the result of reef-building organisms that have overgrown each other over long periods of time and are separated by a sand channel. These spur-and groove formations run perpendicular to shore or the predominant swells (also indicated by the ripples in the sand channel that result from the water movement, and form parallel to the shore and/or predominant swell). This nurse shark was disturbed from under an overhang afforded by corals on the side of the spur.

reef crest are usually dominated by relatively fast-growing, robust, branching corals, which proliferate asexually by establishing new colonies from broken branches. If the branching corals are unable to maintain themselves within this high-energy zone, sheets of blade fire coral (*Millepora complanata*, a calcareous hydrozoan) or algal ridges may dominate. Seaward of the reef crest, an area of rubble may demarcate the landward side of the fore reef. This seaward reef area often consists of fields or lobes of corals growing on a series of one or more terraces with intervening slopes or escarpments (Figure 1.1). A distinct pattern of reef development unique to the fore reef is the spur-and-groove (or tongue-and-groove) formation in which a series of coral ridges oriented perpendicular to the direction of the predominant swells are, in the wider Caribbean, usually separated by sand channels (Figure 1.2). The height of these ridges can reach 10+ m depending, in part, on the depth of the substratum on which they are growing. The shallower fore-reef areas are usually dominated by the slowly growing, boulder-shaped and lobate corals which are gradually replaced by branching corals like *Acropora cervicornis* at intermediate depths (~15 m) and, finally, by flattened foliaceous and encrusting corals at greater depths and decreased light attenuation (~30 m).

ANATOMY OF A CORAL

Despite the many gross differences in the sizes and shapes of individual reefs, their primary framework is constructed of the hard external skeletons underlying the polyps of colonial corals that belong to the cnidarian class Anthozoa, subclass Hexacorallia, order Scleractinia. Each individual coral polyp has tentacles, usually in multiples of six, and secretes a calcium carbonate cup called a corallite to protect its soft delicate body (Figure 1.3).

A coral polyp is made of two true tissue layers: the outer ectodermis is separated from the inner gastrodermis by the mesoglea. Photosynthetic microalgal endosymbionts of the genus *Symbiodinium*, commonly called zooxanthellae, reside in the gastrodermis of reef-building coral polyps. This mutualistic relationship provides the zooxanthellae with an environment safe from predation unlike that of many other dinoflagellates which are a part of the free-living phytoplankton community. Zooxanthellae also have access to a steady supply of organic nitrogen and other nutrients (Trench 1979), which can be scarce resources in open waters. Some species of corals use their tentacles to trap a wide range of food items (depending on its size, from zooplankton to small fish) with which they come into contact (Ruppert and Barnes 1991). Other species, particularly those with tentacles that are reduced (like foliaceous agariciids), or absent altogether (like *Mycetophylli reesi*), utilize a form of suspension feeding and trap zooplankton in mucus secretions (Lewis 1977). Although all corals can also

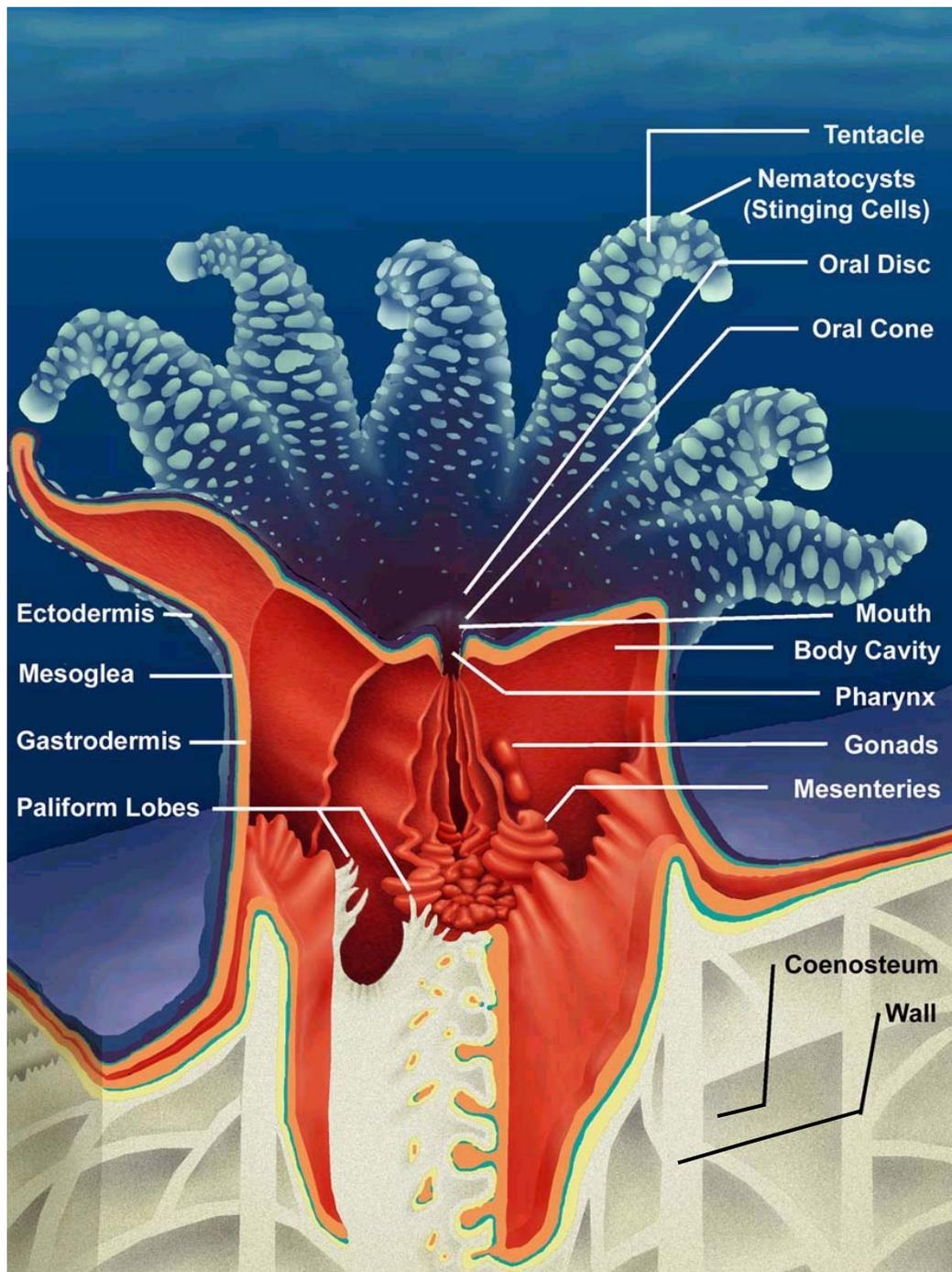


Figure 1.3 Anatomy of a stony coral polyp. The color of the soft-bodied polyp would be dependant upon its population of zooxanthellae and their pigments. The white and gray areas labeled coenosteum and wall areas are the calcium carbonate hard skeletal structure. (By M. Dupler. Adapted from Corals of the World by J.E.N. Veron 2000).

absorb dissolved organic nutrients directly through the ectodermis, the vast majority of their carbon is provided by the endosymbiotic dinoflagellates (Muscatine 1990), whose photosynthetic pigments are also responsible for much of the color of the living tissues in most corals. Corals receive a steady supply of photosynthates from their zooxanthellae, and are also provided with the necessary internal alkaline environment needed for calcium carbonate secretion at the rates required to build their skeleton (Muscatine 1990). This tight cycling of resources greatly contributes to the high gross productivity attributed to coral reefs.

Coral polyps grow into colonies through asexual budding by which the younger polyps form within or between existing polyps as boulder-shaped colonies expand, along the margins of foliaceous and encrusting colonies, and at the tips of elongating branches. Scleractinians are commonly called hard or stony corals and differ from soft corals which belong to the class Anthozoa, subclass Octocorallia, order Alcyonacea. The colonies of soft corals are pliable as their skeleton consists only of isolated, calcareous spicules secreted by cells in the mesoglea, and their polyps have eight pinnate tentacles. Although a few soft corals grow at about 30 m in the Western Atlantic, alcyonaceans are more common at greater depths (Humann 1996), *i.e.*, beyond the no-decompression SCUBA diving limits, and are therefore less accessible for investigation than hard corals. Gorgonian corals in the class Anthozoa, subclass Octocorallia, order Gorgonacea are often called soft corals in the Western Atlantic, however, the term horny corals is more correct since the majority have an internal skeleton primarily

composed of gorgonin, a tanned collagen in addition to calcareous spicules (Ruppert and Barnes 1991).

OTHER IMPORTANT REEF COMPONENTS: THE BENTHIC ALGAL COMMUNITY AND REEF HERBIVORES

Reef-dwelling benthic algae are especially diverse and difficult to identify to the species level in the field. They have therefore been partitioned into three broad functional groups (turfs, macroalgae and crustose algae) for ecological studies, primarily on the basis of their morphology (Littler 1980, Littler and Littler 1980, Steneck and Watling 1982). Turf algae, which have also been referred to as epilithic algal communities (Hatcher and Larkum 1983, Scott and Russ 1987), are attached to the substratum by rhizoids, with erect filaments that are typically between 0.1 cm and 1 cm tall (Steneck 1988, Airoidi 1998). Macroalgae have taller canopy heights, and are anatomically more complex than turfs. Crustose algae include encrusting forms which have a calcareous skeleton (Steneck 1988). These groupings are useful in understanding algal-herbivore interactions and their effects on the entire reef.

Reef herbivores have also been classified into three general categories; scraping, browsing and non-denuding, based on their ability to affect algal community abundance and distribution (see Steneck 1988). Scrapers, like parrotfishes (in the family Scaridae) and some sea-urchins, remove algae and the

top layer of the calcium carbonate substratum on which the algae grow. Scarids, the most common large-bodied herbivores seen on most reefs (Figure 1.4), are characterized by colorful markings and fused teeth which form a beak. Sometimes they also bite living corals (Figure 1.5), possibly to reach the endolithic algae that commonly grow inside coral skeletons. It is the grinding actions in their gullets that allow scarids to extract organic material from the skeleton and tolerate a much higher calcareous content in their diet than most other fishes. This also means that parrotfishes are able to take advantage of a wide variety of algae. *Diadema antillarum*, the long-spined sea-urchin is a key scraping herbivore (Figure 1.6), however, it suffered a Caribbean wide die-off in the early 1980s and is only now starting to recover (*e.g.*, Edmunds and Carpenter 2001).

Browsers are herbivores like surgeonfishes, (family Acanthuridae, Figure 1.7), some damselfishes (family Pomacentridae) and a few others that are able to remove the algae, and leave the substratum bare. Acanthurids can also tolerate high levels of calcareous content since they employ acid digestion to obtain nutrition from their food. Most other pomacentrids are considered non-denuders. They are generally far smaller than acanthurids and scarids, and some species are territorial, gardening a patch of algae that they will protect from all intruders, including humans (Figure 1.8). Males can be particularly aggressive when protecting eggs.

Other species, like the threespot damselfish (*Stegastes planifrons*), actually remove coral tissues in small bites, and allow turf algae to settle onto the bare skeleton in order to establish their algal gardens, causing the death of those portions of the coral (Kaufman 1977). This can lead to fragmentation of the parent colony into smaller daughter colonies, depending on the pattern of tissue mortality and connectedness of live tissue patches (Kaufman 1977).



Figure 1.4 Terminal phase of the Queen Parrotfish, *Scarus vetula*, (family Scaridae). Their fused teeth form the hard beak that are used to scrape algae and the underlying substratum.

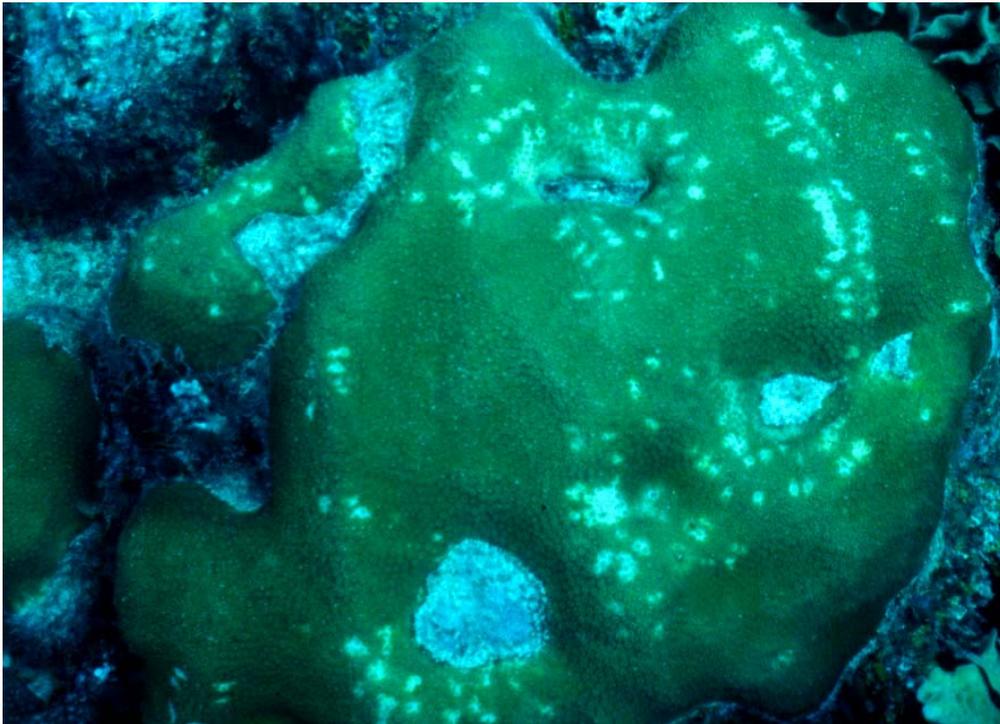


Figure 1.5 Parrotfish bites on a *Montastraea annularis* colony. The numerous paired marks revealing the underlying skeleton are characteristic of focused parrotfish bites.

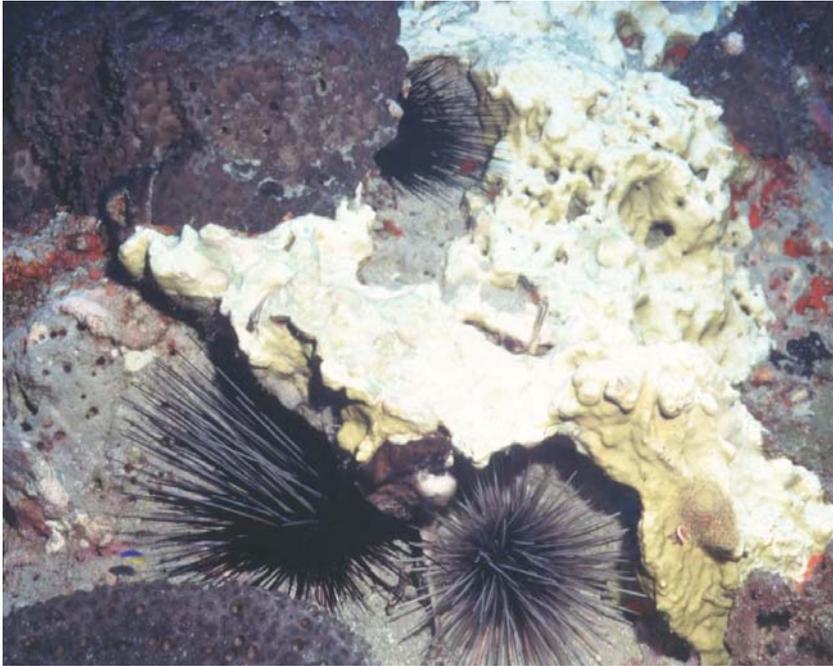


Figure 1.6 Sea-urchins in nooks and crannies of a reef. They remain concealed during the day and forage largely at night to reduce rates of predation.



Figure 1.7 The blue tang, *Acanthurus coeruleus* (family Acanthuridae). These fish employ acid digestion and are therefore able to tolerate higher levels of calcium content in their diet than most other herbivorous fish. (Photo by V. Tomeno).



Figure 1.8 Dusky damselfish, *Stegastes fuscus* (family Pomacentridae). A male protecting its algal territory from intruders (Photo by J. Strong).

OTHER CAUSES OF MORTALITY: BLEACHING, DISEASES AND SEDIMENTS

BLEACHING:

Coral bleaching is currently defined as the reduction in the levels of endosymbiotic populations of *Symbiodinium* (zooxanthellae) and/or their photosynthetic pigments (Douglas 2003). This leaves the coral's tissues paler or even translucent so that the underlying coral skeleton is clearly visible, as though "bleached" (Figure 1.9). Regional and local spatial variation in mass bleaching is apparently partially due to different species or clades (and perhaps genotypes) of zooxanthellae having different threshold temperatures for mortality (Gates and Edmunds 1999, Hoegh-Guldberg 1999, LaJeunesse *et al.* 2003). Many corals can survive if they recover their endosymbionts in at least a portion of their tissues within a few weeks or months, otherwise parts or all of the colony may die. Corals may also survive losing their zooxanthellae so long as other sources of nutrition are available, even though their growth (Goreau and Macfarlane 1990) and reproduction is significantly reduced (Szmant and Gassman 1990).

Both abiotic and biotic factors contribute to bleaching worldwide (Brown 1997). The primary cause for mass bleaching has been largely attributed to gradual increases of seawater temperatures for prolonged periods of time, or large and rapid temperature changes (Jokiel and Coles 1977, Fitt and Warner 1995). It is also becoming more apparent that ultraviolet radiation (UVR), which has

increased over the past few decades due to a reduction of the ozone layer (Stolarski *et al.* 1992, Kerr and McElroy 1993, Glynn 1996), also plays a significant role in triggering bleaching, especially in concert with changes in seawater temperature (Brown and Suharsano 1990, Williams and Bunkley-Williams 1990, Hoegh-Guldberg 1999). Other abiotic factors that cause bleaching are reductions in seawater temperatures (Coles and Fadlallah 1991) and salinity (Goreau 1964, Van Woesik *et al.* 1995). Biotic factors like bacterial (Kushamaro *et al.* 1996) and other infections (Upton and Peters 1986) can also cause corals to bleach.

DISEASES:

Colonies of *Oculina patagonica* that are infected by the bacterium *Vibrio shiloi* bleach at elevated temperatures (Kushamaro *et al.* 1996, 1997), as does the coral *Pocillopora damicornis* when infected by the bacterium *Vibrio coralyticus*, (Rosenberg and Ben-Haim 2002). It is therefore important to consider the cause for bleaching carefully as bacterial-related bleaching must be categorized as a biotic disease rather than solely a direct response to an abiotic factor like high temperature.

Other diseases include black-band disease (BBD), which is caused by a consortium of bacteria (cyanobacteria, sulfur bacteria and heterotrophic bacteria) that sometimes results in whole-colony mortality (Richardson *et al.* 1997). A dark

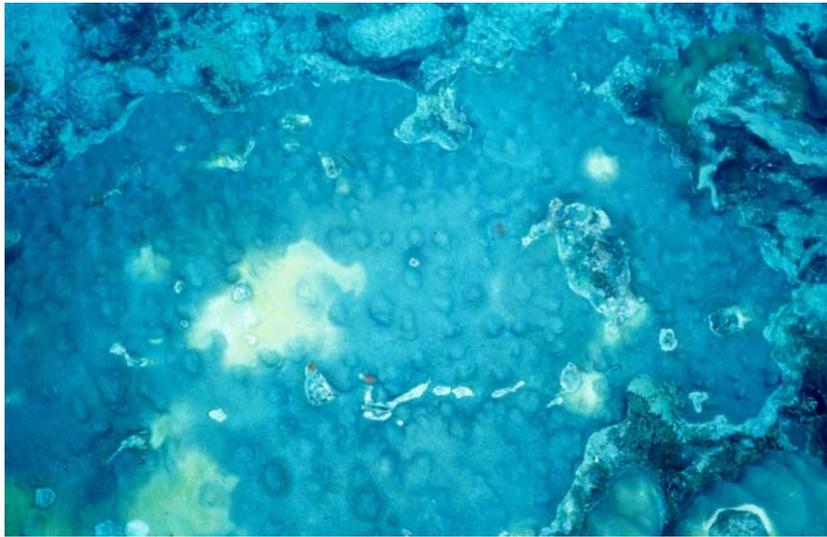


Figure 1.9 Partially bleached tissues of a colony of *Montastraea faveolata*.

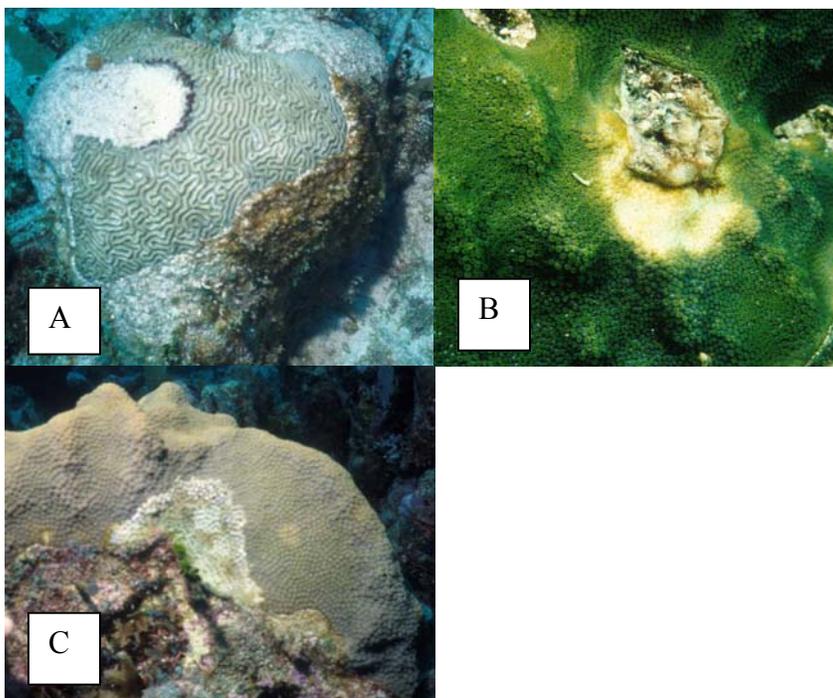


Figure 1.10 Coral diseases **A.** Black-Band Disease (BBD) on *D. strigosa*. **B.** Yellow-Blotch Disease (also called Yellow-Band Disease, YBD); turf algae and cyanobacteria have developed on the exposed skeleton of a colony of *Montastraea faveolata* (Photo by J. Lang). **C.** White Plague (WP), on *M. faveolata*.

red-to-blackish band advances across the coral killing live tissues in front and leaving a denuded skeleton behind which is rapidly colonized by turf algae (Figure 1.10A). BBD primarily affects boulder corals like *Montastraea*, *Diploria* and *Colpophyllia*.

Red-band disease (RBD) is similar to BBD in that it is also caused by a consortium of bacteria. However, its make-up seems to differ with location and host and is reportedly comprised of various cyanobacteria, sulfur bacteria, heterotrophic bacteria, and even the nematode *Araeolaimus sp.* (Santavy and Peters 1996). RBD also causes rapid tissue death, but unlike BBD, at least in one form, will not advance at night (Richardson 1993). It infects stony the corals *Agaricia*, *Colpophyllia*, *Mycetophyllia* and *Stephanocoenia* and also the gorgonian *Gorgonia ventilana* (Bruckner 2004).

Although the causative agent of yellow-blotch (or yellow band) disease (YBD) has not yet been identified, the condition has been reasonably well documented. It can kill whole colonies but usually does so over the course of many years. It starts as a pale yellow to colorless blotch of tissue that gradually expands (Figure 1.10B). Tissues at the disease front pale before dying and sloughing off. YBD primarily affects boulder corals in the genus *Montastraea* but is also found on the brain coral *Colpophyllia natans* (Santavy and Peters 1996, Bruckner 2004) and probably some species of *Diploria* (J. Lang pers. comm.).

White-band disease (WBD) affects acroporids corals and is responsible for having rapidly decimated thick stands of these branching corals around the Caribbean, even leading to local extirpation. The disease seems to advance from the base of the coral (but also sometimes from the middle of the branches in *Acropora cervicornis*), towards the tips. The Type I form of this disease front is clearly demarcated by tissues that peel and slough off, leaving the white skeleton clearly visible beside apparently healthy tissue while Type II has a broader zone in which tissues immediately behind the disease front initially bleach before disintegrating and sloughing off (Ritchie and Smith 1998). YBD is likely caused by aggregates of bacteria (Santavy and Peters 1996, Richardson 1998).

White plague (WP) can be a much more rapid killer and is also highly infectious (Figure 1.10C). At least one virulent form of WP has been proven to be caused by a bacterial pathogen and can cause whole colony mortality of small corals within days as patches of infected tissues die and slough off. WP primarily affects massive boulder and foliaceous corals (Bruckner 2004). (Other diseases like dark spots disease and white pox are also causes for concern but will not be detailed here as these were not prevalent on the reefs in Akumal and full descriptions all such diseases is beyond the scope of this chapter). It is likely that the effect of multiple abiotic and biotic stressors, both natural and anthropogenic, play a large role in the susceptibility of stony corals to infection by these diseases and in their ability to survive.

SEDIMENTS:

The impact of sediment on corals and entire reef communities is well documented. Richmond (1993) divided the detrimental effects of sediment in the water column, on the benthos and on the live surfaces of corals into three basic categories: physical, photosynthetic and chemical.

Corals can suffer physical tissue abrasion (Rogers 1977, Bak and Engel 1979, Dubinsky and Stambler 1996) and mortality due to anoxia and starvation by prolonged burial (Lasker 1980). A reduction in the symbiotic zooxanthellae's rates of photosynthesis caused by increased turbidity in the water column and the presence of sediment on tissue surfaces diminishes a coral's ability to meet its own energy requirements for growth (Rogers 1979, Tomascik and Sander 1985, Rice and Hunter 1992), and reproduction (Tomascik and Sander 1987, Rogers 1990) as limited organic resources are invested in maintenance. With regards to chemicals: lateritic soils (iron-rich red clays) studied in Okinawa, Japan are harmful to corals (Nishihira 1987), as are soils treated with certain pesticides like the organophosphate, Chlorpyrifos (Acevedo 1991). A component of some sediments are pathogenic bacterial communities that also have the ability to damage coral tissues (Hodgson 1990). However sediments can be considered nutritionally advantageous to certain coral species that consume some of the associated organic particles (Lewis 1977, Tomascik and Sander 1985, Sebens 1997).

ACUTE AND CHRONIC STRESSORS ON CORAL REEFS

Acute stressors like disease epizootics or outbreaks and mass bleaching events are easy to identify as important factors in the global decline of coral reefs. However, chronic disturbances like overfishing, increases in sediment, pollution by organic matter, inorganic nutrients, toxic chemicals or pathogens, which often result in macroalgal overgrowth, commonly co-occur and act synergistically, making the effect(s) of each factor hard to distinguish from the others (Hughes and Connell 1999, Jackson *et al.* 2001, McClanahan *et al.* 2002a). In the Florida Keys, where shelf-edge reefs have experienced significant declines in coral cover and species richness, presumably from the effects of multiple stressors (Ogden *et al.* 1994, Porter *et al.* 1999, Barratachea *et al.* 2000), turf algae that bind sediment and form turf algal/sediment (TAS) mats have also been considered yet another source of whole-colony mortality (Dustan 1977, 1999; Abbott 1979, Gittings *et al.* 1992).

Since TAS mats have not been accorded much importance until very recently, no quantitative information of their distribution, abundance, or ecological relationships was available at the initiation of this study. Absence of baseline data makes it impossible to understand their possible contribution to the decline of stony corals on reefs in which TAS mats are currently abundant. Although TAS mats may have been overlooked thus far in light of far more prominent disturbances or may naturally occur on undisturbed reefs, it seems more likely

that, as human populations and their technological interventions in the tropics have burgeoned, TAS mats have emerged as an important, chronic disturbance.

This development may be due to a lag effect of historical overfishing (Jackson *et al.* 2001). Lasting periods of reduced herbivory, combined with more recent increases in sedimentation and/or sediment resuspension (Green *et al.* 1997) and a synergistic result of other chronic stressors (McClanahan *et al.* 2002a), may have allowed TAS mats to expand enough to pose a threat to stony corals. Indeed a recent, reef restoration metamodel proposed by McClanahan *et al.* (2002a), suggests that turf algae can dominate reefs when there is an increase in fishing and sediment loading. The overall reduction in herbivory (Hatcher and Larkum 1983, McCook 1999), which has occurred in the Caribbean due to overfishing and the mass die-off of the regionally important mega-herbivore, *Diadema antillarum* (Lessios 1988), combined with increased sediment retards algal succession by maintaining turfs and preventing progression towards macroalgal dominance (McClanahan 1997). These are conditions under which TAS mats might be expected to flourish.

SUBJECT OF INVESTIGATION

Turf-algal filaments that baffle the laminar water-flow cause suspended sediments to fall out of the water-column, and become entrapped by the turf (Scoffin 1970), forming turf algal/sediment (TAS) mats. This project is focused on TAS mats: their composition, interactions with stony corals (Figure 1.11), and the environment in which they thrive. Akumal, México, a small tourist village where TAS mats visually appeared to be a locally important source of stony coral mortality and the reefs were suspected to be in decline (J. Lang, *pers. comm.*), was chosen as the study site. The relatively easy access to its fore reefs, and minimization of potentially confounding effects of poor water quality in more highly developed areas such as the Florida Keys (e.g., see Griffin *et al.* 1999, Paul *et al.* 2000, Lipp *et al.* 2002) were also important positive factors in studying the reefs in this area.



Figure 1.11 Turf algal/sediment (TAS) mat in contact with a colony of *Montastraea cavernosa*.

Chapter 2: Stony coral communities off Akumal, México

ABSTRACT

Transect surveys were conducted in five fringing reefs near Akumal, México, to assess the condition of coral communities along a developing coastline. Data from line intercept transects (n=74) show that live stony coral cover, density and relative peripheral exposure of colonies to turf algal/sediment (TAS) mats were inversely related to an inferred sediment stress gradient at 13 m. By 2000, live stony coral cover had decreased by 40-50% at two sites studied in 1990 (Muñoz-Chagín and de la Cruz-Agüero 1993). About half of this loss apparently occurred between 1998 and 2000 during an outbreak of white plague disease that mostly affected two key reef framework-builders, *Montastraea faveolata* and *M. annularis*. Whereas densities of carnivorous fishes and herbivores (echinoids, scarids, acanthurids and *Microspathodon chrysurus*) in 2000 were low in belt transects at 10-19 m (n=174), turf-algal gardening pomacentrids were relatively common on these reefs.

INTRODUCTION

Fringing coral reefs along coastlines experiencing uncontrolled development and human population growth have declined worldwide (Ginsburg and Glynn 1994, Wilkinson 2000). Adverse effects of overfishing (Hughes 1994), destructive fishing (McManus 1997), pollution from excess nutrients (Banner 1974, Smith *et al.* 1981, Dubinsky and Stambler 1996), petroleum and minerals (Loya 1976b), heavy metals (Guzman and Jiminez 1992), herbicides (Glynn *et al.* 1984), sedimentation (Rogers 1977), mechanical damage from dredging (Bak 1978) and ship groundings (Gittings *et al.* 1992) have taken their toll on reef systems. Regional die-offs of some important organisms (*Diadema antillarum*–Lessios 1988, *Acropora*-Aronson and Precht 2000) and the effects of bleaching-associated warming events (Wilkinson 2000) have further devastated coral reefs throughout the wider Caribbean. The “Mayan Riviera” on the coastline of Quintana Roo (QR), México attracts large numbers of tourists in part because it still retains some of the natural diversity that has been lost at other Caribbean vacation destinations. Nevertheless, the disruptive ecological effects of inadequate environmental protection programs, and poor enforcement of existing regulations, are beginning to show, particularly in the Cancún-Tulum corridor in the northern region of the state (Jordán-Dahlgren 1993, Lang *et al.* 1998). Mangroves are being replaced by cement, while public access to the shore is privatized at huge resorts. At present, the only legal methods for large-scale (hotel- and resort-size)

sewage disposal are in septic tanks (often without a concrete floor) and “deep-injection wells,” although the limestone bedrock is known for its world-class cenotes (cave systems) created by flowing groundwater that runs out to sea. Turtle nesting beaches are disappearing and fishing has diminished the local invertebrate and fish populations. New pueblos supporting the tourism industry’s workers lack the most basic sanitary facilities, and conditions are hardly better in the longer-established villages (*pers. obs.*). Development alone is not to blame for changes to the QR coastal ecosystems, however, as the Yucatán Peninsula is frequently exposed to hurricanes, of which the most destructive in recent decades were Gilbert in 1988 and Roxanne in 1995.

The fringing-barrier reefs along the QR coastline constitute the northernmost part of the Mesoamerican Barrier Reef System (MBRS). Detailed descriptions of these reefs can be found in Jordán–Dahlgren (1979, 1989, 1993), Gutierrez *et al.* (1995) and other reports; associated sediments were characterized by Nolasco-Montero and Carranza-Edwards (1988). The QR scleractinian coral fauna has been described by Castanares and Soto (1982), Fenner (1988) and Beltrán-Torres and Carricart-Ganivet (1999).

Akumal is a small diving resort about 105 km south of Cancún (Figures 2.1 and 2.2). Its fore reefs have developed as loosely coalesced, spur-and-groove formations on three narrow terraces (Muñoz-Chagín and de la Cruz-Agüero 1993). At depths of ~13 m, a sandy plain which is about 10 m wide separates low-relief (<3 m) spurs on the “inner lobes” (shallowest terrace) from the higher-relief

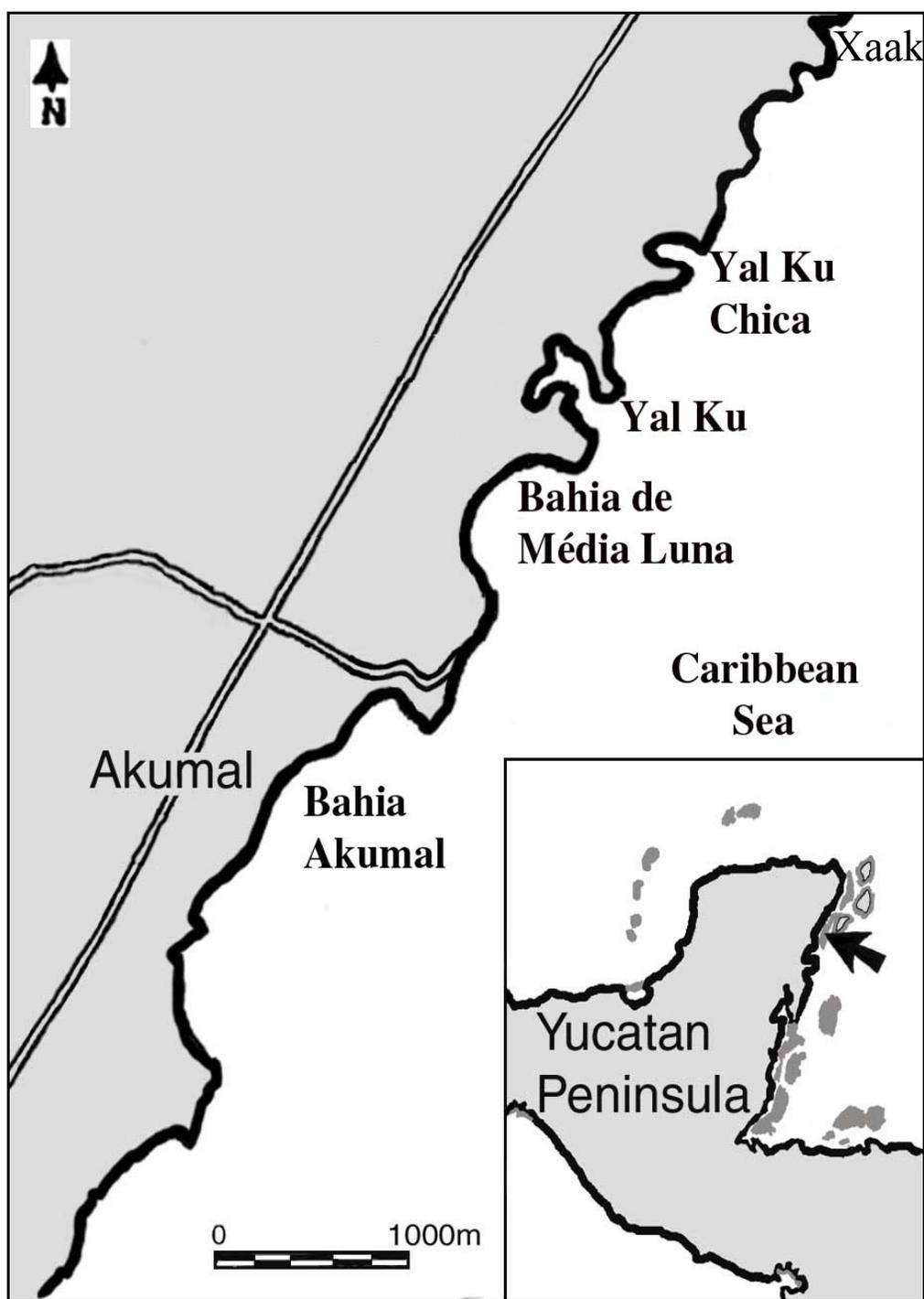


Figure 2.1. Map of study area. Location of bays (Bahia Akumal, Bahia de Média Luna, Xaak) and inlets (Yal Ku, Yal Ku Chica) in the vicinity of the study sites in Quintana Roo, México, part of the Mesoamerican Barrier Reef System (inset) which extends from the Yucatan Peninsula's eastern coast through Belize, to Honduras and Nicaragua (By M. Dupler).

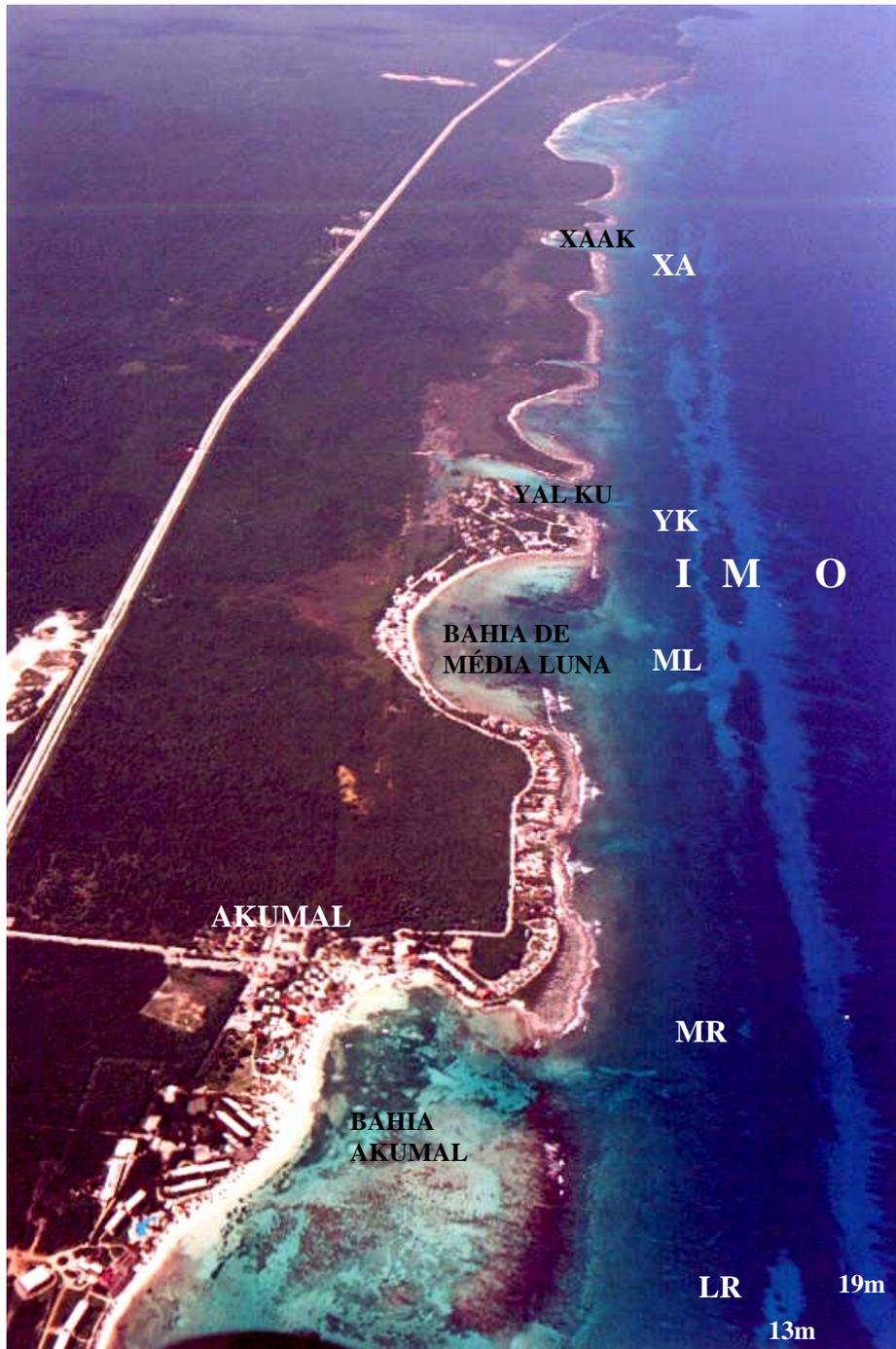


Figure 2.2 Photograph of the Yucatán coastline looking northward from Akumal Bay to Xaak, with survey site locations. See Table 1 for site codes. The spurs on the inner (I) and middle (M) lobes are merged between the northern end of Las Redes and Mérida; the outer lobe (O) is distinct. Depths are means for the sandy plains (light areas) that run parallel to the coastline. Photo by G. Arcila.

(3-5 m) “middle-lobe” spurs, (although there are areas where the two lobes merge). A second sandy plain at ~19 m divides the middle-lobe spurs from the highest-relief (6-9 m) spurs of the “outer lobes.” The outer lobes terminate at >30 m in a hard bottom which slopes off at about 65 m to an escarpment bordering the Yucatan Channel.

In 1990 Muñoz-Chagín’s (*pers. comm.*), area-based estimates of live stony coral cover in two Akumal-area fore reefs (Las Redes and Média Luna, Muñoz-Chagín and de la Cruz-Agüero 1993) averaged 22-24% at 6-18 m and were spatially dominated (40-45%) by *Montastraea annularis* (now species of the *M. annularis* complex, Weil and Knowlton 1994). As elsewhere in the MBRS (Kramer *et al.* 2000), the 1998 ENSO-related mass bleaching event and an outbreak of white plague (WP), a disease which here primarily affected the *M. annularis* complex, were major disturbance events; however, the Akumal-area reefs, sustained relatively little damage from the passage of Hurricane Mitch that October 1998 (S. Slingsby *pers. comm.*). Linear estimates of live coral cover in March 1999 ranged between 13.5% and 21% at 11-18 m on six middle-lobe fore reefs near Akumal (Steneck and Lang 2003). These values are lower than Kramer’s (2003) preliminary estimate of $26 \pm 13\%$ at $10 \pm 3\text{m}$, which was based on 17 live coral coverage assessments (of diverse sample sizes and aerial coverage) of western Atlantic reef areas (including one in Brazil).

Coastal seawater temperatures in the northern QR varied from ~24-30°C between 1994 and 2000 (CARICOMP 1997, D. Linton *pers. comm.*). Nearshore surface currents generally flow to the south, but occasionally shift to the north (*pers. obs.*). Bulk transport of sediment from the shallower terraces into deeper water can occur during the passage of hurricanes (S. Slingsby *pers. comm.*). Sediments are frequently shifted during tropical storms, with depths at known locations on the fore-reef sandy plains changing by as much as ± 0.3 m and, at a finer scale, sediment on the shallowest terrace is routinely suspended by surge (*pers. obs.*). Razo Amoroz (1999) has measured relatively high (10-394 mg/cm²/day) sedimentation rates at 10 m in a fore reef (Shark Caves) off Akumal.

When turf algae (*sensu* Steneck 1988) flourish in areas of high sediment loading and resuspension, they baffle water flow, causing suspended sediment to fall out of the water column and become trapped among their filaments (Scoffin 1970, Carpenter 1986), thereby creating turf algal/sediment (TAS) mats. Turf algae that trap sediments are known to kill live crustose coralline algae (Steneck 1997) and it follows that if TAS mats grow into contact with stony corals, the marginal tissues of the latter may also gradually die (Dustan 1977, 1999, McCook *et al.* 2001). Herbivores (*Diadema* and other grazing echinoids, herbivorous fishes) that would graze algae are relatively scarce on the Akumal-area fore reefs, and estimates of fish herbivory rates in August 1997 were low (Steneck and Lang 2003). TAS mats are conspicuous, particularly in the shallower inner-lobe reefs, where they are frequently in close physical contact with, and even appear to be

overgrowing, stony corals (*pers. obs.*). The possible expansion of TAS mats at the expense of the primary reef constructors adds a previously unstudied dimension to investigations of stony coral mortality in these reef systems.

GOALS

Baseline information about the status of their coral reefs is vital for small communities like Akumal that are financially dependent upon the diving industry. The purpose of this chapter is to describe the scleractinian coral community off a rapidly developing coastline and several, important temporal and spatial characteristics of the ambient physical environment. Stony corals (scleractinians and *Millepora*) in the Akumal-area fore reefs are characterized at two depths and along an inferred sedimentation gradient with respect to species composition, live cover, colony density, and relative exposure to TAS mats. Fish population density and herbivory rates are also assessed. Comparisons between data collected from 1998-2000 are made to previous surveys, intervening perturbations are described, and predictions of future trends are updated.

MATERIALS AND METHODS

LOCATION:

Survey sites on five reefs (Figure 2.2) were chosen according to depth near the seaward margins of the inner (at 13 m) or the middle (at 19 m) fore-reef lobe, and by position along a 5.5 km stretch of coastline extending north from Bahia Akumal to Xaak (Figure 2.1 and Table 2.1). Reefs offshore from shallow sandy bays are considered to receive greater sediment loading than reefs off rocky shores or narrow caletas (inlets) since they are a larger source of sediment, which can be re-suspended and transported to the fore reefs by the local water-flow patterns. Also, since surge decreases with depth, suspended sediment over the spurs on any given reef was markedly less conspicuous at 19 m than at 13 m on any given day (*pers. obs.*) and therefore shallower fore reefs are expected to incur higher sediment loading than the deeper fore-reef sites.

The Las Redes (LR13 and LR19) sites are situated off the 2 km long, <3m deep Bahia Akumal (Figure 2.1 and 2.2), where high levels of small boat traffic frequently resuspend sediments (Muñoz-Chagín and de la Cruz-Agüero 1993). Just south of a natural pass through the reef crest near the northern end of the bay, LR13 is used as a training site for novice scuba divers. Morgan's Reef sites (MR13 and MR19), off a rocky headland marking the northern end of Bahia Akumal, are visited less frequently by recreational divers. The Média Luna (ML13 and ML19) sites are located off the middle to southern side of the smaller

(0.5 km long), shallow (<2 m deep) Bahia de Média Luna. Yal Ku (YK13 and YK19) is directly in front of the Caleta Yal Ku, a major surface outlet of groundwater into the Caribbean Sea. Both ML and YK are popular recreational dive sites. Xaak (XA13), located off a headland on the southern side of a tiny, undeveloped embayment with a narrow beach, is seldom dived by tourists but is frequented by artisanal fishers (J. Lang, *pers. comm.*). I ranked the reefs by a gradient of expected sediment stress at 13m as follows: LR>ML>MR>YK>XA.

ASSESSING ABIOTIC CHARACTERISTICS:

The water temperature at the Las Redes (13 m) site was recorded at hourly intervals with an *in-situ* thermodata recorder (Hobotemp), between July 9 and August 4, 1998, June 4 and August 5, 1999 and June 13 and August 8, 2000. Salinity readings of water samples at the surface and at a depth of 13 m were taken daily between June 9 and July 30 in 1999 using a hand-held refractometer. To obtain a relative estimate of turbidity after tropical storms compared to normal conditions, a number of horizontal Secchi disk readings were taken at a depth of 5 m in 1999. One diver remained stationary holding a spooled tape measure attached at its origin to the Secchi disk. Meantime a second diver swam slowly backwards, holding the disk parallel to and against his/her body allowing the demarcations on the disk to be as clear as possible against the black wetsuit. When the black and white segments were no longer clearly differentiated, the stationary diver took a reading, then tugged on the tape to indicate that he or she

would wind in the tape. A second reading was taken when the black and white segments of the secchi disk became clearly distinguishable again. The final value was obtained by taking the average of the two readings. This method was only viable when the surge was manageable so values given are conservative as turbidity is naturally greater with increased surge.

ASSESSING LIVE CORAL COVER AND TAS MAT ASSOCIATIONS, TEMPORALLY AND SPATIALLY:

Line intercept techniques were used at Las Redes (13 m) in 1998-2000 (with a limited follow-up in March 2001), and at Média Luna (13 m) in 1999 and 2000, to assess any temporal changes occurring in the coral communities at these sites with respect to live cover, species composition, or prevalence and extent of contact with TAS mats. The survey in March 2001 at Las Redes (13 m) was limited to determining changes in cover of the three stony coral species *M. faveolata*, *D. strigosa* and *S. siderea* which are locally important reef framework-builders and integral to subsequent experiments conducted during this investigation.

The same method was used to describe the coral communities at all sites except Yal Ku 19 m, to assess any spatial correlations as might have existed with the previously described inferred sediment stress gradient, between June and August 2000.

Each of the 10 m-long, line intercept transects began at a haphazardly chosen point on the top of a spur and was oriented parallel to its long axis. In rare cases where the spurs were extremely wide, adjacent transects were separated by at least 5 m. All stony corals under the line were identified to species, and the length of their live tissues intercepting the transect was measured. As virtually no colony had >75 to <100% of its periphery in contact with a TAS mat (*pers. obs.*), corals in contact with mats were scored as either partially (~50-75%) or completely (~100%) surrounded.

ASSESSING FISH POPULATIONS AND HERBIVORY RATES:

Fish population densities were surveyed at Las Redes and Média Luna at 13 m in 1999, and at all sites except Xaak in 2000, using a 20 m long x 1 m wide belt-transect method adapted from Fowler (1987). One diver remained stationary while spooling out a line that was attached to a second diver who slowly swam at a constant height of 3-5 m above the reef, holding a 1 m wide PVC T-bar for scale, and a clipboard for recording observations of all visible fishes. Starting from a haphazardly chosen position, transects were restricted to the top of a single spur.

Herbivory was estimated at Las Redes (13 m) in 1999, and at all other sites except Xaak in 2000, with a modified Steneck (1985) fish bite method. The total number of bites observed in a three-minute interval by ‘scrapers’ (scarids), ‘browsers’ (acanthurids and the pomacentrid *Microspathodon chrysurus*) and

'non-denuders' (other herbivorous pomacentrids) was recorded at randomly chosen areas within each site. All estimates of fish density and herbivory rates were made according to the time available, usually from 11:45 a.m.-12:45 p.m. and 3:45-4:45 p.m. Echinoid populations were not surveyed due to their scarcity.

STATISTICS:

Statistical analyses of the all datasets were conducted with SAS version 8.1. Unless stated otherwise, all datasets were tested with one-way ANOVAs after normality was determined (using log or square-root transformations where required and appropriate). Tukey's HSD test was used as a post-hoc test when applicable. However, when examining the relationship with the expected sediment-loading gradient, rather than testing for differences between specific sites, a simple linear regression was conducted as a post-hoc analysis (Motulsky 1995). The percent of coral colonies at just the 13 m sites that were completely surrounded by TAS mats at all sites could not be sufficiently normalized for a parametric test and so Kruskal-Wallis tests, a non-parametric version of the ANOVA, was conducted.

RESULTS

ABIOTIC CHARACTERISTICS:

Despite fluctuations, seawater temperatures in each of the three years generally increase during the summer months between 1998 and 2000 (Figure 2.3). In 1998, seawater temperatures at 13 m varied between 27.14°C and 29.49°C. This range is slightly greater than that found in both 1999 and 2000, when temperatures ranged from 27.73°C to 29.55°C and from 27.55°C to 29.55°C, respectively. Moreover, daily temperatures were generally consistently higher in 1998 than the other two years (particularly evident in 1999) during the same time period (Figure 2.4).

Seawater salinities at 13 m and at the surface ranged between 34‰ and 37‰. The two curves generally paralleled each other, with the bottom water being more saline than the surface waters except for three occasions (Figure. 2.5). Horizontal secchi disk readings were usually far greater than 30 m (the length of the tape measure), with readings of less than 30 m typically only following storms or rough seas. After one memorable storm, which lasted from June 30 to July 3, 1999, the horizontal secchi reading was only 11.4 m although it was 25.6 m the following day.

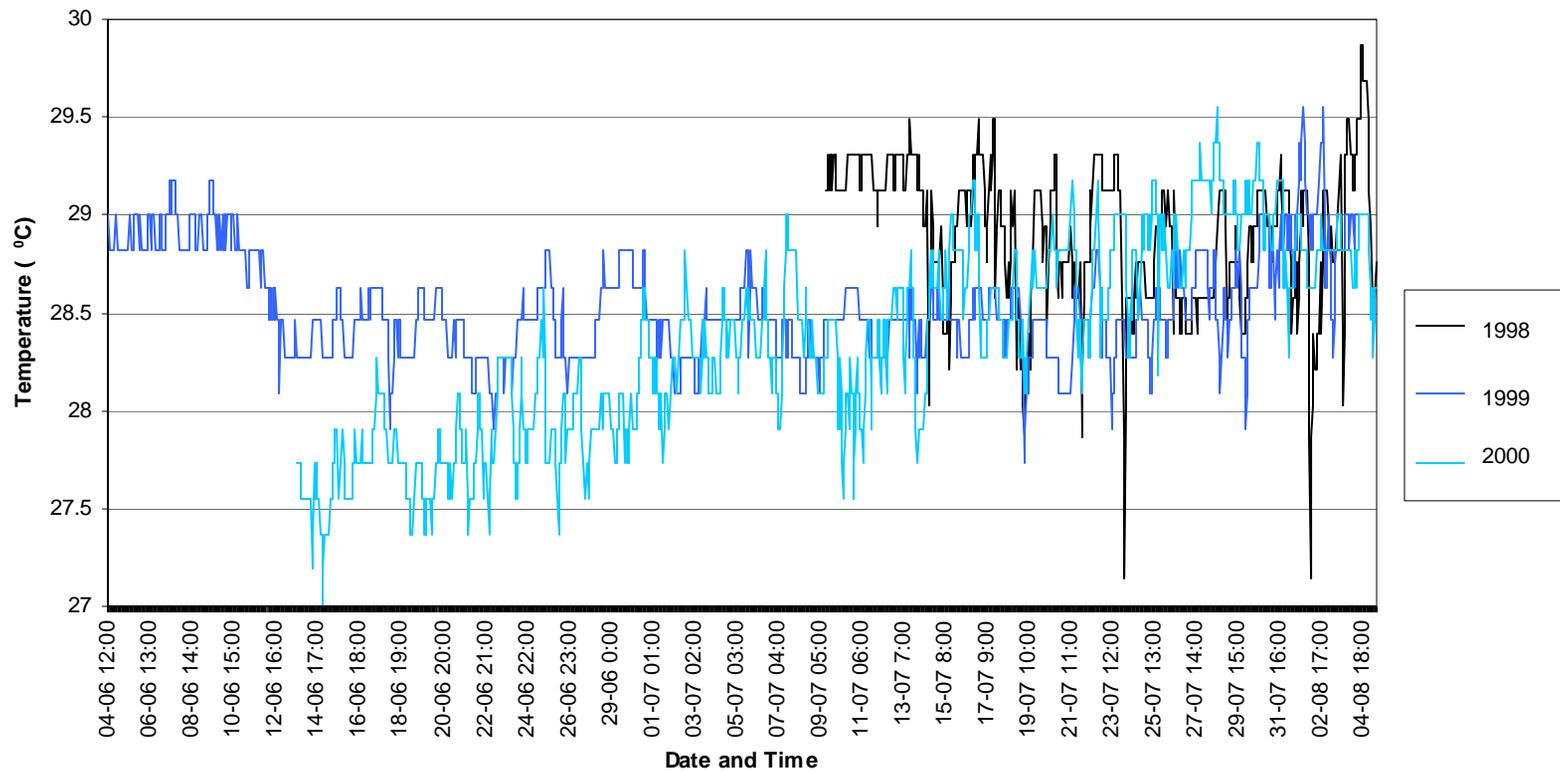


Figure 2.3. Seawater temperatures at Las Redes reef (13 m), between July 9 and August 4, 1998, June 4 and August 5, 1999, and June 13 and August 8, 2000. Data were recorded at hourly intervals with an *in-situ* thermodata recorder (Hobotemp).

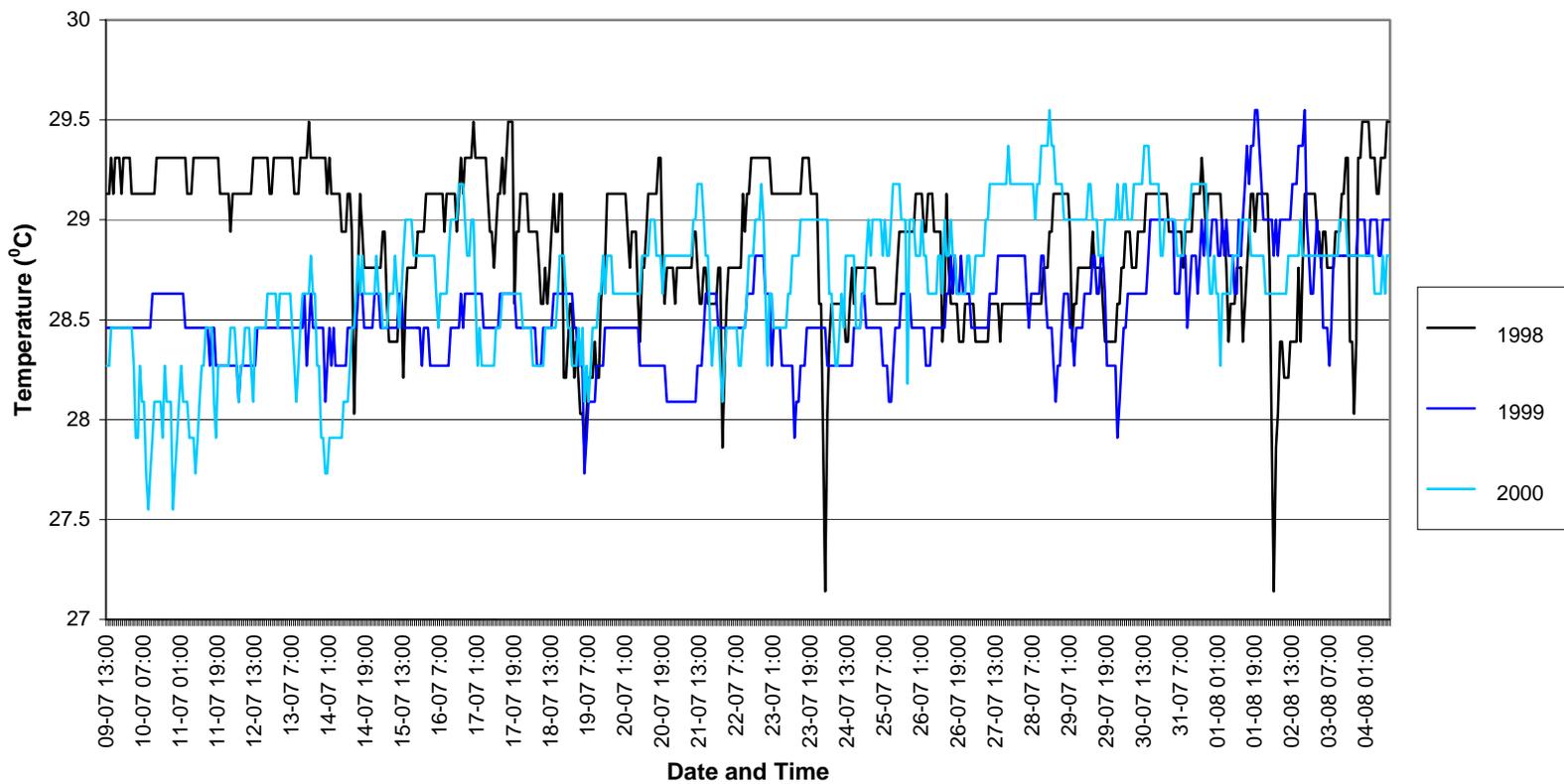


Figure 2.4. Seawater temperatures at Las Redes reef (13 m), between July 9 and August 4, 1998, 1999 and 2000. Data displayed in the graph above was collected at hourly intervals by an *in-situ* data recorder (Hobotemp).

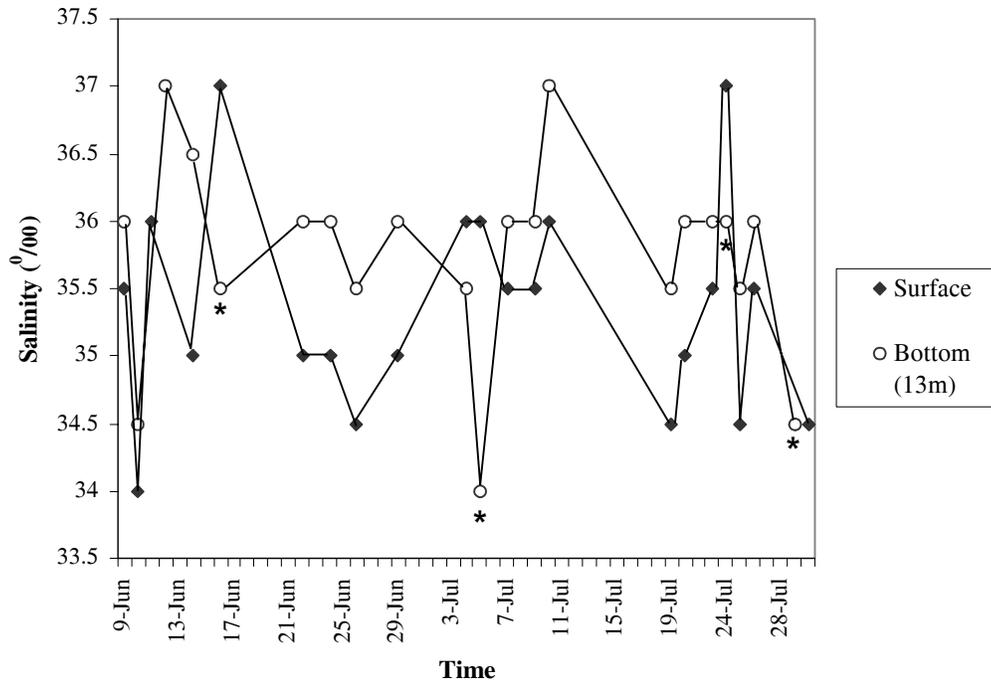


Figure 2.5. Salinity at Las Redes reef (13 m), between June 6 and July 30, 1999. Asterisks below datapoint indicate salinity inversions. (Missing salinity datapoints are due to storms or other factors which did not allow for collection.)

TEMPORAL CHANGES IN LIVE CORAL COVER AND TAS MAT ASSOCIATIONS:

Live stony coral cover at the Las Redes 13 m site (Table 2.1) declined significantly from 19% in 1998 to 10.5% in 2000 (one-way ANOVA, $F=4.19$, $p<0.0221$, Table 2.2) as did the average number of colonies with live tissues/m, from 0.87 colonies/m in 1998 to 0.62 in the same time period (one-way ANOVA, $F=5.35$, $p<0.0086$, Table 2.3). This change was largely due to a loss of over 50% of the live *M. faveolata* cover and about two-thirds of the *S. siderea*; however, restricted surveys in March 2001 indicate that both species appeared to be recovering (Figure 2.6). The Tukey's HSD test indicated that although coral cover was only different between 1998 and 2000, the changes in coral density in 1998 were different from both 1999 and 2000. However, there were no significant changes in the proportion of colonies that were completely surrounded by TAS mat at this site between 1998 and 2000. At Média Luna (13m) between 1999 and 2000, there were no significant changes in the same coral parameters.

In 1998, all of the *D. strigosa* ($n=5$ corals), 93% of the *M. faveolata* ($n=14$ corals) and a third of the *S. siderea* ($n=17$ corals) were completely surrounded by TAS mats at the Las Redes 13 m site (Table 2.4). Although there was little change in the percentage of *D. strigosa* and *M. faveolata* colonies that were completely surrounded by TAS mats in 2000, the percentage of *S. siderea* with this association had doubled to 67% ($n=18$).

TABLE 2.1 Survey site and stony coral transect information, in geographic order from south to north near Akumal, México.

Site name	Site code	Latitude (° ' N)	Longitude (° ' W)	Summer survey date	10 m transects (#)	Stony corals (#)	Live stony corals (mean ± standard deviation)					
							Species (#)	Cover (%)	Density (#/m)	TAS mats around		
										>50-75% (%)	~100% (%)	
13 m												
Las Redes	LR13	20 ⁰ 23.364'	87 ⁰ 18.617'	1998	9	78	13	19.0 ± 8.5	0.9 ± 0.3		60 ± 17	
	"	"	"	1999	11	61	12	13.5 ± 7.5	0.6 ± 0.2	9 ± 16	76 ± 21	
	"	"	"	2000	24	154	18	10.5 ± 7.5	0.6 ± 0.2	18 ± 17	66 ± 22	
Morgan's Reef	MR13	20 ⁰ 23.898'	87 ⁰ 18.310'	2000	15	134	19	15.5 ± 9.0	0.9 ± 0.3	15 ± 12	39 ± 22	
Média Luna	ML13	20 ⁰ 24.145'	87 ⁰ 18.163'	1999	6	44	8	18.0 ± 7.0	0.7 ± 0.2	31 ± 27	43 ± 34	
	"	"	"	2000	12	77	14	14.5 ± 7.5	0.7 ± 0.3	18 ± 20	54 ± 26	
Yal Ku	YK13	20 ⁰ 24.594'	87 ⁰ 17.885'	2000	13	92	15	20.0 ± 15.0	0.7 ± 0.4	21 ± 22	53 ± 32	
Xaak	XA13	20 ⁰ 25.667'	87 ⁰ 17.248'	2000	10	100	18	24.5 ± 17.0	1.0 ± 0.4	32 ± 22	27 ± 16	
19 m												
Las Redes	LR19	20 ⁰ 23.334'	87 ⁰ 18.542'	2000	21	187	20	10.5 ± 7.5	0.9 ± 0.5	20 ± 16	31 ± 22	
Morgan's Reef	MR19	20 ⁰ 23.843'	87 ⁰ 18.234'	2000	12	103	14	10.0 ± 4.0	0.9 ± 0.3	25 ± 29	37 ± 24	
Média Luna	ML19	20 ⁰ 24.087'	87 ⁰ 18.066'	2000	12	120	15	13.5 ± 8.0	1.0 ± 0.6	13 ± 13	28 ± 19	
Yal Ku	YK19	20 ⁰ 24.563'	87 ⁰ 17.809'									

Table 2.2 One-way ANOVA on coral cover at Las Redes (13 m) between 1998 and 2000.

Source	Df	SS	MS	F-value	Pr > F
Model	2	5.04574766	2.52287383	4.19	0.0221
Error	41	24.69241313	0.60225398		
Corrected total	43	29.73816080			

Table 2.3 One-way ANOVA on live coral density at Las Redes (13 m) between 1998 and 2000.

Source	Df	SS	MF	F-value	Pr > F
Model	2	53.5681818	26.7840909	5.35	0.0086
Error	41	205.2272727	5.0055432		
Corrected total	43	258.7954545			

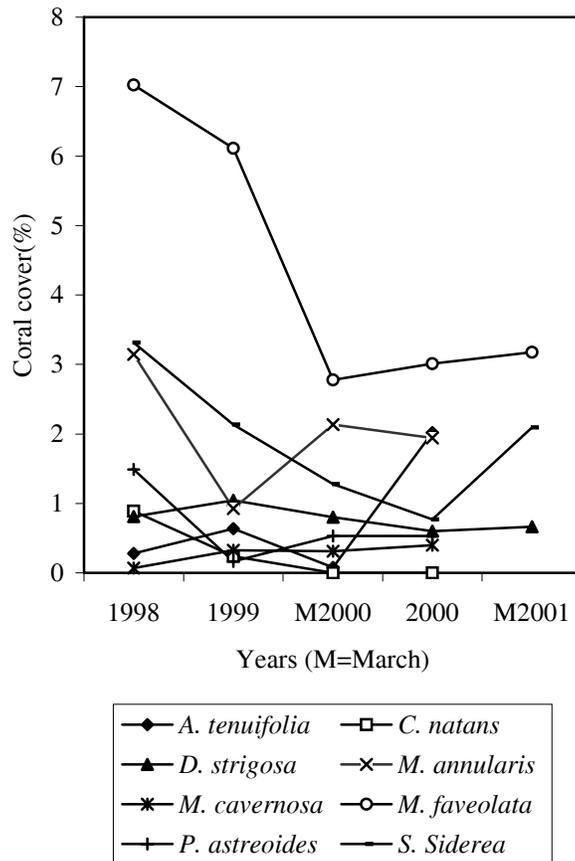


Figure 2.6. Changes in mean percent live cover of the most common species of stony corals at Las Redes (13 m), Akumal, between 1998 and 2000. Number of transects: Summer 1998 = 9; Summer 1999 = 11; March 2000 = 9; Summer 2000 = 24; March 2001 = 20 (for *D. strigosa*, *M. faveolata* and *S. siderea*).

TABLE 2.4 Frequency of species-specific contact with turf algal/sediment (TAS) mats at Las Redes (13 m), from 1998-2000. (Total number of transects in 1998 = 9, 1999 = 11, and 2000 = 24)

Species	1998		1999				2000			
	TAS mats around		TAS mats around				TAS mats around			
	Total # of colonies	~100% (%)	Total # of colonies	~100% (%)	>50%-75% (%)	At least 50% (%)	Total # of colonies	~100% (%)	>50%-75% (%)	At least 50% (%)
Hydrozoa, Milleporidae										
<i>Millepora alcicornis</i>							11	0	0	0
Anthozoa, Scleractinia										
<i>Acropora cervicornis</i>							1	0	0	0
<i>Agaricia agaricites</i>	6	33.33	3	0	0	0	10	80	20	100
<i>A. tenuifolia</i>	1	0	2	50	0	50	6	0	16.67	16.67
<i>Colpophyllia natans</i>	4	100	2	100	0	100				
<i>Dichocoenia stokesii</i>	4	25	1	0	0	0	3	0	33.33	33.33
<i>Diploria labyrinthiformes</i>			3	100	0	100	1	100	0	100
<i>D. strigosa</i>	5	100	7	100	0	100	13	92.31	7.69	100
<i>Madracis decactis</i>							1	100	0	100
<i>Meandrina meandrites</i>	2	50								
<i>Montastraea annularis</i>	10	100	5	80	0	80	24	79.17	20.83	100
<i>M. cavernosa</i>	1	100	4	100	0	100	11	72.73	27.27	100
<i>M. faveolata</i>	14	92.86	15	86.67	6.67	93.33	27	92.59	3.7	96.3
<i>M. franksi</i>							1	100	0	100
<i>Mycetophyllia lamarckiana</i>							2	50	0	50
<i>Porites astreoides</i>	9	22.22	2	50	0	50	13	38.46	46.15	84.62
<i>P. porites</i>	2	0	1	0	0	0	5	40	40	80
<i>Siderastrea radians</i>							1	100	0	100
<i>S. siderea</i>	17	35.29	17	58.82	23.53	82.35	19	68.42	31.58	100
<i>Stephanocoenia intersepta</i>	3	33.33					1	100	0	100

LIVE CORAL COVER AND TAS MAT ASSOCIATIONS IN 2000:

A total of 26 species of stony corals (Table 2.5) were recorded at 13 m (range=14-19/site, n=5 sites) and similar numbers were found at 19 m (22 species, range =14-20/site, n=3 sites). Eighteen of these species were common to both depth intervals. *M. faveolata* was the predominant species at all eight sites in terms of live cover, followed by *M. annularis* at six sites (the exceptions being Las Redes at 13 m, where it was tied for second place with *Agaricia tenuifolia* and Xaak at 13m, where *Acropora palmata* was relatively more abundant, the two sites being on the southernmost and northernmost, respectively, of the surveyed reefs).

The between-site differences in live coral cover at 13m (from 10.5% at Las Redes to 24.5% at Xaak, Table 2.1 and Figure 2.7) were significant (one-way weighted ANOVA, $F= 3.31$ $p<0.0154$, Table 2.6). The density of live corals also varied significantly (one-way weighted ANOVA, $F= 3.96$ $p<0.006$, Table 2.7) among sites, from 0.6/m at Las Redes and Média Luna to 1/m at Xaak (Figure 2.9). Both live cover and stony coral density were inversely related to the inferred sediment stress gradient ($r^2=0.16$, $p=0.0005$, Figure 2.8 and $r^2=0.12$, $p=0.0029$, Figure 2.10, respectively).

Live stony coral cover at the three 19 m sites ranged from 10%-13.5%, (Figure 2.7) and coral densities from 0.8/m-1/m (Figure 2.9). Although the between-depth differences in live coral cover were only significant when

TABLE 2.5 Species-specific relative live stony coral cover by depth (% ± standard deviations) near Akumal, México (2000). (Total number of transects at 13 m = 64, at 19 m=55)

Species	Percent relative coral cover (%)	
	13m	19m
Hydrozoa, Milleporidae		
<i>Millepora alcicornis</i>	0.2 ± 0.1	0.1 ± 0.2
Anthozoa, Scleractinia		
<i>Acropora cervicornis</i>	<0.1	<0.1
<i>A. palmata</i>	0.2 ± 0.4	
<i>A. prolifera</i>	1.1 ± 1.9	
<i>Agaricia agaricites</i>	0.9 ± 0.8	1.3 ± 0.9
<i>A. humilis</i>		<0.1
<i>A. lamarcki</i>	<0.1	<0.1
<i>A. tenuifolia</i>	1.0 ± 1.1	0.1 ± 0.2
<i>Colpophyllia natans</i>	0.7 ± 0.9	0.4 ± 0.5
<i>Dendrogyra cylindricus</i>	0.1 ± 0.1	
<i>Dichocoenia stokesii</i>	<0.1	<0.1
<i>Diploria labyrinthiformes</i>	0.3 ± 0.2	<0.1
<i>D. strigosa</i>	0.6 ± 0.4	0.5 ± 0.5
<i>Eusmilia fastigiata</i>	<0.1	
<i>Madracis decactis</i>	0.1 ± 0.1	<0.1
<i>M. Formosa</i>		<0.1
<i>M. mirabilis</i>		<0.1
<i>Manacina areolata</i>	<0.1	0.1 ± 0.1
<i>Meandrina meandrites</i>	<0.1	
<i>Montastraea annularis</i>	3.6 ± 1.9	2.2 ± 0.3
<i>M. cavernosa</i>	0.5 ± 0.6	0.5 ± 1.0
<i>M. faveolata</i>	5.9 ± 2.6	3.2 ± 0.5
<i>M. franksi</i>	0.2 ± 0.2	0.7 ± 0.9
<i>Mycetophyllia lamarckiana</i>	<0.1	
<i>M. danaana</i>		<0.1
<i>Porites astreoides</i>	0.5 ± 0.2	0.7 ± 0.3
<i>P. porites</i>	0.5 ± 0.5	1.3 ± 0.9
<i>Siderastrea radians</i>	<0.1	
<i>S. siderea</i>	0.5 ± 0.2	0.3 ± 0.3
<i>Stephanocoenia intersepta</i>	<0.1	

Table 2.6. One-way weighted ANOVA on live coral cover among the five shallow 13 m deep sites near Akumal, México (2000). (Data was log transformed to meet normality)

Source	Df	SS	MS	F-value	Pr > F
Model	4	3.20231689	0.80057922	3.31	0.0154
Error	69	16.70034680	0.24203401		
Corrected total	73	19.90266369			

Table 2.7. One-way weighted ANOVA on live coral density among the five shallow 13 m deep sites, near Akumal, México (2000).

Source	Df	SS	MS	F-value	Pr > F
Model	4	262.619614	65.654904	3.96	0.0059
Error	69	1143.3222667	16.569894		
Corrected total	73	1405.942281			

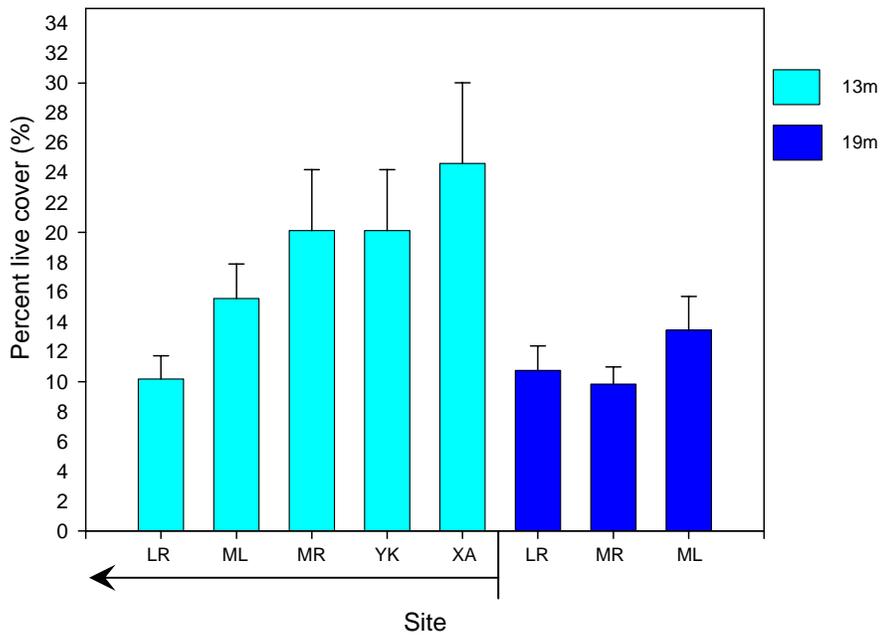


Figure 2.7. Mean percent live coral cover (mean \pm standard error) at different survey sites and depths near Akumal, México (2000). See Table 1 for site codes. Arrow indicates direction of inferred increase in sediment loading at 13m.

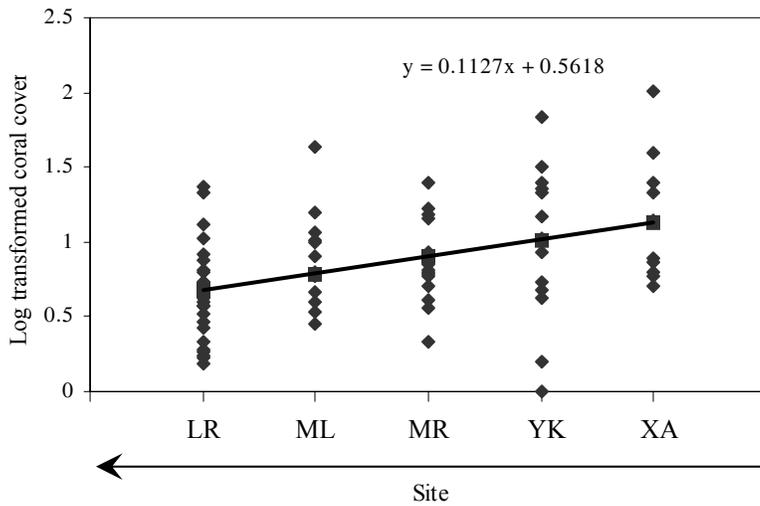


Figure 2.8. Simple regression plot between sites and log transformed live coral cover/transect. Arrow indicates direction of inferred increase in sediment loading at 13m. See Table 1 for site codes.

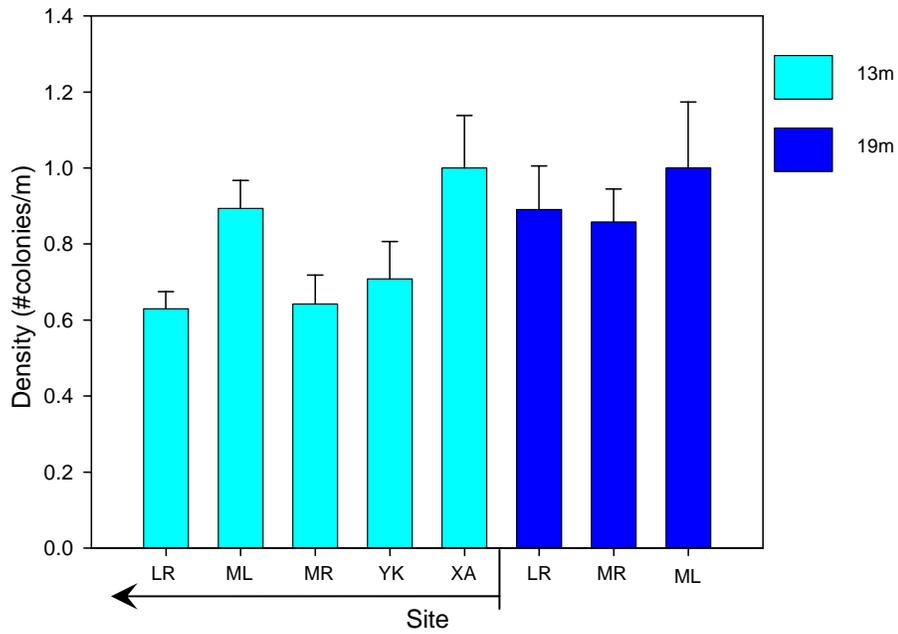


Figure 2.9. Density of live corals (mean ± standard error) at survey sites near Akumal, México (2000). Arrow indicates direction of inferred increase in sediment loading at 13 m. See Table 1 for site codes.

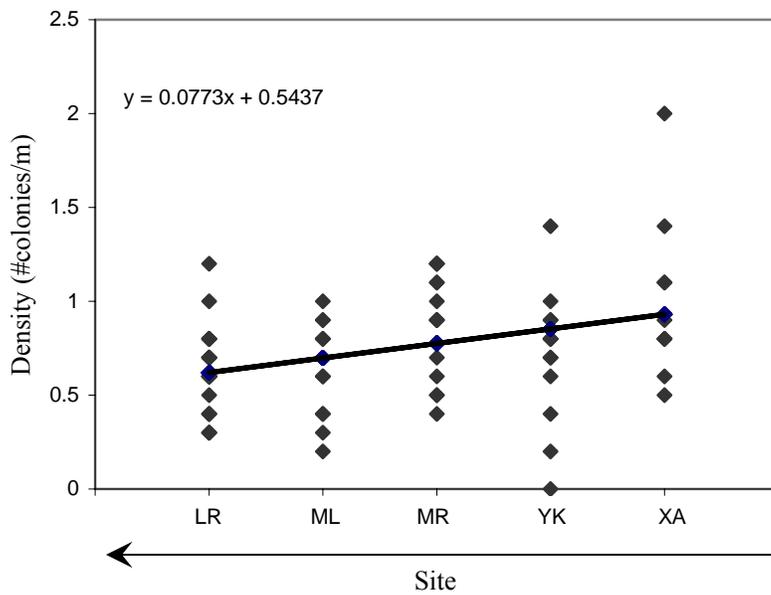


Figure 2.10. Simple regression plot between sites and live coral density. Arrow indicates direction of inferred increase in sediment loading at 13 m. See Table 1 for site codes.

including all sites (one-way weighted ANOVA, $F= 5.07$ $p<0.026$, Table 2.8, Figure 2.7), colony density showed a significant depth effect even just between the three southern reefs (one-way weighted ANOVA, $F= 4.37$ $p<0.039$, Table 2.9, Figure 2.9).

Fifteen to thirty-two percent of the stony corals at the five 13 m sites, and 13-25% of those at the three 19 m sites, had peripheries that were partially (>50%-75%) in contact with TAS mats (Table 2.1 and Figure 2.11); these horizontal and vertical spatial differences were not significant. However, the between-site differences at 13 m for stony corals that were completely surrounded by TAS mats (66% at Las Redes – 27% at Xaak) were significant (one-way weighted ANOVA, $F= 5.86$ $p<0.0004$, Table 2.10, Figure 2.11), and also inversely related to the inferred sediment stress gradient ($r^2=0.18$, $p=0.0001$, Figure 2.12). Only 28-37% of the surveyed corals at 19 m were completely surrounded by TAS mats; moreover, the between-depth differences for this parameter in the three southern reefs were significant (Kruskal-Wallis, $X^2= 9.65$ $p<0.0019$, Table 2.11).

The frequency of corals in contact with TAS mats at the species level also seems to be generally higher at 13 m than at 19 m depths, especially when comparing those corals that showed similar densities at both depths e.g. *Agaricia agaricites* and *Porites astreoides* (Table 2.12).

Table 2.8 One-way weighted ANOVA on live coral cover between 13 m and 19 m near Akumal, México (2000). (Data were log transformed)

Source	Df	SS	MS	F-value	Pr > F
Model	1	0.15559581	0.15559581	5.07	0.0263
Error	117	3.59364614	0.03071492		
Corrected total	118	3.74924195			

Table 2.9 One-way weighted ANOVA on live coral density between 13 m and 19 m near Akumal, México (2000). (Data were square-root transformed)

Source	Df	SS	MS	F-value	Pr > F
Model	1	1.98276593	1.98276593	4.37	0.0392
Error	94	42.63327267	0.45354545		
Corrected total	95	44.61603859			

Table 2.10 One-way weighted ANOVA on the percent of corals completely (100%) surrounded by TAS mats among the five shallow 13 m deep sites, near Akumal, México (2000).

Source	Df	SS	MS	F-value	Pr > F
Model	4	2.34019747	0.58504937	5.86	0.0004
Error	69	6.89460664	0.09992184		
Corrected total	73	9.23480411			

Table 2.11 Kruskal-Wallis test on the percent of corals completely (100%) surrounded by TAS mats between 13 m and 19 m, near Akumal, México (2000).

Chi-square	6.5947
Df	1
Pr > Chi-square	0.0102

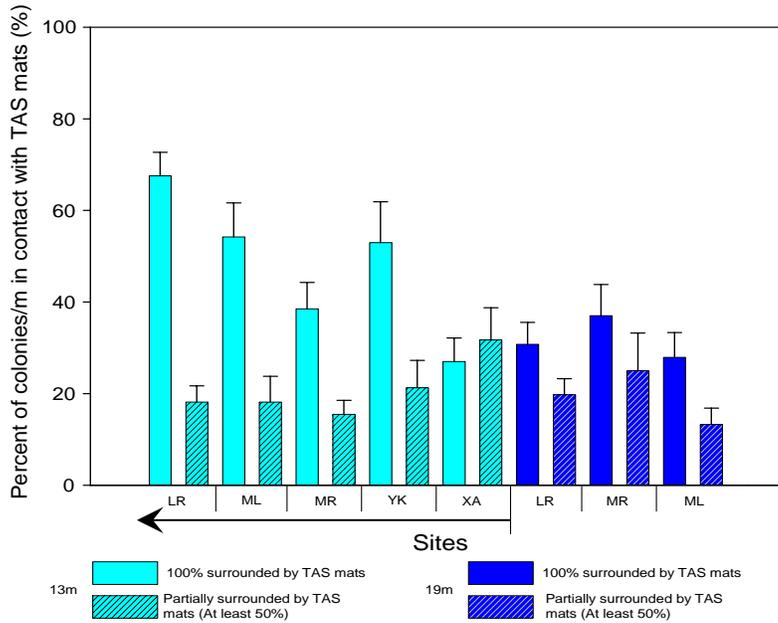


Figure 2.11. Percent of colonies (mean \pm standard error) that are completely (100%) or partially (50% of periphery or more) surrounded by TAS mats at survey sites near Akumal, México (2000). Arrow indicates direction of inferred increase in sediment loading at 13 m. See Table 1 for site codes.

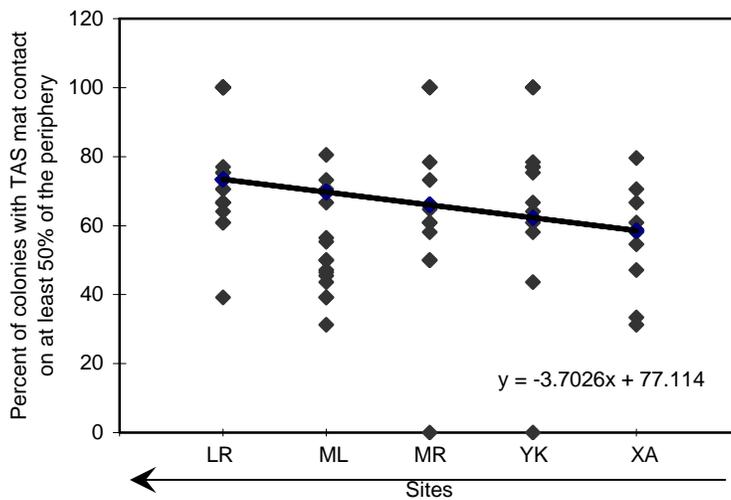


Figure 2.12. Simple regression plot between sites and total proportion of colonies that have at least 50% of their periphery in contact with TAS mats. Arrow indicates direction of inferred increase in sediment loading at 13 m. See Table 1 for site codes.

TABLE 2.12 Frequency of species-specific contact with turf algal/sediment (TAS) mats by depth in 2000.
(Total number of transects at 13 m = 74 and 19 m = 45)

Species	13 m				19 m			
	Total # of colonies	TAS mats around		At least 50% (%)	Total # of colonies	TAS mats around		At least 50% (%)
		~100% (%)	>50%-75% (%)			~100% (%)	>50%-75% (%)	
Hydrozoa, Milleporidae								
<i>Millepora alcicornis</i>	44	0	0	0	30	0	0	0
Anthozoa, Scleractinia								
<i>Acropora cervicornis</i>	4	0	0	0	5	0	0	0
<i>A. palmata</i>	21	9.52	38.1	47.62				
<i>A. prolifera</i>	2	0	0	0				
<i>Agaricia agaricites</i>	66	31.81	36.36	68.18	60	11.67	20	31.67
<i>A. humilis</i>					2	50	0	50
<i>A. lamarcki</i>	1	0	0	0	1	0	100	100
<i>A. tenuifolia</i>	17	0	5.88	5.88	3	0	0	0
<i>Colpophyllia natans</i>	8	50	37.5	87.5	5	60	20	80
<i>Dendrogyra cylindricus</i>	2	0	0	0				
<i>Dichocoenia stokesii</i>	6	33.33	16.67	50	4	50	25	75
<i>Diploria labyrinthiformes</i>	7	100	0	100	3	66.67	0	66.67
<i>D. strigosa</i>	28	78.57	14.29	92.86	12	75	16.67	91.67
<i>Eusmilia fastigiata</i>	2	50	0	50				
<i>Madracis decactis</i>	4	75	25	100	2	50	0	50
<i>M. formosa</i>					1	0	0	0
<i>M. mirabilis</i>					1	0	0	0
<i>Manacina areolata</i>	1	0	0	0	4	0	0	0
<i>Meandrina meandrites</i>	1	0	0	0				

TABLE 2.12 Frequency of species-specific contact with turf algal/sediment (TAS) mats by depth in 2000. *continued.*
 (Total number of transects at 13 m = 74 and 19 m = 45)

	13 m				19 m			
	Total # of colonies	TAS mats around			Total # of colonies	TAS mats around		
		~100% (%)	>50%-75% (%)	At least 50% (%)		~100% (%)	>50%-75% (%)	At least 50% (%)
<i>Montastraea annularis</i>	112	69.64	24.11	93.75	56	60.71	17.86	78.57
<i>M. cavernosa</i>	30	70	16.67	86.67	14	85.71	7.14	92.86
<i>M. faveolata</i>	83	72.29	25.3	97.59	83	54.22	37.35	91.57
<i>M. franksi</i>	9	55.56	33.33	88.89	25	52	20	72
<i>Mycetophyllia lamarckiana</i>	2	50	0	50				
<i>M. danaana</i>					1	100	0	100
<i>Porites astreoides</i>	35	25.71	34.29	60	34	5.89	23.53	29.41
<i>P. porites</i>	29	6.9	10.34	17.24	51	3.92	1.96	5.88
<i>Siderastrea radians</i>	1	100	0	100				
<i>S. siderea</i>	36	61.11	30.56	91.67	15	46.67	40	86.67
<i>Stephanocoenia intersepta</i>	4	100	0	100				

FISH POPULATION DENSITIES AND HERBIVORY RATES:

There were no significant spatial differences between the fish population densities at Las Redes and Média Luna 13 m sites in 1999; however, they were significantly higher in 2000 than in the previous year at both sites (one-way weighted ANOVA for Las Redes, $F= 4.41$ $p<0.04$, Table 2.13 and for Média Luna, $F= 4.80$ $p<0.0337$, Table 2.14).

Of 42 total fish species that were easily visible on reefs near Akumal, 37 species were recorded at 13 m sites and 34 species at 19 m sites in 2000 (Table 2.15). Also, 20 to 31 fish species were recorded in each of the eight sites, most of which were common to all reefs. Total densities of the four most common fish families in 2000 varied from $\sim 100\text{-}175/100\text{m}^2$ on the inner lobes and from $\sim 80\text{-}320/100\text{m}^2$ on the middle lobes (Table 2.16). Pomacentrids were the most common at all sites, acanthurids were generally least abundant, with scarids and labrids usually having densities in the intermediate range (Figure 2.13). Herbivorous fishes (scarids, acanthurids, *Microspathodon chrysurus* and algal-gardening damselfishes), which overall averaged $\sim 70/100\text{m}^2$ ($n=8$ sites), were about as common as all other fish guilds combined ($\sim 80/100\text{m}^2$). No big serranids, lutjanids or other large-bodied carnivores such as *Sphyraena barracuda* were encountered in the belt transects, although individuals were occasionally observed at other times. There were no significant differences in fish population densities among the shallow 13 m sites in 2000 (data from Yal Ku at 19 m was excluded from this analysis because of the low replicate transect number).

Herbivory rates at 13 m (n=4 sites) averaged 107 bites/m²/hour for scrapers, 86 bites/m²/hour for browsers and 42.5 bites/m²/hour for non-denuders (Table 2.17). Corresponding rates at 19 m were 106.3, 82.1 and 20.5 bites/ m²/hour (n=4 sites), respectively. (The number of replicates at Yal Ku 19 m is low, and caution is recommended when considering its fish bite data, especially for non-denuders, since pomacentrid density estimates were relatively high at this site.)

Table 2.13 One-way weighted ANOVA on fish population densities at Las Redes (13 m) between 1999 and 2000. (Data was log transformed to meet normality)

Source	Df	SS	MS	F-value	Pr > F
Model	1	2.46114116	2.46114116	4.41	0.04
Error	60	33.50107578	0.55835126		
Corrected total	61	35.96221692			

Table 2.14 One-way weighted ANOVA on fish population densities at Média Luna (13 m) between 1999 and 2000. (Data was log transformed to meet normality)

Source	Df	SS	MS	F-value	Pr > F
Model	1	2.23834814	2.23834814	4.80	0.0337
Error	44	20.50217028	0.46595842		
Corrected total	45	22.74051842			

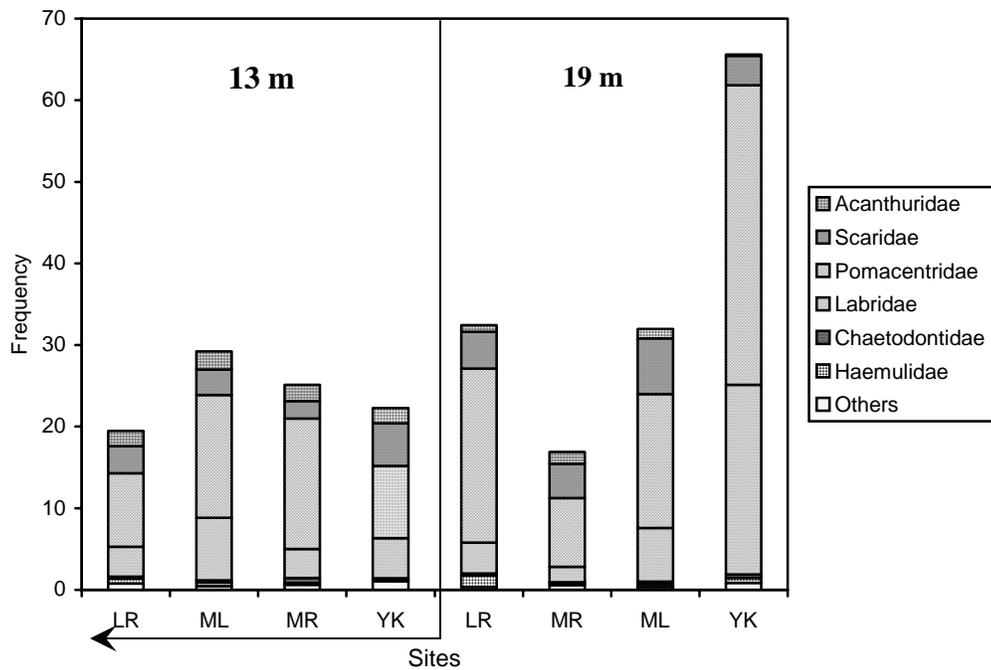


Figure 2.13. Fish family densities at different sites near Akumal, México (2000). The number of replicate belt transects at each site are as follows: at 13 m - LR n=44, ML n=30, MR n=14, YK n=18, at 19 m, LR n=22, ML n=17, MR n=22, YK n=7. Arrow indicates direction of inferred increase in sediment loading at 13 m.

Table 2.15 Fish population densities by species and between depths on reefs near Akumal, México (2000). (Total transect number at 13 m = 106 and 19 m = 68)

Fish family	Fish species	Density (# of individuals/100m ²)	
		13 m	19 m
Acanthuridae	<i>Acanthurus coeruleus</i>	5.4	2.4
	<i>Acanthurus chirurgus</i>	3.9	1.8
	<i>Acanthurus bahianus</i>	0.7	0.2
Aulostomidae	<i>Aulostomus maculatus</i>	0.1	0.2
Balistidae	<i>Balistes vetula</i>	0	0.1
Carangidae	<i>Caranx ruber</i>	0.1	0
Chaetodontidae	<i>Chaetodon capistratus</i>	0.7	0.7
	<i>Chaetodon striatus</i>	0.2	0.5
	<i>Chaetodon ocellatus</i>	0.6	0
Haemulidae	<i>Haemulon flavolineatum</i>	0.8	2.7
	<i>Haemulon striatum</i>	0	0.1
	<i>Anisotremus virginicus</i>	0.2	0.1
Holocentridae	<i>Holocentrus adscensionis</i>	0.1	0.1
Labridae	<i>Lachnolaimus maximus</i>	0.1	0
	<i>Bodianus rufus</i>	0.7	0.4
	<i>Halichoeres bivittatus</i>	0.7	0.6
	<i>Thalassoma bifasciatum</i>	7.9	5.3
	<i>Halichoeres maculipinna</i>	1.1	0.7
	<i>Clepticus parrae</i>	0.9	21.1
	<i>Halichoeres pictus</i>	0.1	0
	<i>Halichoeres garnoti</i>	13.2	16.3
Lutjanidae	<i>Ocyurus chrysurus</i>	1.1	0.5
Mullidae	<i>Mulloidichthys martinicus</i>	0.2	0
Ostraciidae	<i>Lactrophys triqueter</i>	0.8	0.6
Pomacanthidae	<i>Pomacanthus paru</i>	0.1	0
	<i>Holocanthus tricolor</i>	0.4	0.3
Pomacentridae	<i>Chromis cyanea</i>	30.3	51.6
	<i>Stegastes planifrons</i>	3.8	9.8
	<i>Stegastes partitus</i>	12.6	31.5
	<i>Stegastes fuscus</i>	11.1	7.1
	<i>Microspathodon chrysurus</i>	3.3	3.7
	<i>Abudefduf saxatilis</i>	0.1	0
Scaridae	<i>Sparisoma atomarium</i>	0	0.8
	<i>Scarus taeniopterus</i>	1.1	1.5
	<i>Scarus vetula</i>	0	0
	<i>Sparisoma aurofrenatum</i>	2.5	4.2
	<i>Sparisoma viride</i>	7.6	6.6
	<i>Scarus croicensis</i>	6.1	10.7
Serranidae	<i>Serranus tigrinus</i>	0.5	0.2
	<i>Hypoplectrus puella</i>	0	0.1
	<i>Epinephelus adscensionis</i>	1.2	0.7
Tetraodontidae	<i>Sphoeroides spengleri</i>	0.2	0.6
	Total	120.5	183.8

TABLE 2.16 Fish population densities, by family and survey sites, ordered from south to north. See Table 1.1 for site codes.

Site code	Year	Transects (#)	Species (total #)	20 x 1 m belt transects				
				# individuals/100m ² (mean ± standard deviation)				
				Acanthuridae	Labridae	Pomacentridae	Scaridae	Total
13 m								
LR13	1999	18	18	24.7 ± 18.0	7.2 ± 7.1	11.4 ± 9.4	10.6 ± 6.8	53.9
	2000	44	29	9.3 ± 18.1	18.3 ± 24.4	45 ± 40.9	16.6 ± 16.1	177.2
MR13	2000	14	25	10 ± 7.8	17.9 ± 10.3	80 ± 28.4	10.7 ± 9.4	118.6
ML13	1999	16	19	28.8 ± 16.9	7.5 ± 10.3	23.1 ± 14.7	15.6 ± 14.2	75
	2000	30	30	11.2 ± 11.7	38.2 ± 58.8	75.5 ± 63.6	15.5 ± 15.4	140.6
YK13	2000	18	31	9.4 ± 7.8	23.3 ± 23.1	44.2 ± 30.4	26.4 ± 24.2	103.3
19 m								
LR19	2000	22	23	4.1 ± 4.5	18.9 ± 20.1	106.8 ± 88.3	22.3 ± 16.7	152.1
MR19	2000	22	30	7.3 ± 7.2	9.3 ± 12.4	42.1 ± 28.8	21.1 ± 18.6	79.8
ML19	2000	17	22	5.6 ± 8.6	32.9 ± 41.5	82.1 ± 56.7	34.1 ± 42.0	154.7
YK19	2000	7	20	0.7 ± 1.9	116.5 ± 159.5	183.6 ± 89.1	17.9 ± 25.1	318.7

TABLE 2.17 Fish herbivory, by survey sites, ordered from south to north. See Table 1.1 for site codes.

Site Code	Year	Counts (#)	Herbivory			Total
			# bites/m ² /hr (mean ± standard deviation)			
			Scrapers	Browsers	Non-denuders	
13 m						
LR13	1999	74	84.9 ± 187.7	205.9 ± 367.1	83.0 ± 163.2	373.8
	2000	117	58.1 ± 228.0	117.3 ± 298.9	40.7 ± 112.5	216.1
MR13	2000	61	48.5 ± 131.9	81.0 ± 199.8	31.8 ± 84.3	161.3
ML13	2000	56	124.6 ± 310.2	62.5 ± 137.1	68.2 ± 163.6	255.3
YK13	2000	33	197.0 ± 352.6	83.0 ± 159	29.1 ± 57.9	309.1
Mean (2000)			107.1	86.0	42.5	235.5
19 m						
LR19	2000	63	136.5 ± 328.9	89.5 ± 425.9	24.4 ± 97.7	250.4
MR19	2000	77	108.8 ± 273.7	20.8 ± 67.5	39.2 ± 95.2	168.8
ML19	2000	60	90.7 ± 282.5	103.7 ± 519.7	17.7 ± 58.6	212.1
YK19	2000	11	89.1 ± 184.5	114.5 ± 373.3	0	203.6
Mean (2000)			106.3	82.1	20.3	208.7

DISCUSSION

Between 1990 and 2000, live stony coral cover has clearly decreased in the Akumal-area reefs (compare Muñoz-Chagín and de la Cruz-Agüero 1993, with Steneck and Lang 2003, and this chapter). Potential contributing factors include: (a) outbreaks of disease, (b) bleaching related mortality, (c) hurricanes, (d) overgrowth by macroalgae (Figure 2.14), (see Appendix 1 in Steneck and Lang 2003) and/or (e) encroachment by TAS mats (Chapter 3, this dissertation).

The loss of nearly 50 % of the live cover at Las Redes (13 m), between 1998 and 2000 (Figure 2.6) can be attributed primarily to the effects of white plague (WP) disease in the *Montastraea annularis* species complex. It is also believed to have reduced the cover of these species at Média Luna and on other reefs in the immediate Akumal area (J. Bruno *pers. comm.*). WP was less conspicuous in March 2001 (when the live cover of *Montastraea faveolata* at Las Redes (13 m) was about the same as in the previous summer), but was observed in ~2% of all colonies of the *M. annularis* complex (which includes *M. faveolata*) during summer 2002 (J. Bruno *pers. comm.*).

Yellow-blotch (also called yellow-band) disease (YBD), first noticed in a few colonies of Akumal-area *M. faveolata* in 1997 (Steneck and Lang 2003) was very conspicuous at Las Redes (13 m), in March 2000, yet it was less visible a year later (*pers. obs.*). J. Bruno (*pers. comm.*) has estimated that in summer 2002 less than 10% of the *M. annularis* complex in most areas of Akumal were infected



Figure 2.14. Smothering by overgrowth of macroalgae like *Dictyota sp.* on the foliose coral, *Agaricia tenuifolia* on Las Redes at 19 m.

with this disease. Signs of white-band disease (WBD) were seen in several colonies of *Acropora palmata* on the inner lobes at Las Redes and Xaak, (the sites at both ends of the area studied in 2000) by J. Lang in 1997 (*pers. comm.*). WBD, which was considered “fairly common” during 2000-2001 in *A. palmata* and in *A. cervicornis*, (a currently rare genus, Table 2.5), but no examples were seen in summer 2002 (J. Bruno *pers. comm.*).

The susceptibility of stony corals to these diseases, especially the WP outbreak in (*M. faveolata* and *M. annularis*) may have been increased by stresses associated with the 1998 mass bleaching event. The average difference in temperature ranges between 1998 and 1999 are low. However, the often substantially higher temperatures that were consistently recorded prior to the 1998 mass-bleaching event relative to the following year (Figure 2.4), are evidence of sustained thermal stress for the majority of the time between July 9th and August 4th, 1998. Sea surface temperatures collected in 0.5 m at Puerto Morelos (a permanent CARICOMP monitoring station north of Akumal and used commonly as a reference source for the area) in July and August 1999 and June to August 2000, are largely comparable to the average temperatures from 13 m on Las Redes for the same time periods. The only differences between these two sites occurred in July 1999, where Akumal averaged 28.4 °C (0.2 SD) at 13 m was considerably lower than the 29.8 °C reported at Puerto Morelos (D. Linton, *pers. comm.*).

Solar irradiance is also a bleaching trigger (Glynn *et al.* 1992, Gleason and Wellington 1993, Schick *et al.* 1995) that is important under doldrum conditions when light penetration is at its maximum, a factor that is affected by water column turbidity. When a storm occurred, horizontal secchi disk readings could be lowered from >30 m to <12 m. However, the sediments would settle out of the water column in only a few days, returning the area to its normal low-turbidity conditions. Run-off from storms probably does not play a major role in increasing turbidity given the local karst topography, but it can reduce salinity, a factor which has also been cited as a cause for bleaching (Goreau 1964, van Woesik *et al.* 1995). That sea water at 13m was less saline than the surface waters off Akumal on four occasions likely indicates groundwater intrusions (Figure 2.5) , as these reversals each occurred a few days after a storm. However, more detailed data on salinity, groundwater flow, and rainfall patterns in the region would be required to adequately demonstrate this relationship.

Hurricanes are also known to cause severe damage to reefs and have likely played a role in reducing local coral cover. Although Hurricane Gilbert destroyed much of the *Acropora cervicornis* on the Akumal-area fore reefs in 1988 (G. Arcila *pers. comm.*), Mitch in 1998 caused relatively little physical damage to this habitat (S. Slingsby *pers. comm.*).

Large storm systems like hurricanes can also have other effects on benthic communities. After initial removal by turbulence, blooms of macroalgae were conspicuous in the months following the passage of Hurricane Mitch in 1998 (S.

Slingsby *pers. comm.*). The relative abundance of macroalgae on six middle-lobe fore reefs near Akumal was found to have increased from ~25% to 44% between 1997 and 1999 by Steneck and Lang (2003) who discussed increased colonization space on the skeletons of diseased stony corals, the possibility of increased nutrients in groundwater, and decreased herbivory rates as potential explanations for this change. Although Steneck and Lang (*op. cit.*) noted a decline in the relative abundance of algal turfs (from 62~35% between March 1997 and March 1999) at 11-18 m, I found no decrease in the proportion of colonies completely surrounded by TAS mats at the Las Redes 13 m site over the 1998-2000 study period. Indeed, the general trend seemed to be in the opposite direction (Table 2.4) and perhaps is indicative of increases in turf algal cover subsequent to Steneck and Lang's (*op. cit.*) surveys. [Data from a separate study indicate that two of these corals, *M. faveolata* and *D. strigosa*, lose substantial amounts of live tissues to marginal encroachment by TAS mats, whereas a third, *S. siderea*, not only loses tissue at a lower rate, but some colonies have either maintained their original size or have expanded laterally, displacing the mats (Chapter 3, this dissertation).]

The result of chronic TAS mat encroachment is not as conspicuous as that of episodic natural disasters such as hurricanes or disease outbreaks. Nevertheless, it is important to ask why the mats are presently outcompeting what, until recently, have constituted several of the most important reef framework-builders on the Akumal-area fore reefs. A closer look at the species-specific prevalence of contact

with TAS mats indicates that there are some significant differences among species of differing colony shapes (Table 2.4). A consistently smaller percentage of colonies of branching species like *Porites porites* and foliose corals like *Agaricia tenuifolia* are in contact with TAS mats on >50% of their periphery relative to massive corals like *M. faveolata* and *D. strigosa* that grow as mounds, hemispheres, boulders or thick crusts. Although overall coral morphology is a likely factor (Chapter 3, this dissertation), it fails to account for *S. siderea*, another massive species, in which only 35% of its colonies were completely (100%) surrounded by TAS mats in 1998 (Table 2.4). The significantly decreased percentage of corals that were completely surrounded by TAS mats in the 19 m reefs relative to those at 13 m (Table 2.12), is likely due to a combination of reduced light penetration at greater depths lowering rates of photosynthesis in the turf algae and the reduced amounts of sediment in suspension (*pers. obs.*).

Sediment loading on the fore reefs off Akumal bay and Média Luna has likely increased, along with increased human activity, and current local sedimentation rates in the former is relatively high (Razo Amoroz 1999). Although TAS mats are less likely to form in the presence of adequate grazing by herbivores, once established, the sediment bound by the turfs may deter herbivorous fishes (Purcell 2000, *pers. obs.*). So long as the key herbivore, *Diadema antillarum*, remains scarce on these reefs, TAS mats are likely to continue expanding and coming into ever increasing contact with corals and other sessile organisms. The increase in cover and density of live corals and the decreased percentage that were

completely surrounded by TAS mats along the inferred decreasing sediment loading gradient supports this role of sediment (Table 2.1).

Echinoids are important herbivores, and *Diadema antillarum* in particular is quite capable of removing TAS mats from the substratum (Wanders 1977, Carpenter 1986, *pers. obs.*). Most individuals of *D. antillarum* perished throughout the entire western Atlantic during 1983-84 (Lessios 1988). Unfortunately, no quantitative, historical information is available regarding the ecological effects of the loss of this key herbivore from the Akumal area. Although there is a substantial population of *D. antillarum* on the patch reefs in Bahia Akumal during 1998-2000 (*pers. obs.*), only in the summer of 2002 have their densities begun to increase on the fore reefs (R. Steneck *pers. comm.*). All else being equal, the relatively low densities of medium- to large-sized herbivores in the Akumal-area reefs should facilitate the proliferation of benthic macroalgae. Indeed rates fish herbivory (overall averaging ~ 190 bites/m²/hour) in 2000 were essentially identical to the low grazing rates recorded at 10 m in 1988 on the heavily overfished north Jamaican reefs (where scrapers and browsers averaged 155 and 12.5 bites/m²/hour, respectively, Steneck 1993), where macroalgae became the dominant benthic cover (Hughes 1994).

Territorial algal-gardening pomacentrids are known for their ability to cultivate and protect patches of turf algae from other herbivores (Vine 1974, Hixon and Brostoff 1983, Eakin 1988) unless overwhelmed by large schools of acanthurids and scarids (Ogden and Lobel 1978). Moreover, when territorial

damsel fish are experimentally removed from reefs, other herbivores generally show a quick increase in abundance (Hourigan 1986). In the Virgin Islands, at depths of 3-14 m, Nemeth *et al.* (2003) found that the density of large-bodied herbivorous acanthurids and scarids at each site was inversely related to the percentage of stony corals occupied by damselfish. This result may indicate some form of competitive exclusion of larger herbivores by small territorial damselfish or, alternatively, is perhaps an artifact of the belt sampling method, which underestimates the larger-bodied herbivore populations which school and move unpredictably (Nemeth *et al. op. cit.*).

In the Akumal area, aggressively territorial pomacentrids (*Stegastes fuscus*, *S. planifrons* and *S. partitus*) averaged 23% at 13 m and 28% at 19 m of the total fish populations in 2000. Like the acanthurids and scarids, damselfishes have doubtless experienced reduced predation from piscivores, especially groupers and snappers (Randall 1976) that currently are exceedingly rare in this area; in contrast to the latter, they are unlikely to have been fished by humans. Hence, in the absence of significant algal grazing by populations of *Diadema* release of aggressive territorial damselfishes from natural predation may have indirectly promoted the persistence of algal turfs in the Akumal area through the exclusion of larger herbivores from their territories.

In conclusion, fringing reefs near Akumal have declined significantly in recent years. Between 1998 and 2000, *M. faveolata* incurred rapid losses from WP disease (the documentation of which at the Las Redes 13 m site demonstrates

the value of repetitive monitoring before, during, and after major perturbations). In 2000, several attributes of fore-reef condition (live stony coral cover, coral density, and relative exposure to TAS mats) were inversely related to an inferred sedimentation gradient at 13 m (Figures. 2.6-2.12). Less obvious has been the displacement of *D. strigosa* and *M. faveolata* by TAS mats, the formation of which is currently facilitated near Akumal by high sedimentation rates, a relative scarcity of large-bodied herbivores that is partially attributable to overfishing, and possibly by algal-gardening damselfishes. Given the postulated relationships between large herbivorous fishes and aggressively territorial damselfish (see also Hourigan 1986, Nemeth *et al.* 2003) it would seem prudent to include the latter in the species lists for belt-transect rapid assessments (like the AGRRA method, <http://coral.aoml.noaa.gov/agra/>) to better understand reef-ecosystem dynamics. Community leaders in Akumal are already expending considerable effort to restrain environmentally destructive coastal development, support marine ecological research and initiate public outreach education. To reverse current declines, it may also be necessary to implement effective fishing bans, removal of territorial damselfish, and/or programs of artificial stock enhancement for ecologically important herbivores such as *Diadema*, scarids or acanthurids.

Chapter 3: Turf algal/sediment (TAS) mat encroachment over three important framework-building species of stony corals in Akumal, México.

ABSTRACT

Turf algal/sediment (TAS) mats encroached over live stony corals at measurable rates between 1998 and 2000 in a Mexican study site inferred to have a relatively high sedimentation rate. Results of a controlled experiment on the three species studied at 13 m on the Las Redes fore reef near Akumal, showed that *Diploria strigosa* was the most vulnerable to this type of tissue mortality, regressing an average of 1.27 ± 1.78 cm/year (n=42 colonies). Closely following was the primary framework constructor *Montastraea faveolata*, which averaged tissue losses of 0.86 ± 0.84 cm/year. *Siderastrea siderea* also suffered tissue losses due to TAS mat encroachment but at a significantly lower rate than for the other two species (average = 0.24 ± 0.51 cm/year). Time-series photography of 37 tagged *Diploria strigosa* showed an average loss of 70 ± 13.2 cm² of live tissue/coral/year to surrounding TAS mats; 10 of these colonies regressed below their estimated puberty size (*i.e.*, the minimum surface area required to reproduce sexually, Soong 1990). The complete mortality of three of the *D. strigosa* provides further evidence that the present rate of tissue loss is not sustainable for this species.

Coral morphology can be an important factor in avoiding TAS mat encroachment. Branching corals with reduced amounts of live tissue in contact with the benthos, and therefore TAS mats compared to massive boulder corals, seem to escape becoming completely surrounded by them more frequently. TAS mats are a significant, chronic stressor for certain, structurally important, massive coral species on the 13 m Las Redes

reef under current environmental conditions (see Chapter Two this dissertation).

Therefore, it is important to record TAS mat presence and frequency in future assessments of reef health wherever they are prevalent so that appropriate solutions can be developed and implemented.

INTRODUCTION

Spatial competition between stony reef corals and benthic algae is an accepted paradigm, wherein algae are generally considered to be superior competitors under conditions of low herbivory and/or high nutrient loads, (e.g., Littler and Littler 1984, Hughes 1994, Miller 1998). After reviewing the current literature, however, McCook *et al.* (2001) concluded that much of the evidence cited in support of this presumption is indirect, lacking adequate experimental documentation or even detailed descriptions of the competitive mechanisms involved. Indeed, the ability of many scleractinians to overgrow filamentous turf algae (*sensu* Steneck 1988) settling on skeletal areas that are exposed when their soft tissues are removed by some natural (Fishelson 1973, Rogers *et al.* 1982, Lirman 2000) or experimental (Bak *et al.* 1977, Meesters *et al.* 1994) perturbation is well known (Loya 1976a, Meesters *et al.* 1994). Moreover, in a controlled experiment lasting seven months on the Great Barrier Reef, undamaged colonies of the massive coral *Porites lobata* were found to significantly inhibit the lateral expansion of algal turfs along their margins and even encroached over the latter (McCook 2001, see his Figure 4 a). Nonetheless, as also noted by McCook (2001, see also McCook *et al.* 2001), variable outcomes have been reported during diverse natural (non-manipulative) interactions between algal turfs and stony corals (as in Littler and Littler 1997), particularly when sediment carried onto a

reef or re-suspended locally is trapped by algae growing in contact with live coral tissues (Nugues and Roberts, 2003a, 2003b).

Sediment loading alone can be a crucial factor in determining reef community structure. For example, Acevedo and Morelock (1988) showed that communities receiving high rates of sediment input were dominated by stony corals usually found at greater depths in areas less affected by sediment, suggesting that these sites receive reduced light levels. Lower coral cover and diversity were also evident, while the relative abundance of sediment-tolerant species was increased. Recruitment can also be reduced as established larvae are buried and/or newly settling larvae are unable to attach to shifting sediments (Bak and Engel 1979, Rogers *et al.* 1984, Babcock and Davies 1991, Te 1992). In recent decades large areas, even entire reefs, have experienced dramatic losses of live coral cover due to high levels of anthropogenic sediment loading from uncontrolled coastal development and beach replenishment projects, (Endean 1976, Cortes and Risk 1985, White 1987), or dredging for canals and piers (Johannes 1975, Bak 1978, Rogers 1985).

Stony corals are, however, naturally exposed to resuspended sediments during storms and are not entirely defenseless. They possess differing abilities for actively clearing their tissues of debris in one or more of four ways: ciliary action; tentacular utilization; stomodaeal distension; and the secretion and shedding of mucus (Hubbard and Pocock 1972, Stafford-Smith, 1993). Additional passive forms of debris removal related to aspects of the morphology of some coral

species allow gravity and water-flow to assist the disposal process (Lasker 1980). What is not generally recognized, however, is that once sediment and debris reach the edge of the stony coral's live tissues, a new problem potentially occurs if algal turfs are growing in direct contact with its margins (McCook *et al.* 2001). This is because bafflement can result in entrapment of sediment by turf algae, some of which will have fallen directly from suspension in the water column (Scoffin 1970, Carpenter 1986, Purcell 2000), leading to the formation of turf algal/sediment (TAS) mats (Chapter Two this dissertation). Sediments are further bound by the growth of the algal rhizoids on the substratum, as well as in the mucus sheaths that cover some algal filaments (thereby giving them a white powdery appearance). The TAS mats that border stony corals in some areas have been described as potentially superior spatial competitors (Dustan 1977, Abbott 1979; see also Dustan, 1999 for photographic documentation). Furthermore, stony coral recruits on the upper surfaces of settling plates emplaced on reefs off the Caribbean coast of Panama were smothered by sediment trapped by surrounding filamentous algae, unless the latter were grazed by relatively small-sized herbivorous fishes (acanthurids and *Scarus croicensis*) (Birkeland 1977).

GOALS

Shallow fore reefs off Akumal, Quintana Roo, in the Mexican Caribbean, presently have high sediment loading and/or resuspension rates (Razo Amoroz 1999). Abundances of algal turfs that are capable of entrapping these sediments are also fairly high (~25-45% at 11-18 m, n=6 reefs) relative to other algal functional groups (macroalgae and crustose coralline algae) (Steneck and Lang 2003). Species-specific differences in the percentages of colony peripheries that are completely surrounded by TAS mats (Chapter Two this dissertation) are indirect evidence that TAS mats may kill and overgrow massive stony corals on this reef. I recorded and described (1) the mechanisms by which TAS mats interact with live coral tissues, (2) any role that colony morphology played in avoiding TAS mats, and (3) quantified species-specific rates of encroachment, and effects of this competition for three different species that are major framework builders on the shallow fore reefs. I also attempted to experimentally determine the relative significance of the turf algae versus the sediment in TAS mats during these competitive encounters. In addition, since size determines a coral's ability to reproduce sexually (Soong 1990, Lirman 2001a), and other important functions like competition, regeneration, growth rates and survivorship (Loya 1976b, Highsmith *et al.* 1980, Lang and Chornesky 1990, Lirman 2001a), I also investigated the relationship between initial size and percent area tissue lost per year at the live coral-TAS mat interface in photographed *D. strigosa* corals.

MATERIALS AND METHODS

The Las Redes reef site, which is located at 20^o 23.364'N and 87^o 18.617'W in a depth of 13 m (range = 11.5-13m) off the 2-km long Bahia Akumal described in Chapter two, was chosen for its accessibility and the ubiquity of extremely conspicuous TAS mats in this habitat.

A. OBSERVATIONS OF INTERACTIONS BETWEEN TAS MATS AND STONY CORALS:

I. SPECIFIC MECHANISMS BY WHICH TAS MATS ENCROACH OVER CORALS

The specific mechanisms by which TAS mats interact for space with stony corals was determined in *Diploria strigosa*, *Montastraea faveolata* and *Siderastrea siderea* by close daily observations underwater, and amplified by close-up photography of the coral-TAS mat interfaces where possible.

II. RELATIONSHIPS BETWEEN STONY CORAL MORPHOLOGY AND CONTACT WITH TAS MATS

Qualitatively assessing any existing relationships between stony coral morphology and susceptibility to TAS mat encroachment by close daily observation.

B. QUANTIFYING THE RATES AND EFFECTS OF SPATIAL
COMPETITION BETWEEN TAS MATS AND THREE SPECIES OF
FRAMEWORK-BUILDING REEF CORALS:

I. EXPERIMENTAL DESIGN IN 1998

In 1998, I initially chose to study the massive brain coral, *D. strigosa* because of its relatively high population density (~0.05/m) and the extremely high prevalence (100% during 1998-2000, Table 3.4), of colonies that are completely (100%) surrounded by well-developed TAS mats. Pairs of randomly generated numbers were used to determine kick-cycles and compass headings. Once each pair was completed, the nearest healthy *D. strigosa* that was completely surrounded by a TAS mat was selected. In total, twenty colonies were tagged and positioned on a map of the study site by 4 July, 1998. Two stainless steel pins were placed ~5 cm apart in each TAS mat, near its border with the living coral tissue, to serve as stationary reference points from which I used a ruler to measure changes in the distance from each pin to the live coral margin with an accuracy of ± 0.5 mm. The colonies were then divided into four spatial blocks (each with five corals) in relatively close proximity to each other in order to control for locally varying environmental factors such as water flow patterns, sedimentation patterns and overall depth. Within each block, each tagged coral was assigned one of the five treatments to yield four replicates/treatment.

II. CONTROLS AND EXPERIMENTAL MANIPULATIONS OF THE TAS MATS AT THE INTERFACE WITH LIVE STONY CORALS

For all treatments, the dependant variable was the distance from the pin to the live coral border. Five treatments (two controls and three manipulations) were applied (Figure 3.1).

Controls

Control (C1) – To examine the ambient rate of encroachment by an established TAS mat over live corals, for one coral in each block, the portion of the mat within at least a 5cm radius around the steel pins remained untouched as a non-manipulated control;

Disturbance control (C2) – To control for the disturbance experienced by the TAS mats in manipulations M1 and M2 (see below), the sediment in the portion of the mat within at least a 5 cm radius around the steel pins was lightly dusted away. Then a comparable amount of sediment occurring naturally on the substratum near these colonies was collected by hand and added to the disturbed area of the TAS mat.

Manipulations

Of the three manipulations performed, two were implemented to assess the effect of sediment in the TAS mat and the subsequent rate of encroachment over the adjacent corals. The third manipulation was to assess whether TAS mats were actively expanding over the corals or passively expanding into newly available substrata as the corals died due to factors other than contact with the TAS mats.

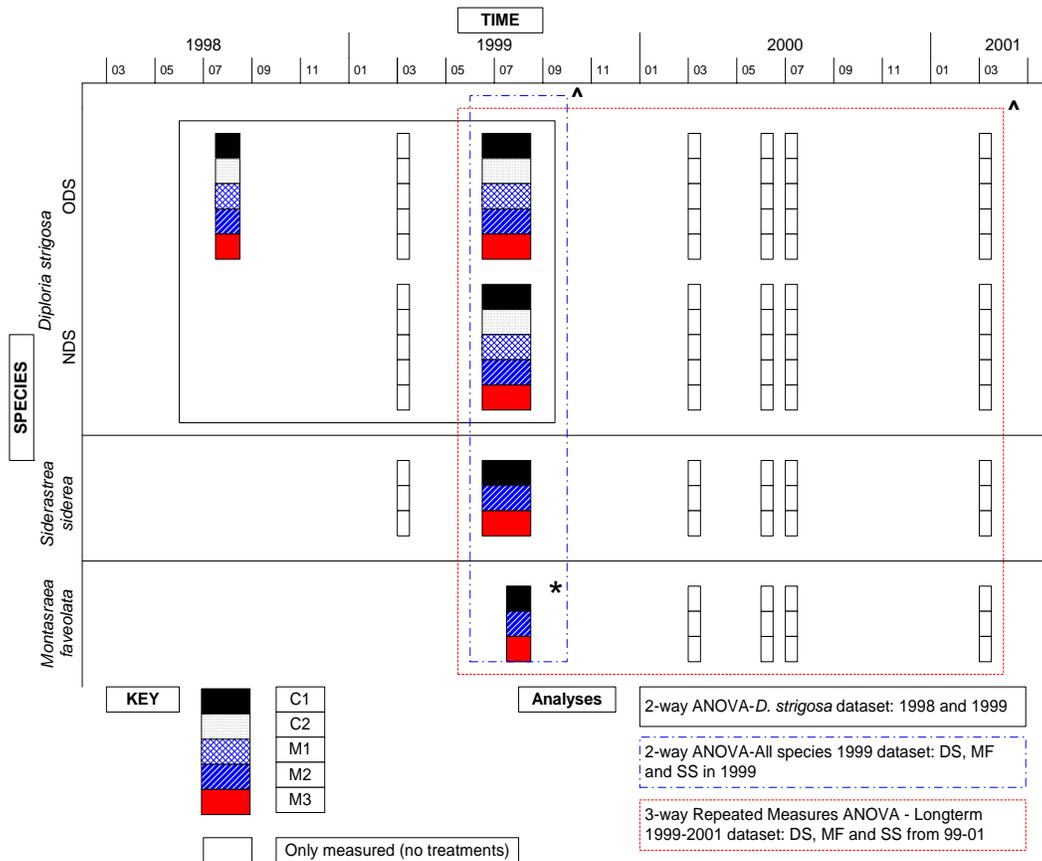


Figure 3.1. Experimental design and groupings for analyses in the three stony corals *Diploria strigosa* (two groups ODS – old *D. strigosa* and NDS – New *D. strigosa*), *Siderastrea siderea* and *Montastraea faveolata* from 1998 – 2001.

^ - only C1, M2 and M3

* - All three treatments were administered to each *M. faveolata* colony, at laterally spaced intervals of at least 50cm (in contrast to the other two species in which only one treatment was administered per colony)

Sediment addition (M1) – to test for encroachment rates of TAS mats under higher levels of sedimentation, about 100 g of additional sediment was added to the portion of the mat within at least a 5 cm radius around each steel pin;

Sediment removal (M2) – to assess the encroachment rates by the algal components (and thus the role of sediment by inference), the sediment in the portion of the TAS mat within at least a 5 cm radius around the steel pins was lightly dusted away leaving only the turf algae in contact with the coral tissue;

TAS mat removal (M3) – to compare changes at a live tissue border when not in contact with a TAS mat, the portion of the mat within at least a 5cm radius around the steel pins was completely scraped away, exposing the underlying coral skeleton.

Prior to the start of the experiment in 1998, one of the colonies from the M3 manipulation group could not be located after a storm, so a replacement was tagged and pinned. Four days later, when the experimental observations began, the original colony was found, so the appropriate manipulation was re-established and data for this coral was collected from July 10 to August 9, resulting in data from five colonies in the M3 group. Any necessary manipulations or maintenance were re-established, observations were recorded and the distance separating each pin from the edge of the live coral tissues during the experiment was measured at least once every 2-3 days between July 10 and August 9, 1998 (n=21).

III. EXPERIMENTAL DESIGN IN 1999

In 1999, the sample size for *D. strigosa* was doubled based on results from the previous year. 20 new colonies (randomly selected as described above) were divided into four new spatial blocks, resulting in at least eight replicates/treatment (nine replicates in M3 for reasons given above). Two other species, *Siderastrea siderea* and *Montastraea faveolata* were added to the study but only a subset of the treatments were applied. For *S. siderea*, C1, M2 and M3 were applied to a total of 24 corals with eight replicates/treatments. For *Montastraea faveolata*, C1, M2 and M3 were applied at laterally spaced intervals of at least 50 cm, to each of nine corals (nine replicates/treatment), due to its large size and relative scarcity at this site. These three treatments, C1 control and the two (M2 and M3) manipulations were chosen because they exhibited the largest differences among groups in 1998 (see Results) and because they tested for direct effects.

These particular species were added not only because they are both important contributors to the benthic cover locally (Chapter Two this dissertation), but also because results of the line intercept transects showed that only 35% of *S. siderea* colonies were completely surrounded by TAS mats in 1998 in contrast to 93% of the *M. faveolata* (Table 2.4, this dissertation) suggesting different susceptibilities to TAS mats among these species. Also, given the large sizes of *M. faveolata* sizes at Las Redes, where colony diameters at 13 m commonly exceed 1.5 m (*pers. obs.*), this species significantly enhances the reef's three-dimensional structural complexity and habitat heterogeneity, adding to its relevance as a

subject for investigation. However, these methodological modifications placed additional constraints on the inspection schedule. Due to limitations in manpower, time and funding, inspections were made at a longer interval than in the previous year.

Necessary manipulations or maintenance were re-established, observations recorded, and changes in the distance from the pins to the live tissue border were measured 1-2 times a week from June 10 to August 5, 1999 (n=41 colonies) for *D. strigosa*. The same inspections were made between June 10 and August 5, 1999 for the 24 *S. siderea*, (which were tagged and prepared in March 1999), and between July 8 and August 6, 1999 for the nine *M. faveolata*, (which were tagged and prepared during June 1999), as shown in figure 3.1. Means for each colony were obtained by averaging the change in distance for both pins over the specified period of time.

Additional distance measurements were made when all tagged colonies were observed once in each of March 1999 and March 2000, once a month in June and July 2000, and once in March 2001 (Figure 3.1). The data for each colony (or each treatment in the case of *M. faveolata*) were obtained by averaging the change in distances from the pins to the coral tissues as described above.

C. PHOTOGRAPHY:

Contact between TAS mats and live tissues in a total of 42 randomly chosen and tagged colonies of *D. strigosa* at LR13 were photographed once or twice in

1998 (when n=18 corals) and in 1999-2001 (when n=37 corals). The slides were digitized and analyzed with the Scion Beta 4.0.2 version of NIH Image to extract temporal changes in surface area. The two nails emplaced in the TAS mat for the *in-situ*, tissue regression measurements were also used as fixed reference points and their actual measured separation distances used to set the scale of each image. Due to slight differences in the orientation of the slides, the unique ridge pattern of most colonies was used to draw an outline of the 2001 image over the initial image to calculate the net difference in surface area between the two time intervals and the results were standardized to cm² of tissue change/year. Other illustrative photographic images were also captured where possible.

STATISTICS:

The experimental design did not allow for a single comprehensive analysis of all the data gathered. It was therefore separated into three datasets for three separate analyses (Figure 3.1). The first dataset (*D. strigosa* 1998 and 1999) was comprised of results from experimental manipulations in *D. strigosa*, in 1998 and 1999. The second dataset (All species 1999, with experimental treatments C1, M2 and M3), was comprised of comparable data from the experimental manipulations on all three species in 1999. The third dataset (Long-term 1999-2001) consisted of measurements of the long-term rate of tissue loss, primarily without manipulation, from 1999 to 2001.

i. *DIPLORIA STRIGOSA* 1998 AND 1999 ANALYSIS:

The “*D. strigosa* 1998 and 1999” dataset was first organized into three groups:

- ODS98 – data from all 21 colonies in 1998
- ODS 99 – data from the original 21 colonies (which had now undergone two seasons of manipulations)
- NDS99 – data from the 20 newly tagged colonies in 1999.

These data were first standardized to the average tissue loss per 30 days by calculating the average loss of tissue/day during the experimental period and multiplying that by 30, to allow comparability between years. As some of the data were negative, 1 was added to all datapoints for log transformation to meet normality (Figure 3.6), and then analyzed in a two-way fixed effects ANOVA with interactions. The two factors were treatments (5 levels) and groups (3 levels), which account for year and group in this case.

ii. ALL SPECIES 1999 ANALYSIS:

The “All species 1999” experimental dataset was also standardized to the average tissue loss per 30 days for comparability and log transformed (after 1.06 was added to all datapoints to ensure that all data were positive) to meet normality initially (Figure 3.8a and b). Once an outlier became apparent, careful review of the raw data showed that it was likely a mistake. The outlier represented one set of values taken from *M. faveolata* coral tag# 299 M2 treatment on August 6th, 1999. Were these values accurate, they would indicate that the *M. faveolata*

tissues displaced TAS mats and grew over 1.2 cm towards the left pin and 0.7 cm towards the right pin, in only 9 days. This rate of growth is inconsistent with coral growth rates for *M. faveolata* even at a growing margin (Cruz-Piñón *et al.* 2003), therefore this outlier was excluded from this and all further analyses, and the current transformation was re-done (Figure 3.8c).

Once transformed, data from *D. strigosa* (n=25: C1 n=8, M2 n=8, M3 n=9), *M. faveolata* (n=9/treatment in C1 and M3, n=8/treatment in M2) and *S. siderea* (n=21: C1 n=7, M2 n=7, M3 n=7), were tested in two-way fixed-effects ANOVA with interactions. The two factors were species (3 levels) and treatments (3 levels). (Three colonies of *S. siderea* with data that was incomplete for various reasons including loss of nails and gaps in data collection were not used in this analysis.)

iii. LONG-TERM 1999-2001 ANALYSIS:

The “Long-term 1999-2001” dataset for tissue loss in *D. strigosa* (n=24: C1 n=8, M2 n=7, M3 n=9), *M. faveolata* (n=9/treatment) and *S. siderea* (n=12: C1 n=5, M2 n=4, M3 n=3) was compiled only from those colonies with complete data (with all measurements taken from the original reference point, over the same time period and all still alive at the end of the study). After the data were log transformed to meet normality (Figure 3.10), they were analyzed with a two-way fixed-effects repeated measures ANOVA with interactions, (utilizing a compound symmetric covariance structure).

All statistical analyses were conducted in SAS version 8.2, and results were based on Type III SS (appropriate for unbalanced designs). Post-hoc tests that were conducted when necessary are detailed in the Results. Graphs were plotted in Sigma Plot 2001 and enhanced in Visio Professional 5.0b.

The relationship between initial area of live tissues and percent area of soft tissue loss in the photographic time series data of *D. strigosa* (n =37 colonies) was investigated with a simple regression analysis.

RESULTS

A. OBSERVATIONS OF INTERACTIONS BETWEEN TAS MATS AND STONY CORALS:

I. SPECIFIC MECHANISMS BY WHICH TAS MATS ENCROACH OVER CORALS

I have observed three ways in which TAS mats displace live coral tissues. The first occurs when their algal filaments extend up to 3 cm immediately above the live coral surface without anchoring to it, thereby coming into contact with tissues several centimeters from the mat border. The extended portion of the TAS mat, moving in response to the local surge and current flow patterns, brushes these tissues, likely abrading their surface and perhaps depositing fine sediments or

other materials shaken loose from the mat (Figure 3.2). The second occurs when individual filaments at the border of the live coral stretch as far as 2 cm across its surface, trapping sediments in mucus sheaths and remaining in close contact with the coral (Figure 3.3). These filaments are mostly attached to the surface of the coral tissues in contrast to the mechanism described above. In the third method, algal filaments growing in the coral skeleton emerge through the live coral tissues within millimeters of its border with the TAS mat, causing tissue damage that eventually is exploited by the adjacent mats (Figure 3.4). However, these seemingly solitary filaments have only been seen thus far when the TAS mat has been pulled back from the edge of the live coral tissues over which they are hanging.

Constant irritation caused by any one of these methods, induces the coral to produce large amounts of mucus and presumably diminishes its energy stores while it has no visibly negative effect on the TAS mat. Another source of significant energetic costs to the coral are the required repairs to damaged tissue. Restricted access to sunlight, oxygen, nutrients and other exogenous resources could gradually lead to the death of the coral's soft tissues (Aller and Dodge 1974, Tomascik and Sander 1985, Richmond 1993). Once the dead tissue sloughs off, the turf algal rhizoids presumably attach so quickly to the newly available substratum that no margin of exposed skeleton has been observed thus far between the two competitors, a marked difference from that expected were the coral tissue killed by mechanical damage or most diseases (Figure 3.5).

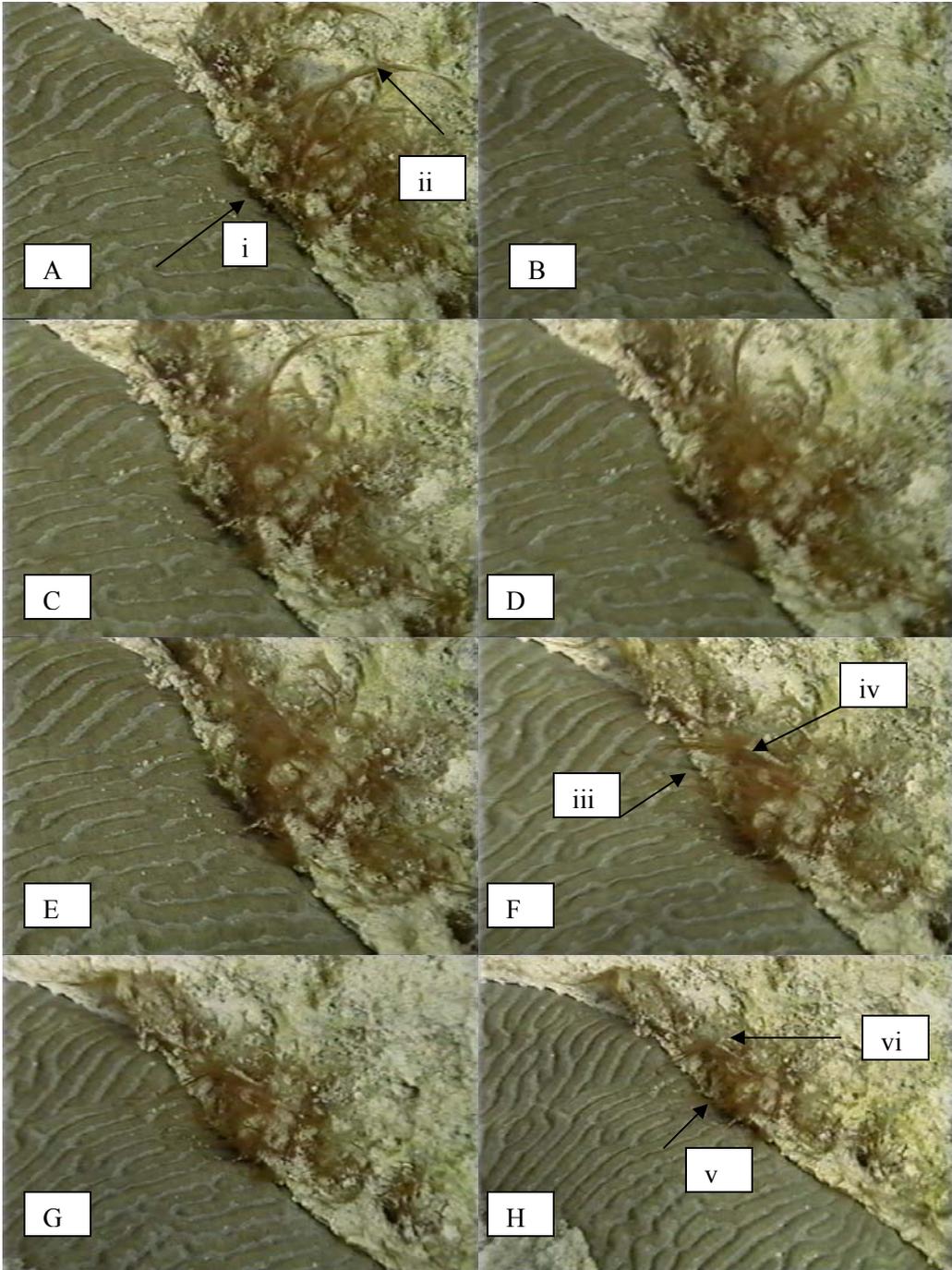


Figure 3.2 A-H. Sequential images (from video), of TAS mat on coral. Portion of mat extends over live tissues, moving on and off coral with the local water flow patterns, (without anchoring to substratum).

A. Arrow i-Space between TAS mat and coral, **arrow ii**-algal filaments caught in the water flow, with enough drag to pull portion of TAS mat off the coral tissues.

F. Arrow iii-TAS mat is in contact with coral, as shown by **arrow iv**-filaments moving in the opposite direction from that shown by arrow ii (A).

H. Arrow v-TAS mat starts to lift again, **arrow vi**-filaments are moving back to position in arrow ii (A).



Figure 3.3. A *Diploria strigosa* coral (tag#78), with turf algal filaments stretching across the tissue surface. These filaments trap sediment while remaining in close contact with the coral. Arrows indicate a few of the turf algal filaments that have trapped sediments and are mostly attached to the coral tissue surface

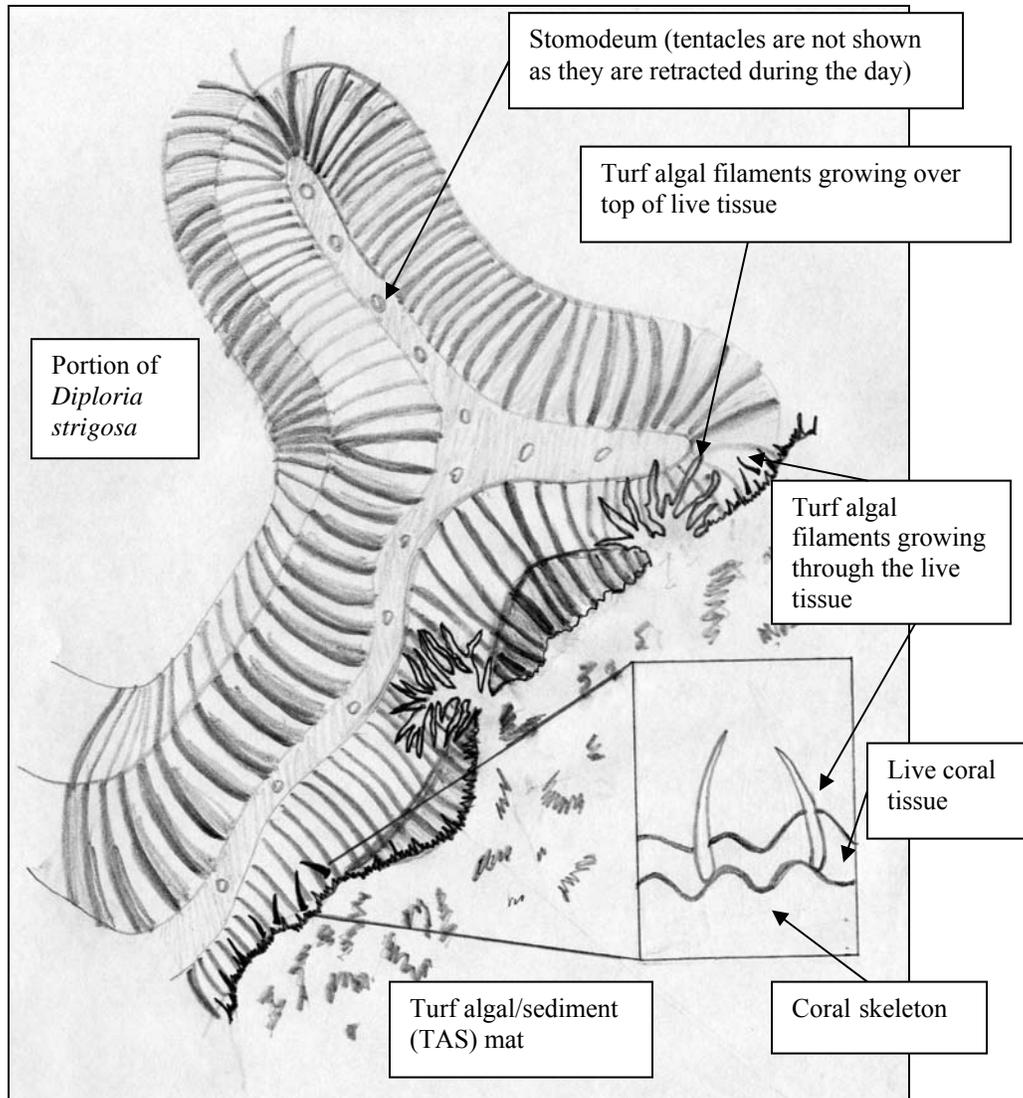


Figure 3.4 Diagram of the border of *Diploria strigosa* and turf algal/sediment (TAS) mat showing turf algal filaments growing through the coral tissue within millimeters of the TAS mat border. *In-situ* observations did not reveal connections among these filaments, and since observations of how these filaments grow through the skeleton in this particular case were not possible, portions below the skeleton surface have not been drawn.



Figure 3.5. Black-band Disease (BBD) in a colony of *Diploria strigosa*. The dark broad band closer to the center of the picture is the rapidly advancing disease front which is destroying the coral tissues, and leaving behind the bare, bright-white coral skeleton. The thinner drawn black line demarcates the front of an incipient TAS mat, which is following the disease and opportunistically monopolizing the newly available substratum.

II. RELATIONSHIPS BETWEEN STONY CORAL MORPHOLOGY AND CONTACT WITH TAS MATS

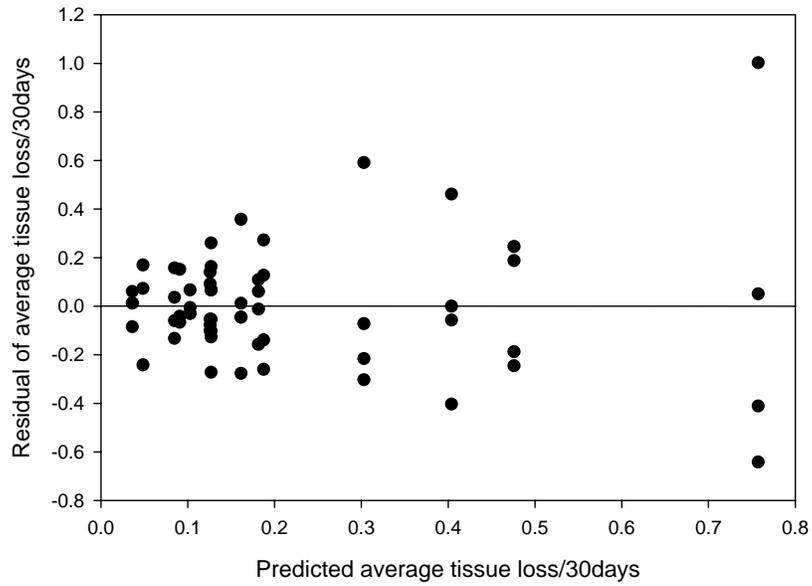
There seems to be a relationship between different coral morphologies and contact with TAS mats. Massive, boulder corals like *Diploria strigosa* and *Montastraea faveolata* are more commonly completely (100%), surrounded by TAS mats compared to branching corals like *Porites porites*. Mushroom-shaped corals like some *Porites astreoides* which have its live tissues raised off the substratum on which it is growing, also seem to avoid contact with TAS mats that might be growing on the same substratum more often than the massive corals.

B. RATES AT WHICH TAS MATS OVERGROW THREE SPECIES OF FRAMEWORK-BUILDING REEF CORALS:

i. *DIPLORIA STRIGOSA* 1998 AND 1999:

In the two-way ANOVA, there were no significant differences among treatments nor was there an interactive effect between treatment and group; however, there was a significant difference among groups (Table 3.1). A Tukey's HSD test on the groups indicates that the tissue loss in 1998 (in the group ODS98) is significantly different from the tissue loss in the other two groups in 1999 (Figure 3.7). (Data from 1998 was excluded from any further analysis given that it was also a year during which elevated seawater temperatures resulted in a mass-bleaching event. This added stress probably contributed to the significantly higher rates of tissue loss for the *D. strigosa* in 1998 than during the following year.)

a. Prior to transformation



b. After log transformation

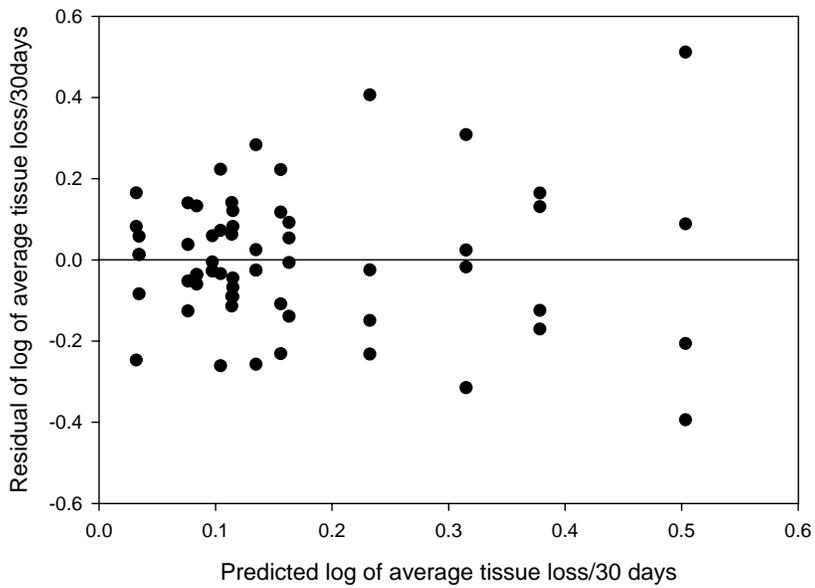


Figure 3.6. Plots of residuals vs. predicted average of tissue loss/30days before (a) and after log transformation (b) for *Diploria strigosa* (all colonies) in 1998 and 1999.

Table 3.1 Two-way ANOVA testing the three groups of *D. strigosa* and the treatments conducted in 1998 and 1999. Data was standardized to average tissue loss per 30 days and then log transformed to meet normality.

Source	DF	SS	MS	F-value	Pr>F
Model	14	0.98675445	0.0704826	1.93	0.0480
Error	46	1.68157432	0.03655596		
Corrected Total	60	2.66832877			

Source	DF	Type III SS	MS	F-value	Pr>F
Group	2	0.65734920	0.32867460	8.99	0.0005
Treatment	4	0.09924559	0.02481140	0.68	0.6102
Group*treatment	8	0.28372153	0.03546519	0.97	0.4709

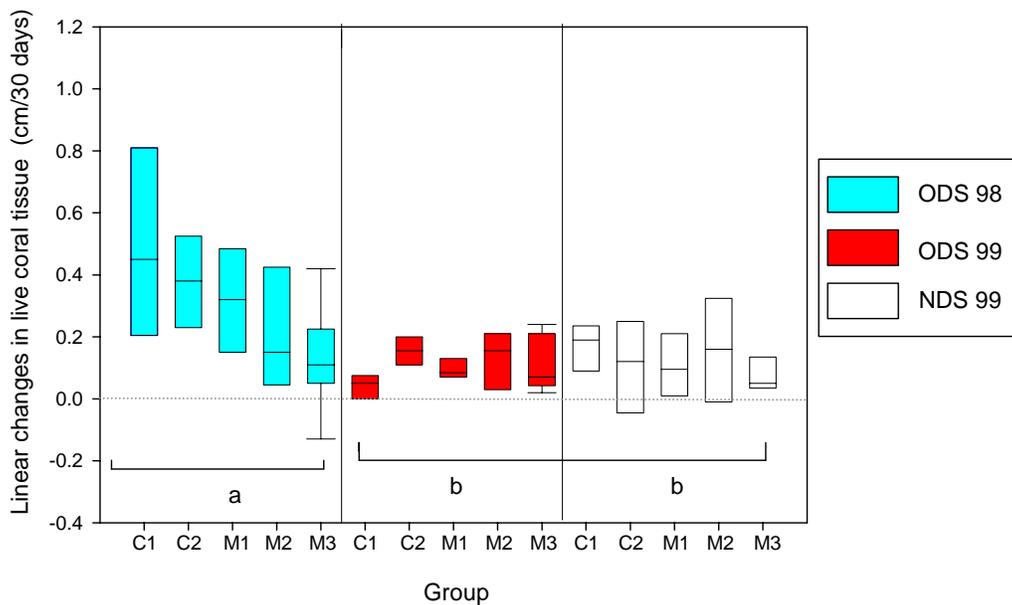


Figure 3.7. Linear changes in coral tissue between years and treatments in *Diploria strigosa*, 1998 and 1999. Groupings a and b indicate the groups between which there are significant differences according to the post-hoc Tukey's HSD test. Standard error bars appear only on those boxes that had more than five data points from which to calculate this statistic and horizontal bars represent the median statistic. (ODS98 – Old *D. strigosa* group in 1998, ODS99 – Old *D. strigosa* group in 1999, NDS99 – new *D. strigosa* group in 1999)

ii. ALL SPECIES 1999:

The two-way ANOVA to test for differences among the three coral species, the three treatments, and an interactive effect between the two factors from 1999, showed no significant differences in any of these categories (Table 3.2 and Figure 3.9). However, when the same analysis was conducted after the removal of an outlying datapoint from the M2 group in *M. faveolata* (plotted in Figure 3.9), there was a marginally significant interactive effect between species and treatments (Table 3.3), which also altered the significance of the difference between species in this second analysis. A post-hoc one-way ANOVA of only the interaction effects and Tukey's HSD test indicate that the only significant difference occurred between the *S. siderea* M2 (the group in which sediment was removed from the TAS mat) and *M. faveolata* C1 (the group in which the TAS mat was unmanipulated). The *S. siderea* M2 group is the only one in which coral tissues were able to consistently grow by displacing TAS mats compared to the *M. faveolata* C1 group, which experienced the most linear tissue loss (Figure 3.9).

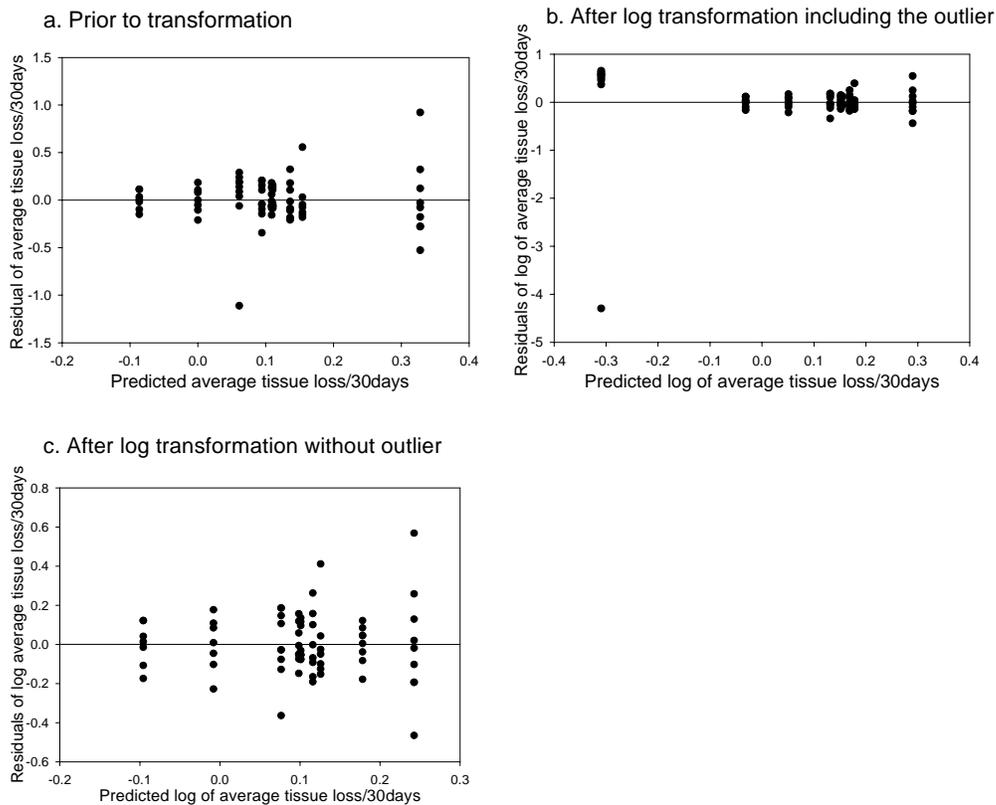


Figure 3.8. Plots of residuals vs. predicted average tissue loss/30 days before (a) and after log transformation of the data with the outlier (b) and without the outlier data point (c) for *M. faveolata* (tag #299) from dataset of all three species in 1999.

Table 3.2 Two-way ANOVA testing for differences between the three species and the three treatments (C1, M2, M3) in 1999. Data were standardized to average tissue loss per 30days and then log transformed to meet normality (with outlier).

Source	DF	SS	MS	F-value	Pr>F
Model	8	2.09705245	0.26213156	0.75	0.6740
Error	64	22.35499340	0.34929677		
Corrected total	72	24.45204584			

Source	DF	Type III SS	MS	F-value	Pr>F
Species	2	0.20207863	0.10103931	0.29	0.7498
Treatment	2	0.74972120	0.37486060	1.07	0.3480
Treatment*species	4	1.02963995	0.25740999	0.74	0.5702

Table 3.3 Two-way ANOVA testing for differences between the three species and the three treatments (C1, M2, M3), in 1999, without outlier. Data was standardized to average tissue loss per 30days and then log transformed to meet normality.

Source	DF	SS	MS	F-value	Pr>F
Model	8	0.59313178	0.07414147	2.65	0.0143
Error	63	1.76370125	0.02799526		
Corrected total	71	2.35683303			

Source	DF	Type III SS	MS	F-value	Pr>F
Treatment	2	0.02576831	0.01288416	0.46	0.6332
Species	2	0.29279591	0.14639795	5.23	0.0079
Treatment*species	4	0.27755462	0.06938865	2.48	0.0529 [^]

[^] Since the Treatment*species interaction is marginally significant, the corrected Type F value (for species) is 2.11 and is therefore not significant.

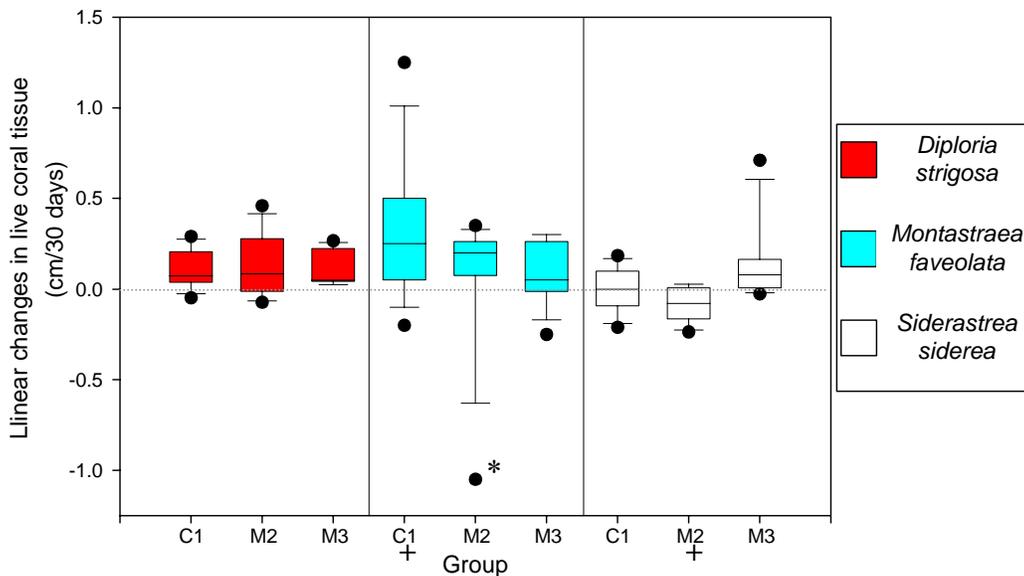


Figure 3.9. Linear changes in coral tissue between treatments in three stony corals, *Diploria strigosa*, *Montastraea faveolata* and *Siderastrea siderea*, 1999. Data has been graphed with standard error bars around the median and outliers.

* *M. faveolata* (tag#299) outlier is plotted here but was excluded from analysis

+ Only differences between these two groups are marginally significant

iii. LONG-TERM 1999-2001:

The three-way repeated measures ANOVA with interactions on the long-term data showed significant differences among species, treatments and over time but there were no interactive effects between these three main factors (Table 3.4). A post-hoc Tukey-Kramer test indicate that rate of tissue loss in *S. siderea* is significantly less than in the other two species (Figures 3.11 and 3.12), which lose tissues at a similar rate. Among treatments, the Tukey-Kramer showed a significant difference between C1 and M2, as control groups have lost the most tissues and the M2 groups (sediment removal from TAS mat) have lost the least (possibly due in large part due to the increase in tissues in the M2 group of *S. siderea*). The loss of tissue over time beginning in July 1999, is not significant by August of the same year, but is significant by the next time measurements were taken in March 2000, according to the post-hoc Tukey-Kramer.

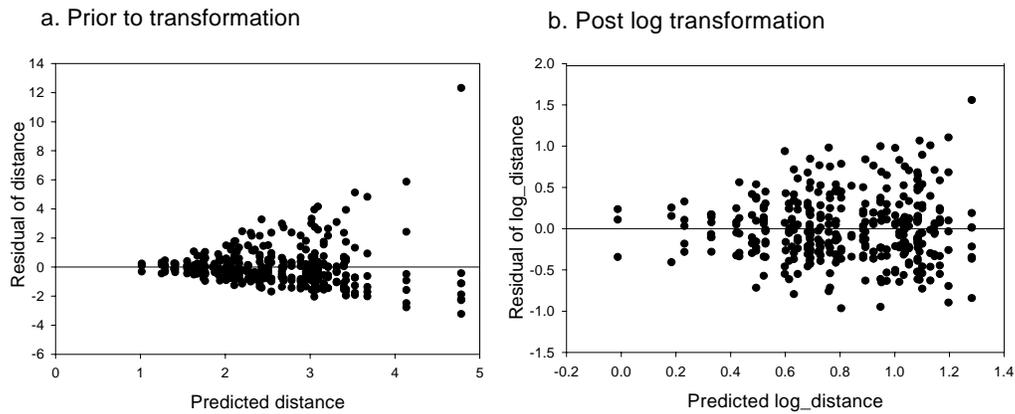
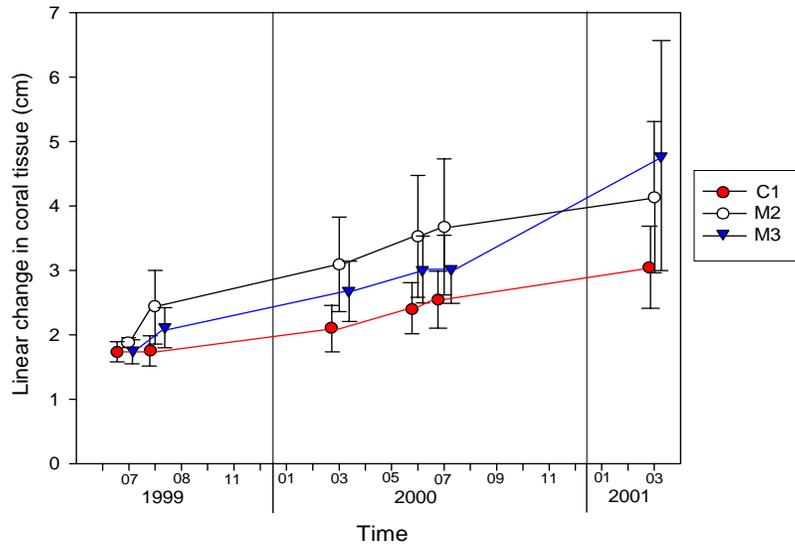


Figure 3.10. Plots of the residual versus the predicted distance before (a) and after the log transformation (b) of the long-term dataset of the loss of tissue over time in *D. strigosa*, *M. faveolata* and *S. siderea*, 1999-2001. (Outlier was excluded)

Table 3.4 Three-way, repeated measures ANOVA, testing for differences in the rates of tissue loss between July 1999 and March 2001, among species, over time and between the three treatments C1, M2 and M3. Data was log transformed to meet normality and the outlier datapoint (from *M. faveolata* tag #299) was excluded.

Effect	NumDF	DenDF	F-value	Pr>F
Species	2	304	18.78	<0.0001
Time	5	304	9.51	<0.0001
Treatment	2	304	5.56	0.0042
Species*time	10	304	0.24	0.9925
Treatment*species	4	304	2.01	0.0936
Treatment*time	10	304	0.60	0.8143
Treatment*species*time	20	304	0.35	0.9961

a. *D. strigosa*



b. *S. siderea*

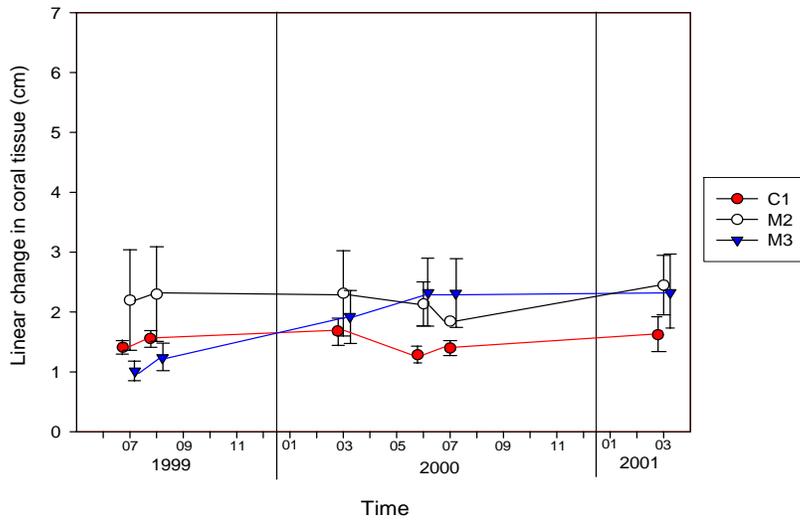
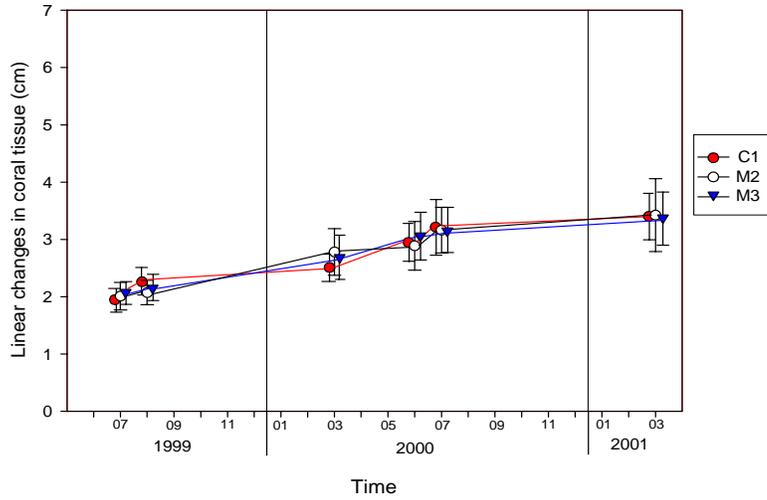


Figure 3.11. Linear changes between treatments in *Diploria strigosa* and *Siderastrea siderea* from July 1999 to March 2001. A post-hoc Tukey-Kramer test indicates that the rates of tissue loss between these two species is significantly different. Although all treatments were measured at the same time, they have been separated slightly to clarify the plots.

a. *M. faveolata*



b. *S. siderea*

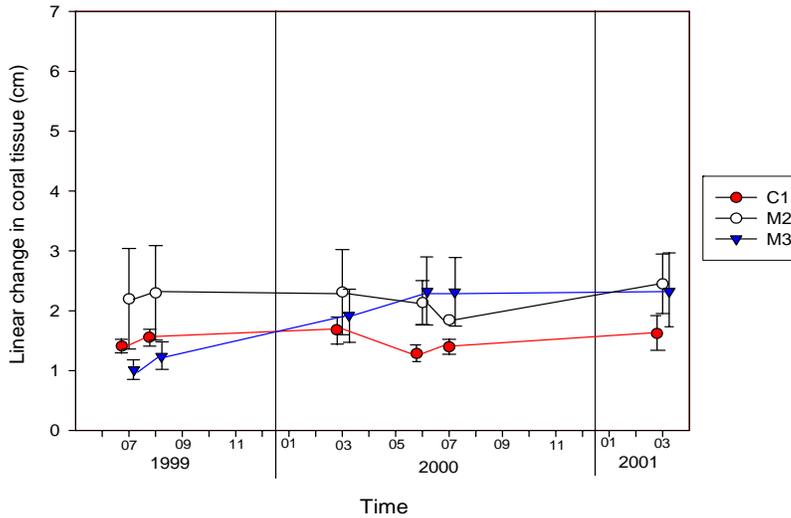


Figure 3.12. Linear changes between treatments in *Montastraea faveolata* and *Siderastrea siderea* (same data for the latter as shown in Figure 3.11) from July 1999 and March 2001. A post-hoc Tukey-Kramer test indicates that the rates of tissue loss between these two species is significantly different, however there were no significant differences between *D. strigosa* (in Figure 3.6) and *M. faveolata*. Although all treatments were measured at the same time, they have been separated slightly to clarify the plots.

C. PHOTOGRAPHY:

Data for five of the photographed *D. strigosa* at LR13 are incomplete. Although all tagged corals may have grown vertically, between 1998 and 2001 none of the remaining 37 corals showed any lateral expansion in live surface area, nor even maintained its original live tissue coverage. Including three that died by 2001 (e.g. *D. strigosa* tag #78, Figure 3.13), these 37 colonies lost an average of $70 \pm 13.2 \text{ cm}^2$ of live tissues/coral/year (Figure 3.14). (When only considering the eight C1 corals, the average tissue loss/coral/year is $67 \pm 35.48 \text{ cm}^2$.) However, the size of the colonies did not seem to play a role in their ability to compete with TAS mats, as the results of the simple regression (after linearization by log transformation), were not significant ($F = 0.54$, $P < 0.468$, $R^2 = 0.0151$, Figure 3.14).

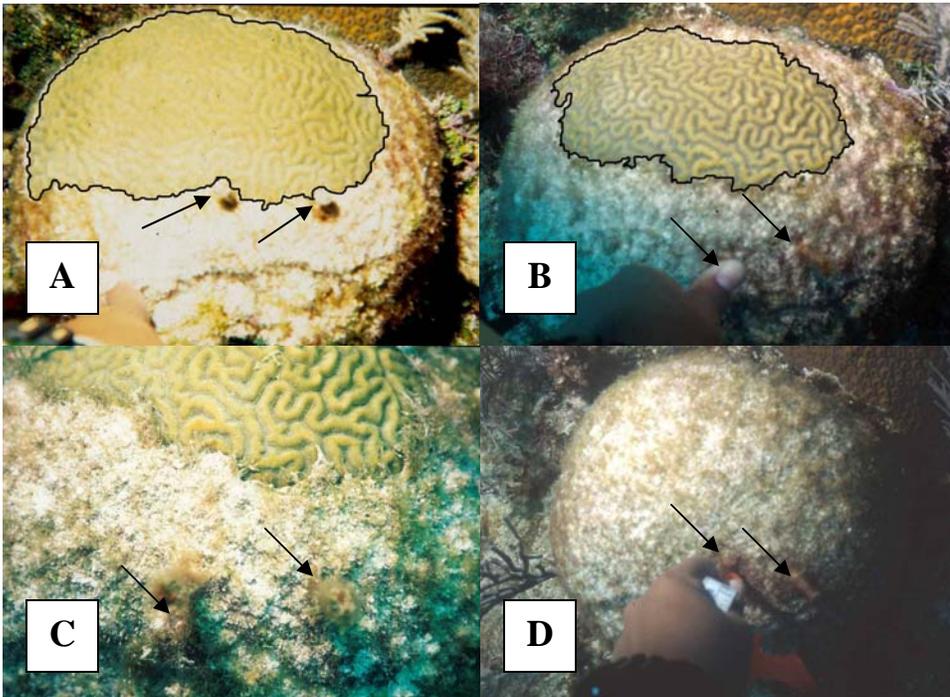


Figure 3.13. Time series photography of a colony of *Diploria strigosa* (tag#78) at Las Redes (13 m) that was completely surrounded by a turf algal/sediment (TAS) mat. Nails are shown by arrows and borders of live tissues outlined in A and B.
A Nails in TAS mat, 5 cm apart from each other and 1 cm from the live tissue, July 1998;
B Nails are now 4.4-4.5 cm from the live tissues July 1999;
C Close-up of sediment bound in turf-algal filaments, stretching across live tissue, August 1999;
D Whole colony has died, March 2000.

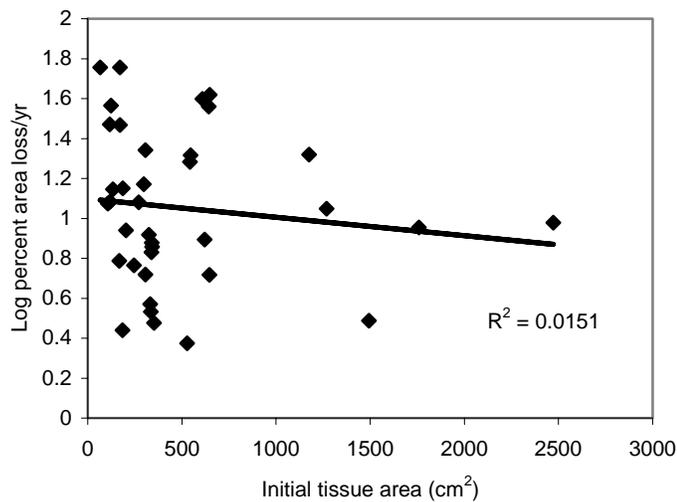


Figure 3.14. Log of area of live coral tissue lost per year in *D. strigosa* as a percent of the total area at the start of the experiment (n=37).

DISCUSSION

Close daily observations of the three ways in which TAS mats encroach over coral (detailed above) during the field seasons have lead me to believe that TAS mats are not simply opportunistic. Massive corals like *D. strigosa*, *M. faveolata* and *S. siderea* continue to expand laterally throughout life unless stressors like disease and physical damage reduce the energy available for growth (Meesters *et al.* 1994). Lateral expansion rates are also reduced when corals in contact with adjacent organisms engage in competition for space (Lang and Chornesky 1990). Since most corals overgrow algal turfs (*e.g.*, Fishelson 1973, Rogers *et al.* 1982, Lirman 2000), the steady attrition of their tissues at the interface of expanding TAS mats in the absence of other signs of damage or disease in 1999 and 2000 is a clear indication that the addition of sediments reverses the competitive outcome.

Other stressors may, however, exacerbate the interaction between TAS mats and corals. In 1998, ~2.5 to 3.5 cms of tissue around a majority of the *D. strigosa* corals that were 100% surrounded by TAS mats, were slightly paler than the tissues further in from the periphery (Figure 3.15). Presumably rates of photosynthesis by the zooxanthellae located along their margins were correspondingly reduced. This paling may have been a result of stresses associated with the elevated water temperatures (Figures 2.3 and 2.4) having been superimposed upon the energetic cost of the on-going competition with the TAS mats. Assuming the peripheral energetic requirements of these colonies were not

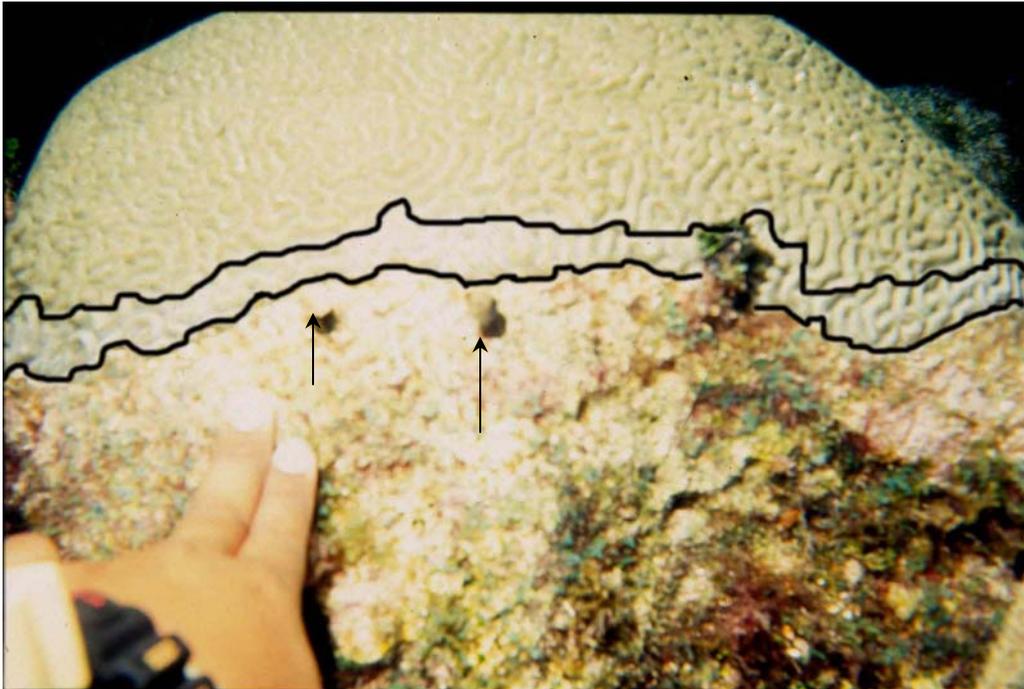


Figure 3.15. Photograph of a *Diploria strigosa* colony (Tag# 91), in 1998 with a ring of paler tissues around its edge indicated by the black lines. (Arrows indicate the two pins placed ~5 cm apart within the TAS mat area and ~1 cm from the border, indicated by the lower line, with the live *D. strigosa* tissues).

being met at this time, the higher rates of tissue loss in summer 1998 than the following summer for *D. strigosa* are perhaps explained.

Analysis of tissue loss among all three coral species in 1999 showed that there was only a marginally significant interactive effect between species and treatment. That post-hoc analyses indicated the largest differences occurred between the M2 group in which sediment was removed from the mat in *S. siderea* and the C1 control group in *M. faveolata* (Figure 3.9) suggests that the sediments entrapped in TAS mats play a significant role in their ability to encroach over *S. siderea*. That M2 was also the only group where the corals were able to extend their margins by displacing TAS mats, supports McCook (2001), in that turfs without trapped sediments are at disadvantage, at least in the case of *S. siderea*. Although caution is advised given that the possible effect was only marginally significant, the fact that it appeared in such a small experimental population leads me to believe that it is probably a real relationship.

My long-term dataset (Table 3.4, Figures 3.11 and 3.12) clearly validates Dustan (1977, 1999)'s earlier observations that TAS mats are capable of displacing live coral tissues. Differences among species, with *D. strigosa* and *M. faveolata* at the 13 m Las Redes reef incurring both significantly higher rates of tissue loss (Figure 3.11 and 3.12) and more frequent contact with TAS mats (Table 2.4) than neighboring colonies of *S. siderea*, have not been described previously. As these corals lose their live tissues, their ability to reproduce sexually is endangered, more so for the smaller *D. strigosa* colonies, than the

locally much larger *M. faveolata*. A third of 30 live experimental colonies of *D. strigosa* corals analyzed with the image analysis program were below the 195 cm² estimate of puberty size (Soong 1990), three of which fell below that minimal area during my study. Eventually, complete colony mortality can result (Figure 3.13), as also observed in three of the *D. strigosa*.

Colonies of *M. faveolata* are larger and, all else being equal, should persist longer, having greater resources for maintenance and regeneration (Highsmith *et al.* 1980, Hughes and Jackson 1985, Hughes and Connell 1987, Lirman 2001a). However, its populations on the Akumal-area reefs have been significantly affected by white plague and yellow-blotch diseases in recent years, and live cover by colonies of *M. faveolata* decreased by over 50% between 1998 and 2000 at Las Redes 13 m (figure 2.6). Even hardy *S. siderea*, known for its ability to recover from sediment damage (Torres and Morelock 2002) and, of the three species, apparently the only one capable of expanding over sediment-depleted TAS mats during short-term experiments (Figure 3.9), still lost tissues overall, albeit at significantly slower rates (Figures 3.11 and 3.12).

In trying to predict which corals are most threatened by TAS mats, it is necessary to understand the circumstances under which contact is reduced or avoided. All else being equal, close proximity to sand patches seems to increase exposure to suspended sediments and facilitate the formation of TAS mats, whereas height above the substratum has the opposite effect. Corals with near-vertical or vertical edges seem more able to maintain their space when in contact

with TAS mats (*pers. obs.*) possibly because it is harder for turf algae to trap sediments on steeply inclined surfaces than on horizontal substrata. Indeed, upright branching and foliose corals, like some branching acroporids and foliaceous agariciids, are completely surrounded by well-developed TAS mats less frequently than massive corals (Table 2.12). The mushroom growth-form of some small *Porites astreoides* found in shallow water (~2-13 m) where, due to the effects of bioerosion, only a small base remains attached to the substratum, also has the effect of reducing potential competition with TAS mats. Furthermore, over a two and a half year time period, I observed part of the edge of a *D. strigosa* which was in contact with a particularly thick TAS mat as it slowly turned upward, growing away from the contact area, suggesting that with enough time and low TAS mat encroachment rates, colonies of this species may be able to avoid this form of algal competition. These observations add more detail to relationships between coral morphology and benthic algae

With macroalgae, Hughes (1989) and Tanner (1995), proposed that massive, boulder coral morphology conferred an advantage against macroalgal overgrowth. They explained their results by reasoning that massive corals like *Diploria* and *Colpophyllia* have more of their tissues away from the periphery where it might come into contact with macroalgae compared to the encrusting and semi-encrusting forms of *Acropora* sp. and are therefore less likely to be overgrown.

Another important factor in predicting tissue loss due to algal overgrowth is the likelihood of damage and partial mortality within the live tissue borders of massive corals (Lirman 2001b). Partial-mortality disturbance events that are too small to kill entire stony corals result in dead patches (Meesters *et al.* 1996, Lirman 2000), which, if colonized by macroalgae, may successfully compete with the surrounding tissues (Lirman 2001b), particularly if grazers are scarce (e.g., Bythell *et al.* 1993). Turf algae also colonize lesions created by corallivores (Bak *et al.* 1977), herbivores (Diaz-Pulido and McCook 2002) or any other source of mechanical damage (Meesters and Bak 1993, Meesters *et al.* 1994). These patches of turf algae may bind sediment and, if a TAS mat forms, will similarly expand at the expense of the adjacent coral's tissues. When colonies are already regressing marginally from contact with TAS mats, as is true of *D. strigosa* corals on Las Redes (13 m) reef site, complete mortality of the colony (Figure 3.16) may be hastened.

Another factor that might be expected to affect the rate of tissue loss is colony size. However, it does not seem to confer an advantage (Figure 3.14). The lack of a clear relationship may be an indication that coral are unable to compete with TAS mats regardless of the available resources. It may also be that the size range and distribution of corals used here were too restricted. Our understanding would likely be enhanced by assessing the tissue lost at regular intervals rather than only as an average at the end of several years, as the latter does not provide any information as to the rate of tissue loss from a coral's entire perimeter.

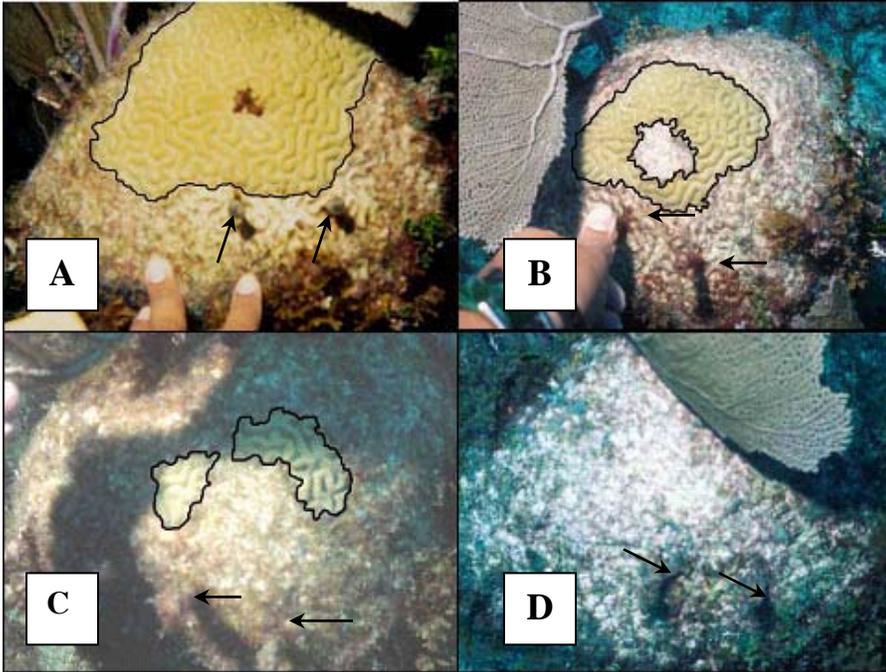


Figure 3.16. Time series photography of a *Diploria strigosa* coral (tag# 22).

A. Colony in 1998, with a *Spirobranchus giganteus* (tube-dwelling polychaete) near the center of the colony and a margin that is entirely surrounded by a TAS mat.

B. In 1999, coral #22 with only a TAS mat in the center (worm has disappeared) that is spreading outward as the TAS mat on the periphery is encroaching inward.

C. In 2000, two small patches of live tissue are left after the central TAS mat has merged with the one on the periphery.

D. By March 2001, the colony is completely dead.

Black lines in A-C outline the living tissues and arrows point to pins placed 5 cms apart and initially ~1 cm from the live tissue border in the peripheral TAS mat.

Variability in encroachment rates of TAS mats over the three studied coral species was highly variable under the various natural and experimental conditions. Some of this variation may be dependent on the specific composition of the turf algae in the mats and possible differences in their ability to tolerate or bind sediments, a question I began to address in Chapter Four (this dissertation).

I have observed that some TAS mats carry a much higher sediment load than others, which is likely have repercussions as to how easily the mats are grazed (Purcell 2000). The amount of sediment that was bound in the TAS mats also seemed to have an effect on its rate of encroachment (*pers. obs.*). Mats with extremely high sediment loads as a whole did not encroach very rapidly over coral in comparison to the other mats with less sediment. These new considerations of the specific character of the sediment load, and the algal composition of the TAS mats, also became the subject of further investigation in Chapter Four (this dissertation).

These results have significant implications for future management plans for Las Redes and similar sites. The rates of encroachment found in this study suggest that TAS mats are either a recent development locally or that their rates were much slower prior to this study given that *D. strigosa* and *M. faveolata* still occur in this area. However, the rates of tissue loss in these two species are not sustainable in the long run, especially in combination with the other stressors these species experience locally. Therefore, TAS mats must clearly be recognized

as a source of chronic stony coral tissue mortality today and should be included as such in future assessments of reef health.

Future research should include assessments of encroachment rates in conjunction with other disturbances given that it already seems as though thermal stress elevates rates of tissue loss. It would also be important to study the microbial component of TAS mats and the role that these mats might play in incubating pathogenic bacteria and disease outbreaks. Seasonality is also likely to be an important factor in predicting rates of tissue loss in corals. Information gathered from these lines of investigation would increase our predictive power and help assess longer term consequences for these reefs.

Chapter 4: The effects of sediment on the development and composition of turf algal/sediment (TAS) mats on the Las Redes reef in Akumal, México.

ABSTRACT

Turf algal/sediment (TAS) mats grown on tiles at 13 m in a reef off Akumal, México, responded to short-term changes in sediment loading during June – August, 2000. TAS mats were allowed to recruit to paired sets of terracotta tiles placed at the Las Redes fore-reef study site for a year prior to conducting an experiment in which sediment levels on half of the tiles were manipulated by either the addition or removal of sediment while adjacent controls were left unperturbed. Notwithstanding the passage of a tropical storm in the last few days of the experiment, both turf algal filament height (mean = 2.5 mm) and dry weight (mean = ~61 g/m²) were significantly and positively related to the amount of sediment still remaining on the tiles. Across treatments, sediment averaged 14 times the weight of the turf in which it was embedded.

A total of 61 species of rhodophytes, phaeophytes, chlorophytes and cyanobacteria were identified from both experimental tiles and natural rubble, 31 of which were not reported at these depths according to Littler and Littler (2000) and 15 of which are new reports for the Western Caribbean region, (Schneider and Searles 1991, Littler and Littler 2000). There were no significant differences between treatments in either species richness or species similarity of the turf

algae. Moreover, there were no significant effects of sediment manipulations on percent cover when all species that had recruited to the tiles were grouped by one of six cover types, the aggregate means for which are: larger turf algae = $36.7 \pm 35.5\%$; diminutive turf algae = $27.5 \pm 21.8\%$; macroalgae = $1.8 \pm 2.6\%$; encrusting cover = $28.4 \pm 21.1\%$; calcareous serpulid worms = $0.5 \pm 2.2\%$; and bare substrata (microalgae and protists) = $4.3 \pm 6.4\%$.

However, the treatments did have a significant effect on the frequency of occurrence of different algal and cyanobacterial genera. Whereas the cover of most genera was inversely related to the sediment load, that of a few genera was lower than controls in both treatments, and one genus (*Dichothrix*) had higher cover under both treatments. Three of the five genera that ran counter to main trends were also among the five most frequently occurring genera in controls, suggesting that sediment can influence the predominant composition of TAS mats. Though the causes of these idiosyncratic responses were not investigated, it is likely that the different sediment treatments altered competitive outcomes across genera.

INTRODUCTION

Turf algal communities are highly productive components of shallow coral reefs to depths of about 15 m (Odum and Odum 1955, Smith and Marsh 1973, Wanders 1977, Carpenter 1985). They can constitute a significant portion (from 100% at 1 m back reef sites to 30% at 10+ m, fore reef sites) of the live cover on a coral reef (Wanders 1976, Benayahu and Loya 1977, Carpenter 1981), and therefore are potentially major contributors to a reef's primary production (Johannes *et al.* 1972, Smith and Marsh 1973, Wanders 1977, Adey and Steneck 1985). Although the algae in these communities, which are also referred to as epilithic algal communities (Hatcher and Larkum 1983, Scott and Russ 1987), encompass a wide variety of growth habits, the modern definition of turf algae is restricted to those which are attached to the substrate by rhizoids and have erect filaments that are typically between 0.1 cm and 1 cm tall (Carpenter 1986, Airoidi 1988). However, in areas of potentially reduced herbivory, or even within damselfish territories, turf algal filaments can grow as tall as 3 cm, forming very dense mats (*pers. obs.*).

The abundance, distribution, density, and high productivity of the turf algal component of the phytobenthic community have been examined in some detail. Their development and maintenance at a given site have been explained by their ability to rapidly invade available substrate (Diaz-Pulido and McCook 2002), remove nutrients from the water-column across boundary layers (Littler and

Littler 1984, McCook 1999, McClanahan *et al.* 2002b), their response to light (van Tussenbroek and Collado Vides 2000), and season (Klumpp and McKinnon 1989, Ferreira *et al.* 1998, van Tussenbroek and Collado Vides 2000).

Grazing levels also affect the abundance and distribution of turf algal communities (Littler and Littler 1984, Carpenter 1986, Lewis 1986). Grazers range from associated mm-sized micrograzers like amphipods (Brawley and Adey 1981, Duffy and Hay 2000) to large (meter-sized) roaming herbivorous fishes (Ferreira *et al.* 1998). Nevertheless, turf algae can provide the dominant benthic algal cover on reefs with moderate levels of herbivory and/or high populations of territorial pomacentrids (damselfish) because of their ability to regenerate rapidly. Protection by damselfish not only limits grazing by other herbivores but also reduces competition from macroalgae, which the damselfish will remove from their territory. Moderate levels of grazing can enhance the productivity and biomass of turf algae (Brawley and Adey 1977, Carpenter 1983, Steneck 1988, Klumpp and Polunin 1989), as is often the case in damselfish gardens. Under high-rates of herbivory, as in the presence of the key Western Atlantic echinoid, *Diadema antillarum*, grazing-resistant crustose coralline algae, which are otherwise often outcompeted by turfs, (Hatcher 1983, Steneck 1997, van Tussenbroek and Collado Vides 2000), become dominant (Steneck and Dethier 1994 and Steneck 1997).

Unlike crustose coralline algae, many established colonies of stony corals are able to outcompete turfs. During regeneration corals can successfully overgrow

algal turfs that have settled on their skeletons at sites of damage (Fishelson 1973, McCook 2001), unless the lesion is too large relative to the area of their remaining live tissues (Loya 1976a, Meesters *et al.* 1994). However, as shown in Chapter 2 (this dissertation), turf algae that have entrapped and bound sediments to form turf algal/sediment (TAS) mats can kill stony corals, (as well as crustose coralline algae) and yet these mats have been largely unstudied (Steneck 1997).

Sediment can have several different effects on this phytobenthic community, which includes the smothering of turf algae (Adey and Goertmiller 1987, van Tussenbroek and Collado Vides 2000), and shifting the composition towards those macro and turf algal species that are more shade and burial tolerant (Gorostriaga and Diez 1996), like some ceramiaceous algae, *Pterosiphonia pennata* and *Champia parvula*. Sediment can also protect a turf algal community from grazing, as most herbivores are unable to tolerate much in their diets (Randall 1976, Purcell 2000), and may provide an important source of the limiting nutrient phosphorous. [Turf algae can potentially take advantage of the small amounts of soluble phosphorus released during the breakdown of insoluble apatite (Smith *et al.* 1978, Entsch *et al.* 1983) and the breakdown of organic detritus (Purcell and Bellwood 2001) by microorganisms present in coral reef sediments.]

TAS mats develop as the turf algae bind sediments settling out of suspension in the water column. Such accumulation can occur under conditions of extremely high local re-suspension from local water flow (Airoldi *et al.* 1996), particularly during storms that can temporarily create enough surge to resuspend bottom

sediments and, as during hurricanes, even translocate large amounts of sediment across reef systems (e.g. van Tussenbroek and Collado Vides 2000, for the effects of hurricane Roxanne in the Mexican Caribbean). These processes have been recorded locally on the shallow Las Redes fore reef and are considered among the more important contributing factors to the high frequency of TAS mats on reefs off Akumal, México (Chapter 2 this dissertation).

During this investigation, I had noted qualitative differences in the types of TAS mats surrounding the monitored corals. Some of the mats had a relatively high load of accumulated sediment, which obscured the algal filaments, while others had less sediment and a more clearly visible, dense stand of erect filaments. Mats with the higher sediment load seemed to be closer to the grooves or other pockets in which sediments were relatively abundant and easily re-suspended, such as in the grooves of the reef, while mats with less sediments were usually on the tops of the spurs and relatively distant from areas of sediment accumulation.

Relatively high and low amounts of sediment in TAS mats seems to result in slower rates of encroachment over corals compared to intermediate levels of sediment (*pers. obs.*) For example, in one particular case, a *D. strigosa* coral in contact with a very sediment-rich TAS mat was able to grow away from contact with the mat by turning upward. It is also possible that sediment-related differences in encroachment rates are related to the composition of the algae in the TAS mats, should turf algae vary in their ability to tolerate shading and burial as suggested by Gorostriga and Diez (1996).

Kendrick (1991), has already elucidated some relationships between sediment loading and scouring conditions on the recruitment of turf algae, in a shallow (> 3 m deep) lagoon in the Galapagos. Turf algal biomass was significantly lower under scouring conditions, (which were dominated by crustose coralline algae), than the different sediment treatments and the unmanipulated control. Although it was the highest in the sediment removal treatment, turf algal biomass was not significantly different from that in the sediment addition treatment. Differences in sediment loading also caused a shift in the dominant recruiting algal species. Building on these results and those from Chapters 2 and 3 (this dissertation), it is important to study the effect of sediment on developed turf algal communities, especially within the context of TAS mats.

GOALS

TAS mats are a common component of the phytobenthic cover in the Las Redes 13 m reef, where they are also in contact with a large proportion of the corals at this site (Chapters 2 and 3 this dissertation). By experimentally manipulating the sediment loads in TAS mats growing on artificial substrata under natural conditions, I sought to better understand those characteristics of the turf algae, in particular their biomass and species composition, that may help us to better understand why some TAS mats appear to encroach on stony corals more rapidly than others.

MATERIALS AND METHODS

FIELD WORK – PREPARATION AND EXPERIMENTATION:

In July 1999, 10 porous terracotta tiles (each 15 cm x 15 cm) were cut with a tile-cutting water saw into four equally sized pieces (7.5 cm x 7.5 cm).

Unfortunately, one of the smaller tiles was broken during the cutting process leaving only 39 tiles. These were soaked in seawater for over 48 hours to allow any chemicals as might prevent recruitment of turf algae to leach out and to saturate the tiles with seawater in preparation for their use as settling plates. The tiles were taken to the 13 m Las Redes reef study site (Chapter Two), where locations for placement were chosen randomly (by swimming randomly generated pairs of compass headings and kick-cycles). Each location was recorded on a map of the study site. The tiles were affixed in pairs within the nearest TAS mat, using the underwater cement, Z-spar, after appropriately sized areas had been scoured clean with a wire brush to ensure firm attachment.

Pairing of tiles allowed one to be used as a control while its pair was manipulated with one of the two treatments, either sediment addition (M1) or sediment removal (M2). This design was intended to control for small-scale variations in the turf algal communities as differences in their species composition might occur even over distances as short as a few meters. The odd tile was included with the last pair of tiles cemented to the reef.

The 18 pairs of tiles and one set of three tiles were allowed to recruit TAS mats from July 26, 1999, to June 8, 2000, when the experiment was started. These 39 tiles were randomly allocated into one of the following two groups:

(a) For 15 pairs - one tile in each pair was the control (unmanipulated) and the other either had ~ 100 g of sediment added (M1 n=7 pairs) or had the sediment removed by lightly dusting the TAS mat (M2 n=8 pairs e.g. Figure 4.1) to artificially create TAS mats with different sediment loads.

(b) In case the TAS mats were more homogeneous in species composition than suspected, the remaining tiles had either M1 (n=4) and M2 (n=5) treatments to increase the replicate size of manipulated tiles which could be compared to the controls in the paired tiles. (Data from these tiles were only used to find averages for treatments M1 and M2 overall and not analyzed as part of the paired design)

The tiles were manipulated at least twice a week to maintain the experimental conditions through August 8, 2000, when they were collected just hours after a tropical storm had passed through the area. Unfortunately this storm not only resuspended and redistributed substantial amounts of sediment, presumably also displacing sediment-associated, invertebrate microfauna across the study site but it also destroyed four tiles. Two controls and one treatment tile from the paired M1 group and one treatment tile from the unpaired M1 group were broken, turned over or washed away.

The remaining 35 intact tiles (paired tiles: M1 n=4 and M2 n=8, unpaired tiles: M1 n=5 and M2 n=5, when including two M1 treatment tiles as their paired controls were lost and the one, now unpaired, control tile), were gently detached from the reef surface using a chisel and hammer, and carefully placed in a pre-labeled Ziploc bag while minimizing any disturbance to its TAS mat. Three pieces of loose rubble covered with TAS mats were also collected to compare the composition of their turf algal communities with those on the tiles. Once at the surface, the samples were fixed in seawater and 4% formaldehyde for transport to the laboratory and subsequent storage prior to analysis. During transport, the unpaired control tile was broken but I was able to remove its TAS mat and sediment components for weighing as described in section C below, now leaving a total of 34 tiles.

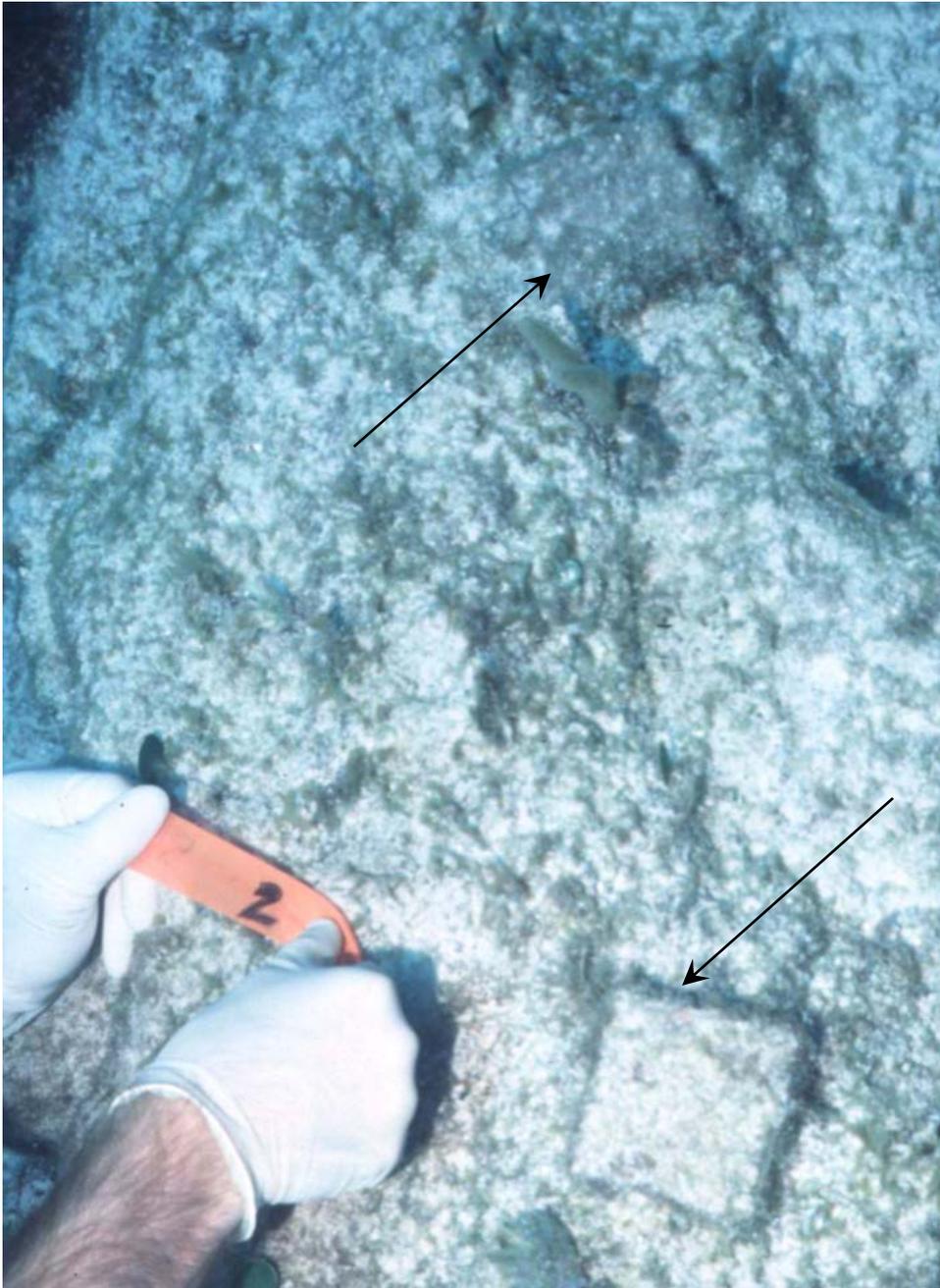


Figure 4.1. Paired tiles at the start of manipulations on Las Redes reef (13 m), June 2000. Arrows are pointing to tiles of Pair #2 – upper tile has its sediment removed and lower tile is the control.

A. BENTHIC COVER ON THE INTACT TILES:

Each of the remaining 34 tiles was washed several times with a fresh solution of 31⁰/₀₀ Instant Ocean (hereafter referred to as seawater) and lightly dusted with fingertips to transfer as much sediment and associated invertebrates as possible from the attached turf algae into a 200 µm mesh sieve. The tiles were then placed in lidded, plastic Ziploc containers, with seawater and 4% formaldehyde, making sure that all the algae were fully submerged. Materials collected in the sieve were transferred to labeled screw-cap vials which also contained the same seawater-formaldehyde solution.

To assess the cover of benthic organisms on the tiles, 50 sample points (circles, each 2 mm in diameter), were randomly plotted on a graph (7.5 x 7.5 cm to match the dimensions of the tile), using two sets of randomly generated numbers as Cartesian co-ordinates. This procedure was repeated 18 times to give 18 patterns of randomly placed sampling points and printed out as 6 patterns/transparency. A haphazardly chosen pattern was then laid over a tile and the presence/absence within each of the 50 circles was identified and recorded according to the following categories:

1. Macroalgae
2. Larger turf algae - more than 1-10 mm tall
3. Diminutive turf algae - <1mm tall
4. Encrusting cover - crustose coralline algae and encrusting elionid sponges

5. Serpulids (calcareous tube-worms)

6. Bare substrata (-microalgae and protists)

(At this time an unpaired M2 tile was also lost, leaving only 33 complete tiles for further analysis.)

To determine adequacy of sampling, this procedure was initially performed using only 20, 30 or 40 circles per sampling point pattern for three randomly selected tiles and then this procedure was repeated with each of 30, 40 or 50 random circles on another three tiles. Percent cover did not change markedly above 40 points/tile, therefore fifty data points were considered an adequate sampling size (Table 4.1).

B. ALGAL IDENTIFICATIONS:

Six randomly located samples, each 0.25 cm x 0.25 cm, were scraped off each of the 33 tiles and from each of the three pieces of rubble with a razor blade. These were placed in separate, labeled, screw-cap vials. This sampling effort was considered adequate based on the results for the first six tiles examined among which there was a low occurrence of new species by the sixth sample (Table 4.2). Directly comparable data on cover, turf algal height and turf algal weight/unit area, and sediment load/unit area could not be collected for the rubble given their irregularities of size, shape and surface morphology relative to the tiles.

Samples were decalcified in 5% hydrochloric (HCl) acid solution for at least 24 hours before mounting in a Palmer–Maloney chamber cell for identification

under a Zeiss upright light microscope. Digital images were captured with a ProgRes3008 camera and manipulated in Adobe Photoshop 7.0. Measurements of filament diameter, segment length, branching intervals and reproductive bodies as appropriate, were recorded to ensure that identifications were consistent. Algae were identified to species where possible, using four keys (Taylor 1976, Woelkerling 1976, Schneider and Searles 1991, Littler and Littler 2000), and their presence was recorded (as their growth habits preclude the identification of individuals). Algae that could not be identified were designated as unknowns.

C. TURF ALGAL HEIGHT AND WEIGHT MEASUREMENTS:

Prior to the sampling in B, each tile had been placed in a clear container with a solution of fresh seawater and 4% formaldehyde. Ten measurements of turf algal filament height had been haphazardly made with a transparent plastic ruler. After sampling in B, each of the 33 tiles was meticulously scraped with a razor blade, either to its surface or to the surface of any encrusting cover. The detached material was washed with seawater into a 200 μm mesh sieve. (Adjustments were made in subsequent calculations for the six 0.25 cm^2 samples of tile cover removed from each tile for algal identifications in section B). Materials collected in the sieve were transferred to a labeled, vial and decalcified with 5% HCl acid solution for at least 72 hours, to remove any calcium carbonate sediments that were still bound to the turf algae. In some larger samples, the neutralized solution had to be partially exchanged with fresh acid to dissolve remaining debris.

Table 4.1 Assessment of sampling effort on benthic cover estimates for six, randomly chosen tiles. The type of cover was determined within 20, 30, 40 or 50, 2 mm diameter circles that had been randomly plotted on a graph matching the dimensions of the tiles. Data is shown as percent cover.

Tile ID (treatment)	<u>14</u> (M2)			<u>16</u> (M2)			<u>18</u> (M2)			<u>3</u> (M1)			<u>13</u> (M1)			<u>17</u> (C)		
Sample (#)	20	30	40	20	30	40	20	30	40	30	40	50	30	40	50	30	40	50
Macroalgae															2			
Larger turf algae				100	100	92.5	5	0	7.5				20	32.5	28	6.7	10	8
Diminutive turf algae	50	53.3	57.5				55	50	37.5	80	85	80	46.7	37.5	44	56.7	47.5	44
Encrusting cover	50	46.7	42.5				35	43.3	47.5	20	15	20	26.7	20	18	36.6	42.5	44
Serpulid (calcareous tube-worm)																		4
Bare substrata						7.5	5	6.7	7.5				6.6	10	8			

Table 4.2 Assessment of sampling effort on detection of species present on a single tile. Each sample was a randomly chosen 0.25 cm x 0.25 cm portion of the tile. Values given are numbers of new species recorded with each successive sample that had not been recorded in previous samples of the same tile.

Sample order	Tile ID (treatment)					
	4 (C)	6(M2)	11(M2)	13(M2)	20(M1)	7(C)
First	5	3	6	5	3	10
Second	7	1	0	1	0	5
Third	2	2	2	2	2	5
Fourth	0	1	4	4	4	3
Fifth	4	0	1	2	1	1
Sixth	1	2	2	1	0	1

After decalcification, the turf algal samples in each vial were drained, transferred to pre-weighed pieces of aluminum foil and weighed to obtain algal wet weights. They were then placed in an oven at 70⁰C and dried to constant weight (for at least 24 hours) to obtain algal dry weights. (Adjustments were made in the subsequent calculations for the previously described six samples of the tile cover removed from each tile in section B). Material from the broken control tile was also used in this section, bringing the sample size to 34.

D. SEDIMENT WEIGHT:

Sediment samples from each of the 33 tiles were transferred to pre-weighed aluminum foil trays and dried at 70⁰C for at least 24 hours, to constant weight. The sample from the broken control tile was also used in this section, bringing the sample size to 34.

E. ENCRUSTING COVER ON SCRAPED TILES:

Removal of all the upright algae and TAS mats from the 33 remaining intact tiles exposed any underlying crustose coralline algae and encrusting clionid sponges that are otherwise obscured *in-situ* by erect organisms of the benthic community. Thus I took advantage of the opportunity to directly re-measure the percentage of encrusting cover on each tile, using the circle plot graphs described above in A, for comparison with the initial estimates for the intact tiles.

STATISTICS:

I. EFFECT OF TREATMENTS ON (TYPE OF) BENTHIC COVER

Given the paired design, the dependant variable was calculated as the differences in average percentage of cover on the tiles for the six different categories of organisms between the manipulation and its paired control. This yielded dependant variables that were either M1 (add sediment – control, n=4) or M2 (remove sediment – control, n=8) across six cover types. Data were analyzed by one-way MANOVA with two treatment levels, in PAST version 1.15 (Hammer *et al.* 2000) as well as a principle component analysis in SAS version 8.2.

II. PHYSICAL CHARACTERISTICS OF TURF ALGAE AND SEDIMENT LOAD

i. EFFECT OF TREATMENTS ON PHYSICAL CHARACTERISTICS OF TAS MATS

The dependant variable was calculated as the differences in average turf algal filament height, dry weight and trapped sediment weight between the manipulation and its paired control tile. This yielded dependant variables that were either M1 (add sediment – control, n=4) or M2 (remove sediment – control, n=8) across these three physical parameters. Data were analyzed by one-way

MANOVA with two treatment levels, in PAST version 1.15 (Hammer *et al.* 2000) as well as a principle component analysis in SAS version 8.2.

ii. GENERAL RELATIONSHIPS BETWEEN PHYSICAL CHARACTERISTICS OF TAS MATS

To ascertain general relationships between turf algal filament height and algal dry weight, with sediment dry weight, regardless of treatment, simple linear regressions were conducted in Excel 2000.

III. EFFECT OF TREATMENTS ON SPECIES COMPOSITION

Differences in turf algal species composition were assessed in three ways:

i. GENUS-LEVEL EFFECTS

Differences in the average frequency of occurrence of algal genera between paired tiles was assessed. These data were obtained as follows. The six presence/absence datapoints for each genus, per tile, were used to compute a frequency of occurrence/cm² of that genus for each tile. These data were then used to find the mean difference between treatment-control pairs in the frequency of occurrence/cm² of each genus. A Wilcoxon signed rank test was conducted on the differences in the average frequencies of occurrence of each genus between treatments to assess treatment effects at the genus level.

For a general view of the composition of TAS mats, the overall average of frequency of occurrence at the genus level was also calculated, using all M1 tiles (n=9), M2 tiles (n=12) and control tiles (n=12) by ignoring the paired design.

ii. SPECIES SIMILARITY

Because of the very high variance in species presence (most being rare), it was not appropriate to perform a test for detailed effects. However, the data were amenable to an overall test for the species similarity between control and treatment tiles within the same pair. The algal species presence/absence data were used to obtain Dice, Jacard, Simpson association similarity indices by comparing random pairings of samples from the control and its paired manipulation using PAST version 1.15 (Hammer *et al.* 2001). This provided six similarity index values for each set of paired tiles within the treatment group M1 (add sediment n=4 pairs) or M2 (remove sediment n=8 pairs). These similarity index values were used as characteristic differences between the paired tiles and submitted to a one-way, fixed effects, repeated measures ANOVA in SAS version 8.2 (as were all other ANOVAs in this chapter).

iii. SPECIES RICHNESS

A second type of overall comparison could be made for species richness (again ignoring the detailed responses for each species individually as most were too rare to occur on every experimental tile). The differences in average number of species/cm² between paired tiles, either M1 (add sediment – control, n=4 pairs) or M2 (remove sediment – control, n=8 pairs), was submitted to a one-way ANOVA. The dataset was log transformed to comply with normality.

IV. ASSESSING FIELD UNDERESTIMATIONS OF ENCRUSTING COVER

Estimates of the percentage of encrusting cover in a benthic community in the presence of canopy organisms (similar to field estimates of undisturbed substrata) can vary greatly from more accurate estimates of their cover in the absence of the same. To assess the level of disparity, a two-sample t-test (in SAS version 8.2), was conducted on the average percentage of encrusting cover before and after all the other types of erect, obscuring cover (except tube worms and sponges) were removed by hand.

RESULTS

I. EFFECT OF TREATMENTS ON (TYPE OF) BENTHIC COVER

The average differences between manipulated tiles and their paired controls in the percent coverage of the six benthic categories showed the following trends: overall the cover seemed higher for larger turf algae when the sediment was removed and for encrusting cover when sediment was added (Figure 4.2). However, the variances for all categories within each treatment were large, and the MANOVA detected no significant treatment effects in the percent coverage of these six categories of benthic organisms (Table 4.3). The principle component analysis supports the MANOVA, in showing that the manipulations M1 and M2 do not significantly fall out into clusters (Table 4.4 and Figure 4.3).

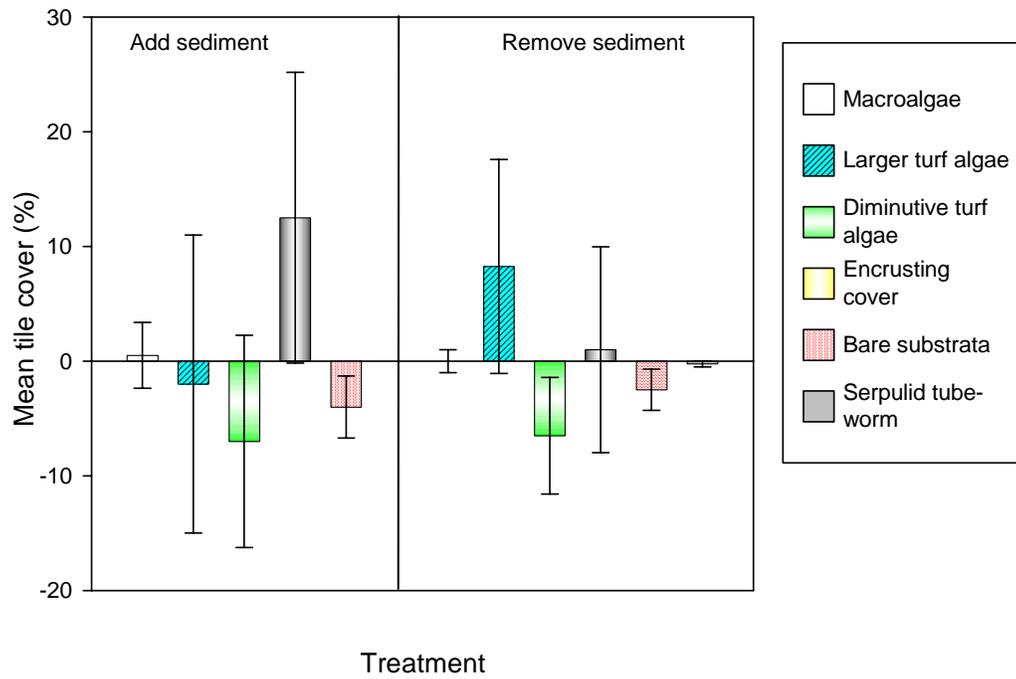


Figure 4.2. Average changes in types of benthic cover between manipulations and their paired controls (M1 Add sediments n=4, M2 Remove sediments n=8).

Table 4.3 One-way MANOVA on the differences between the manipulation and its paired control in the averages of the six benthic cover types.

Wilk's lambda	0.6857
Df1	6
Df 2	5
F-value	0.3819
p (same)	0.8636
Eigenvalue 1	0.4546
Eigenvalue 2	0.0001107

Table 4.4 Correlation matrix of the principle component analysis of the differences in the percent of the different types of benthic cover on tiles, between paired tiles, for treatments M1 (n=4) and M2 (n=8).

	Larger turf algae	Diminutive turf algae	Macroalgae	Encrusting cover	Bare substrata	Calcareous serpulid worm
Larger turf algae	1.0000	-0.1046	-0.5386	-0.7934	-0.4785	0.2813
Diminutive turf algae		1.0000	0.0473	-0.4760	-0.1936	0.5319
Macroalgae			1.0000	0.2977	0.3763	0.0140
Encrusting cover				1.0000	0.3547	0.5973
Bare substrata					1.0000	-0.1886
Calcareous serpulid worm						1.0000

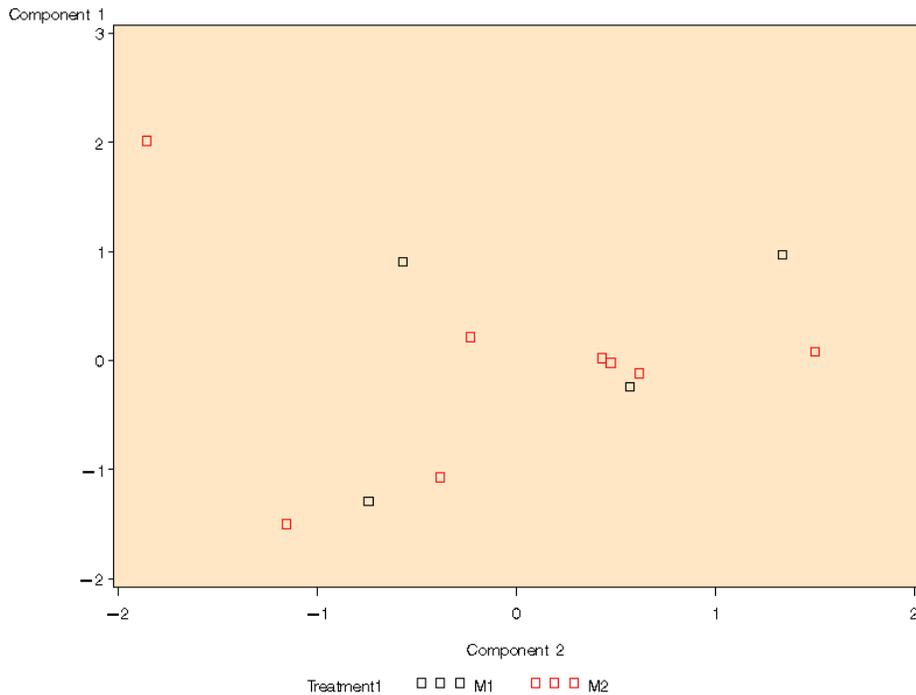


Figure 4.3 Graph of principle component analysis for correlations between the differences in the percentage of different types of benthic cover on tiles, between paired tiles, for treatments M1 and M2. (Component 1 – Larger turf algae, component 2 – Diminutive turf algae)

II PHYSICAL CHARACTERISTICS OF TURF ALGAE AND ITS SEDIMENT LOAD

i. EFFECT OF TREATMENTS ON PHYSICAL CHARACTERISTICS OF TAS MATS

The MANOVA showed no overall significant effect of treatments on the differences in average turf algal filament height, algal dry weight and sediment weight between paired tiles (Table 4.5). The principle component analysis supports the MANOVA, in showing that manipulations M1 and M2 do not fall out into clusters (Table 4.6 and Figure 4.4).

ii. GENERAL RELATIONSHIPS BETWEEN PHYSICAL CHARACTERISTICS OF TAS MATS

When the paired design was ignored and all the information for a treatment was averaged, the mean turf algal dry weight (± 1 standard deviation) was $88 \pm 117.4 \text{ g/m}^2$ on tiles to which sediment had been added (all M1 tiles $n=9$), $54 \pm 94.4 \text{ g/m}^2$ on those from which sediment had been removed (all M2 tiles $n=12$), and $57 \pm 114.4 \text{ g/m}^2$ in the controls (all control tiles $n=12$). Corresponding values for sediment dry weight averaged $599.1 \pm 726.7 \text{ g/m}^2$ on the sediment addition tiles, $367.1 \pm 631.6 \text{ g/m}^2$ on the sediment removal tiles, and $506.8 \pm 587.4 \text{ g/m}^2$ in the controls. Sediment weight was, on average, 14.4 times higher than the turf algal biomass by which it was entrapped. It was also positively related to the average turf algal filament height ($R^2=0.325$ $F=14.924$ $p<0.001$, $n=33$, Figure 4.5), and turf algal dry weight ($R^2=0.5172$ $F=34.279$ $p<0.000$, $n=34$, Figure 4.6).

Table 4.5 One-way MANOVA on the differences between the manipulation and its paired control in the averages of three TAS mat physical parameters (turf algal filament height, algal dry weight and sediment weight), M1 (n=4) and M2 (n=8).

Wilk's lambda	0.7294
Df1	3
Df 2	8
F-value	0.9895
p (same)	0.4453
Eigenvalue 1	0.371
Eigenvalue 2	0.00001973

Table 4.6. Correlation matrix of the principle component analysis for the differences in the average algal filament height, algal dry weight g/cm² and sediment dry weight g/cm² between paired tiles for the treatments M1 and M2.

	Average filament height	Average algal dry weight	Average sediment dry weight
Average filament height	1.00	0.5712	0.2534
Average algal dry weight		1.00	-0.0251
Average sediment dry weight			1.00

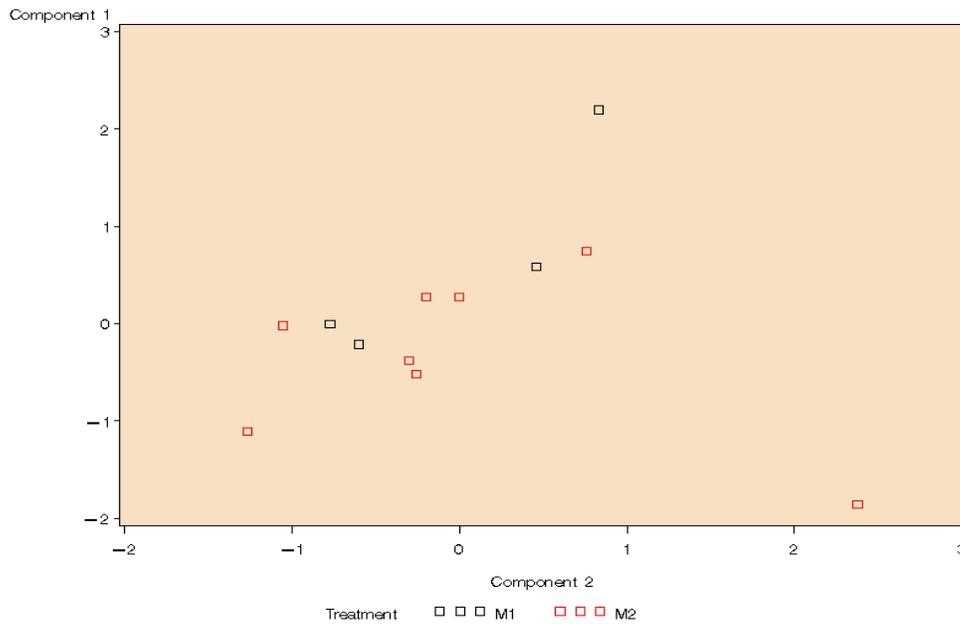


Figure 4.4. Graph of principle component analysis for correlations between differences in the average algal filament height, algal dry weight (g/cm²) and sediment dry weight (g/cm²), between paired tiles, for the treatments M1 and M2. (Components 1 and 2 are the first two of the three parameters mentioned.)

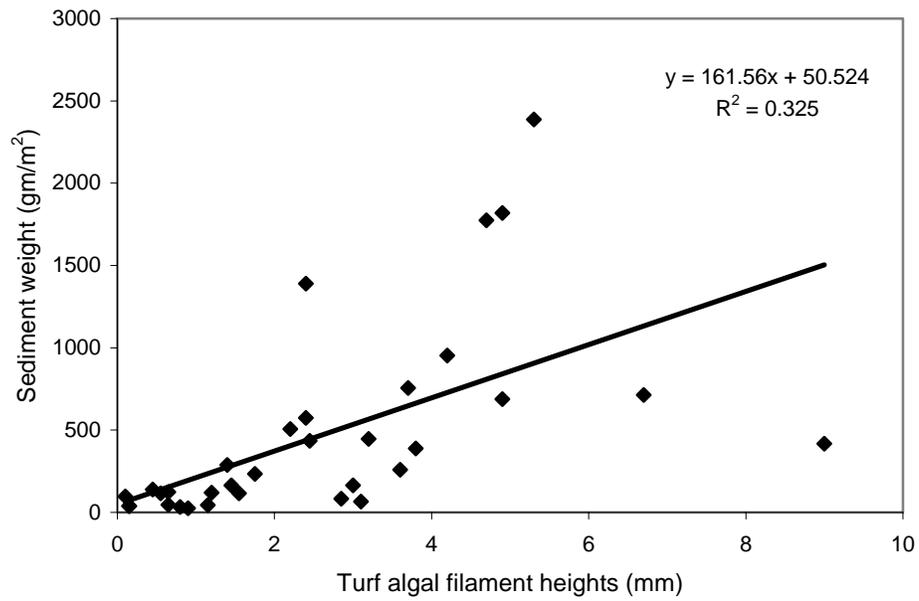


Figure 4.5. Simple linear regression of turf algal filament height by sediment weight (n=33).

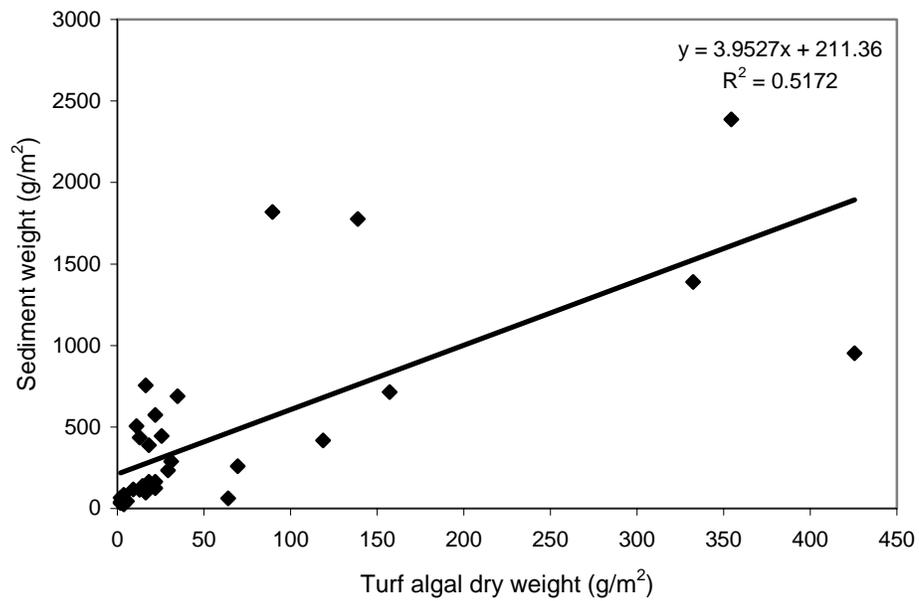


Figure 4.6. Simple linear regression of turf algal dry weight by sediment weight (n=34)

III. EFFECT OF TREATMENTS ON SPECIES COMPOSITION

i. GENUS LEVEL EFFECTS

There was a significant effect of sediment manipulations on turf-algal community composition when measured at the genus level (Wilcoxon signed ranks test, $w=2.92$, two-tailed $p=0.00273$). Although this test does not allow for detailed post-hoc analyses, inspection of the rankings indicates substantial differences in response to treatments across genera (Figure 4.7 and Table 4.7).

The greatest differences in frequency of occurrence between treatments were in the genera *Jania*, *Polysiphonia*, *Pleonopodium* and *Gelidiopsis*. Overall, *Jania*, *Polysiphonia*, *Wurdemannia* and 12 other genera were more frequently found on tiles with reduced sediments relative to their paired controls, whereas *Lophosiphonia* and *Herposiphonia* (rhodophytes), and *Cladophora* (a chlorophyte) occurred far less frequently under lower sediment levels. On tiles with added sediment, as with most (80%) algal genera, the frequency of occurrence of *Ceramium* and *Digenea* (which are both rhodophytes) was lower relative to their paired control tiles. *Dichothrix* (a cyanobacteria), *Amphiroa* and *Jania* (branching coralline rhodophytes), were exceptions, showing higher frequencies under higher levels of sediment. *Lyngba* was less frequent under both experimental conditions in comparison to its paired controls. The four genera, *Polysiphonia*, *Cladophora*, *Herposiphonia* and *Lophosiphonia*, which show the greatest difference in occurrence between treatments, are among the top five most commonly occurring genera in controls (Table 4.8).

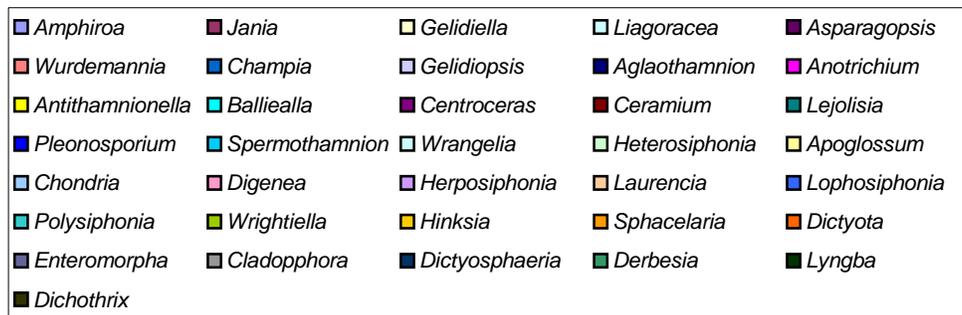
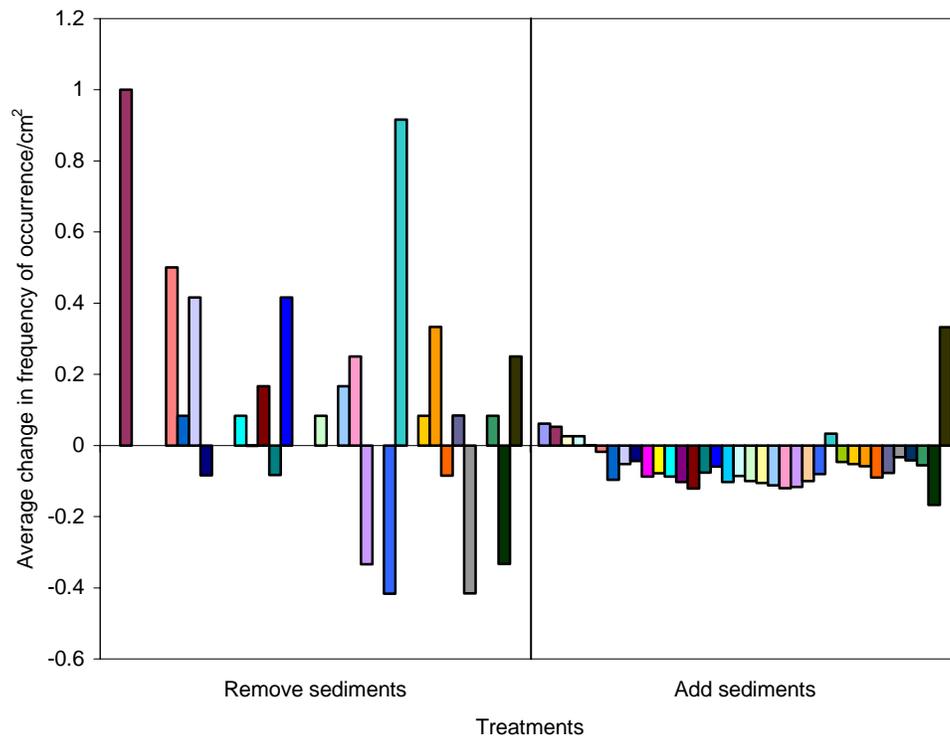


Figure. 4.7. Differences in frequencies of algal and cyanobacterial genera based on differences between controls and their paired manipulations, M1 (n=4) and M2 (n=8).

TABLE 4.7 Differences in average frequency of occurrence of algal and cyanobacterial genera/cm² between manipulated tiles and their paired controls.

Genus	Frequency of occurrence/cm ²	
	Remove sediments	Add sediments
RHODOPHYTA		
<i>Amphiroa</i>	0	0.06
<i>Jania</i>	1	0.05
<i>Gelidiella</i>	0	0.03
<i>Liagoracea</i>	0	0.03
<i>Asparagopsis</i>	0	0
<i>Wurdemannia</i>	0.05	-0.02
<i>Champia</i>	0.08	-0.1
<i>Gelidiopsis</i>	0.42	-0.05
<i>Aglaothamnion</i>	-0.08	-0.04
<i>Anotrichium</i>	0	-0.09
<i>Antithamnionella</i>	0	-0.08
<i>Balliealla</i>	0.08	-0.09
<i>Centroceras</i>	0	-0.1
<i>Ceramium</i>	0.17	-0.12
<i>Lejolisia</i>	-0.08	-0.08
<i>Pleonosporium</i>	0.42	-0.06
<i>Spermothamnion</i>	0	-0.1
<i>Wrangelia</i>	0	-0.09
<i>Heterosiphonia</i>	0.08	-0.10
<i>Apoglossum</i>	0	-0.11
<i>Chondria</i>	0.17	-0.11
<i>Digenea</i>	0.25	-0.12
<i>Herposiphonia</i>	-0.33	-0.12
<i>Laurencia</i>	0	-0.10
<i>Lophosiphonia</i>	-0.42	-0.08
<i>Polysiphonia</i>	0.92	0.03
<i>Wrightiella</i>	0	-0.05
PHAEOPHYTA		
<i>Hinksia</i>	0.08	-0.05
<i>Sphacelaria</i>	0.33	-0.06
<i>Dictyota</i>	-0.09	-0.09
CHLOROPHYTA		
<i>Enteromorpha</i>	0.08	-0.08
<i>Cladophora</i>	-0.42	-0.03
<i>Dictyosphaeria</i>	0	-0.04
<i>Derbesia</i>	0.08	-0.06
CYANOBACTERIA		
<i>Lyngba</i>	-0.33	-0.17
<i>Dichothrix</i>	0.25	0.33

Table 4.8 Average algal and cyanobacterial frequency of occurrence/cm² at the genus level on tiles and rubble.

Genus	Frequency of occurrence/cm ²			
	Control	Remove Sediment	Add Sediment	Rubble
RHODOPHYTA				
<i>Amphiroa</i>	0.08	0.15	0.13	0.17
<i>Jania</i>	0.25	0.38	0.41	0.33
<i>Gelidiella</i>	0.01	0.00	0.02	0.00
<i>Liagoracea</i>	0.00	0.00	0.02	0.00
<i>Asparagopsis</i>	0.00	0.01	0.00	0.00
<i>Wurdemannia</i>	0.33	0.33	0.39	0.06
<i>Champia</i>	0.00	0.01	0.00	0.00
<i>Gelidiopsis</i>	0.04	0.12	0.04	0.17
<i>Aglaothamnion</i>	0.01	0.00	0.09	0.06
<i>Anotrichium</i>	0.00	0.00	0.00	0.06
<i>Antithamnionella</i>	0.00	0.00	0.00	0.06
<i>Balliealla</i>	0.00	0.01	0.00	0.11
<i>Centroceras</i>	0.24	0.32	0.33	0.22
<i>Ceramium</i>	0.24	0.26	0.17	0.22
<i>Lejolisia</i>	0.10	0.14	0.06	0.00
<i>Pleonosporium</i>	0.06	0.21	0.02	0.33
<i>Spermothamnion</i>	0.03	0.01	0.04	0.00
<i>Wrangelia</i>	0.00	0.00	0.02	0.00
<i>Heterosiphonia</i>	0.00	0.01	0.00	0.00
<i>Apoglossum</i>	0.00	0.00	0.00	0.17
<i>Chondria</i>	0.31	0.29	0.26	0.17
<i>Digenea</i>	0.08	0.13	0.02	0.00
<i>Herposiphonia</i>	0.42	0.29	0.44	0.00
<i>Laurencia</i>	0.08	0.06	0.07	0.28
<i>Lophosiphonia</i>	0.40	0.25	0.19	0.28
<i>Polysiphonia</i>	1.00	1.00	1.00	0.17
<i>Wrightiella</i>	0.00	0.00	0.02	0.00
PHAEOPHYTA				
<i>Hinksia</i>	0.00	0.03	0.00	0.00
<i>Sphacelaria</i>	0.06	0.10	0.15	0.00
<i>Dictyota</i>	0.06	0.03	0.00	0.00
CHLOROPHYTA				
<i>Enteromorpha</i>	0.30	0.15	0.30	0.28
<i>Cladophora</i>	0.50	0.51	0.43	0.00
<i>Dictyosphaeria</i>	0.00	0.00	0.00	0.06
<i>Derbesia</i>	0.00	0.01	0.06	0.11
CYANOBACTERIA				
<i>Lyngba</i>	0.49	0.42	0.37	0.83
<i>Dichothrix</i>	0.07	0.18	0.11	0.00

ii. SPECIES SIMILARITY

The one-way repeated measures ANOVA comparing the Dice, Jacard, Simpson similarity indices between the two manipulations M1 and M2 was not significant (F-value 3.18, $p < 0.7087$). A total of 61 species of algae and cyanobacteria were identified (Table 4.9) on the 33 tiles and three pieces of rubble, not including the three types of algae identified only to the genus level and 10 of which could not be identified. Rhodophyta was the predominant group with at least 46 identified species (and two only to the genus level), three of which were calcareous branching algae. Seven of the remaining species were chlorophytes, four species and one taxon identified only to genus were phaeophytes, and five were cyanobacteria. Several of these either had never been reported in the Western Caribbean [14 species by Littler and Littler (2000) and one by Schneider and Searles (1991)] or at this depth (31 species) according to Littler and Littler's (2000) identification guide (Table 4.9).

iii. SPECIES RICHNESS

The TAS mats averaged 11.6 ± 4.5 species/cm² on all groups of tiles and 9.6 ± 3.4 species/cm² on the rubble. (The data had 6.5 added to each datapoint before log transformation to meet normality because one of the manipulated tiles had an average of 6.5 fewer species than its paired control.) Differences between paired tiles in the number of species/cm² were not significant in a one-way weighted ANOVA (Table 4.10).

TABLE 4.9 List of species recorded, known distribution, source and new records

Order	Family	Genus	Species	Distribution	Depth (m)	Source	New record
RHODOPHYTA							
Corallinales	Corallinaceae	<i>Amphiroa</i>					
		<i>Jania</i>	<i>capillacea</i>	WC	15	L&L	
		<i>J.</i>	<i>pumilla</i>	WC	15	L&L	
Gelidiales	Gelidiaceae	<i>Gelidiella</i>	<i>setacea</i>	WC	1	L&L	**
Nemaliales	Liagoraceae					L&L	
			(Falkenbergia stage)				
Bonnemaisoniales	Bonnemaisoniaceae	<i>Asparagopsis</i>	<i>taxiformis</i>	WC	30	L&L	
Gigartinales	Wurdemanniaceae	<i>Wurdemannia</i>	<i>miniata</i>	WC	30	L&L	
Rhodymeniales	Champiaceae	<i>Champia</i>	<i>parvula</i> var. <i>prostrata</i>	WC	15	L&L	
Gracilariales	Lomentariaceae	<i>Gelidiopsis</i>	<i>intricata</i>	WC	10	L&L	**
		<i>G.</i>	<i>variabilis</i>	WC	2	L&L	**
Ceramiales	Ceramiaceae	<i>Aglaothamnion</i>	<i>herveyi</i>	****	1	L&L	**
		<i>Anotrichium</i>	<i>tenue</i>	WC	30	L&L	
		<i>Antithamnionella</i>	<i>breviramosa</i>	****	35	L&L	
		<i>Balliella</i>	<i>pseudocorticata</i>	WC	5to10	L&L	
		<i>Centroceras</i>	<i>clavulatum</i>	WC	5	L&L	**
		<i>C.</i>	<i>internitens</i>	WC	18	L&L	
		<i>Ceramium</i>	<i>cimbricum</i>	WC	40	L&L	
		<i>C.</i>	<i>cimbricum</i> f. <i>flaccidum</i>	WC	40	L&L	
		<i>C.</i>	<i>flaccidum</i>	WC	22	L&L	
		<i>C.</i>	<i>nitens</i>	****	10	L&L	**
	<i>Lejolisia</i>	<i>exposita</i>	WC	32	L&L		
	<i>Pleonosporium</i>	<i>boergesenii</i>	WC	12-30	L&L		
	<i>P.</i>	<i>flexuosum</i>	****	18-27	L&L	**	

Table 4.9 List of species recorded, known distribution, source and new records (*continued.*)

Order	Family	Genus	Species	Distribution	Depth (m)	Source	New record	
RHODOPHYTA	Ceramiales	Ceramiaceae	<i>Spermothamnion</i>	<i>gymnocarpum</i>	WC	10	L&L	**
			<i>Wrangelia</i>	<i>bicuspidata</i>	WC	40	L&L	
		Dasyaceae	<i>Heterosiphonia</i>	<i>crispella</i>	WC	20	L&L	
		Delesseriaceae	<i>Apoglossum</i>	<i>ruscifolium</i>	****	20-40	L&L	**
		Rhodomelaceae	<i>Chondria</i>	<i>baileyana</i>	WC	5	L&L	**
			<i>C.</i>	<i>curvilineata</i>	****	40	L&L	**
			<i>C.</i>	<i>floridiana</i>	WC	40(-80)	L&L	
			<i>C.</i>	<i>leptacremon</i>	WC	15	L&L	
			<i>Digenea</i>	<i>Simplex</i>	WC	20	L&L	
			<i>Herposiphonia</i>	<i>bipinnata</i>	WC	15	L&L	
			<i>H.</i>	<i>cf. parca</i>				
			<i>H.</i>	<i>pecten-veneris</i>	WC	2	L&L	**
			<i>H.</i>	<i>Secunda</i>	WC	2	L&L	**
			<i>H.</i>	<i>tenella</i>	WC	2	L&L	**
			<i>Laurencia</i>	<i>cervicornis</i>	****	45	L&L	
			<i>Lophosiphonia</i>	<i>cristata</i>	****	2	L&L	**
			<i>L.</i>	<i>obscura</i>	****	2	L&L	**
		<i>Polysiphonia</i>	<i>atlantica</i>	WC	1	L&L	**	
		<i>P.</i>	<i>ferulacea</i>	****	36	L&L		
		<i>P.</i>	<i>howei</i>	WC	SI-I	L&L	**	
	<i>P.</i>	<i>pseudovillum</i>	****	3	L&L	**		
	<i>P.</i>	<i>scopulorum</i>	WC	3	L&L	**		
	<i>P.</i>	<i>subtilissima</i>	WC	1	L&L	**		
	<i>Wrightiella</i>	<i>tumanowiczii</i>	****	55	L&L			

Table 4.9 List of species recorded, known distribution, source and new records (*continued.*)

	Order	Family	Genus	Species	Distribution	Depth (m)	Source	New record
PHAEOPHYTA							L&L	
	Ectocarpales	Ectocarpaceae	<i>Hincksia</i>	<i>mitchelliae</i>			L&L	
	Sphacelariales	Sphacelariaceae	<i>Sphacelaria</i>	<i>tribuloides</i>	WC	3	L&L	
	Dictyotales	Dictyotaceae	<i>Dictyota</i>	<i>pulchella</i>	WC	70	L&L	
CHLOROPHYTA							L&L	
	Ulvales	Ulvaceae	<i>E</i>	<i>flexuosa</i> sbsp. <i>paradoxa</i>	****	5	L&L	**
			<i>E</i>	<i>lingulata</i>	WC	LI	L&L	**
			<i>E</i>	<i>prolifera</i>	WC	1	L&L	**
	Cladophorales	Cladophoraceae	<i>Cladophora</i>	<i>albida</i>	****	2	L&L	**
			<i>C</i>	<i>montagneana</i>				
			<i>C</i>	<i>pellucidoidea</i>	****	16-20	S&S	**
		Siphonocladaceae	<i>Dictyosphaeria</i>	<i>cavernosa</i>	WC	40	L&L	
	Bryopsidales	Bryopsidaceae	<i>Derbesia</i>	<i>fastigiata</i>	WC	1m	L&L	**
CYANOBACTERIA								
	Oscillatoriales	Oscillatoriaceae	<i>Lyngba</i>	<i>confervoides</i>	WC	2	L&L	**
			<i>L</i>	<i>majuscula</i>	WC	2	L&L	**
			<i>L</i>	<i>polychroa</i>	WC	2	L&L	**
			<i>L</i>	<i>sempi plana</i>	WC	2	L&L	**
			<i>Dichothrix</i>	<i>bornetiana</i>	WC	I-2	L&L	**

WC – Western Caribbean

L&L – Littler and Littler (2000); S&S – Schneider and Searles (1991)

I = intertidal; LI = lower intertidal; SI = shallow intertidal

**** - New distribution in WC (based on L&L and S&S)

** - New record at 12-13m depth (based on L&L and S&S)

IV. ASSESSING FIELD UNDERESTIMATIONS OF ENCRUSTING COVER

A comparison of encrusting cover values before and after removing all other erect organisms, showed a significant difference in a two-sample t-test (Table 4.11). Percent cover of benthos by encrusting cover (\pm standard deviation), was significantly higher when the obscuring erect organisms had been removed (average $70.24 \pm 34.55\%$) than when the erect benthic community was intact (average $28.36 \pm 21.2 \%$).

Table 4.10 One-way ANOVA on the effects of sediment load on the average species richness of algae and cyanobacteria (n=33). (Data was log transformed to meet normality)

Source	Df	SS	MS	F-value	Pr > F
Model	1	0.11094408	0.11094408	0.12	0.7328
Error	10	8.99826096	0.89982610		
Corrected total	11	9.10920504			

Table 4.11 Two-sample t-test analysis for differences in estimated percentage of encrusting cover before and after removal of erect, canopy organisms (n=33).

If variances are	t-statistic	Degrees of freedom	Pr>t
Equal	-5.943	64	<0.0001
Not equal	-5.943	52.96	<0.0001

DISCUSSION

Although the MANOVA did not detect significant treatment effects on the average percent cover of the different categories of benthic organisms, the non-significant trends of higher percent coverage of encrusting cover under increased sediment loads and of higher coverage by the larger turf algae under lower sediment levels (Figure 4.2) were in the direction expected by previous work at shallower depths (Kendrick 1991, van Tussenbroek and Collado Vides 2000).

Several explanations are possible for the surprising finding that there were no significant effects of the sediment addition and removal on the average height, and dry weight of the turf algal filaments, or on sediment dry weight. Possibly one or more of the following modifications in the experimental design would produce significant differences: (a) more frequent maintenance of the different manipulations; (b) a greater difference in sediment levels between the two treatments; and (c) longer exposure times. Moreover, not only had the tropical storm increased sediment re-suspension levels in the study area immediately prior to the collection of the tiles but it is also likely that any TAS mat-associated sediment that was not entrapped by algal filaments had been washed away.

However, when treatments are ignored, the amount of sediment trapped by turf algae is clearly related to the average turf algal filament height (Figure 4.5) and turf algal dry weight (Figure 4.6) as would have been expected (Purcell 2000). Moreover, the sediment load carried on the tiles, averaging 14.4 times the

dry weight of the turf algae by which it was entrapped, was nearly three times greater than the 5:1 ratio reported by Kendrick (1991). Although cause and effect relationships were not examined in this experiment, it is likely that small increases in sediment load may require that the turf algal filaments grow taller to intercept light for photosynthesis, which, in turn, would provide more than three-dimensional space in which sediments could become entrapped.

That the average turf algal dry weight (from 54g/m^2 , on sediment removal tiles to 88g/m^2 , on sediment addition tiles) was far lower than $120 - 550\text{g/m}^2$ reported in Kendrick (1991) is at least partially explained by their lower productivity due to the lower ambient light levels at 13 m than is expected at > 3 m. The proportionately greater sediment load on the Las Redes reef would have further reduced the turfs' access to radiant energy and may also have contributed to the lack of significant treatment effects in contrast to Kendrick (1991)'s study in which similar treatments were employed.

Based on my results, the specific composition of the algae in the Las Redes TAS mats appear to be relatively stable and resistant to short-term changes in shading and/or sediment load in seeming contrast to the findings of Gorostriga and Diez (1996) in the Mediterranean. The lack of significant differences in turf algal dry weight between treatments also suggests that their ability to regenerate under less than optimum conditions either was not greatly affected or that it was at least adequate to the levels of grazing and damage experienced locally.

The small differences between species richness, algal biomass and filament height on the rubble compared to the tiles is perhaps explained by the fact that the pieces were loose and likely tumble under conditions of high surge such as had occurred the day prior to their collection. Scouring reduces turf species number, biomass and filament height compared to more stable substrata (Kendrick 1991, Airoidi *et al.* 1996). Other differences between the two kinds of substrata may be due to the more porous nature of the rubble than the terracotta tile (as endolithic algae in coral skeletons may have a significant role in the development of algal turfs in nature) and to any differences between the ages of the mats on the rubble pieces and those on the tiles.

In terms of composition, red algae are clearly dominant in TAS mats on Las Redes, which seems unusual in comparison to the description of other turf algal mats (e.g. Hackney *et al.* 1989, Kendrick 1991, van Tussenbroek and Collado-Vides 2000). This may be an indication of sediment tolerance in general or an earlier stage of succession, although 12 months is considered adequate time for succession to be complete in this community (van Tussenbroek and Collado-Vides 2000). All else being equal, the relative dominance of red algae, which is also characteristic of turf algal patches protected by territorial pomacentrids (Ogden and Lobel 1978), the Las Redes TAS mats should also be appealing to other herbivorous fish given that rhodophytes are generally more easily digested than their chlorophyte and phaeophyte equivalents (Lassuy 1984). [However,

apart from the pomacentrids, local herbivore populations are relatively low (Chapters 2 and 3 this dissertation).]

Steneck (1988) suggested that the cover of turf algae is greatest in areas that are protected from intense grazing so that they are able to maintain themselves by rapid regeneration. However, there must also be an adequate level of grazing to remove fleshy macroalgae that might otherwise become dominant. These conditions are somewhat in contrast to the relative dominance paradigm of Littler and Litter (1984) who had earlier proposed that microfilamentous algae (equivalent to turf algae), would only dominate in areas of low herbivore activity and low nutrient levels while crustose coralline algae would dominate in areas of both high herbivory and nutrient levels.

TAS mats in the Las Redes reef seem to flourish under somewhat different conditions than have been previously described for turf algae alone. Ambient nutrient conditions within the mats, currently unknown, may actually be relatively high (see Introduction, this chapter). Moreover, grazing on turf algae is suppressed by the lack of medium- to large-sized herbivorous fishes (acanthurids and scarids), possibly by the relatively large populations of resident pomacentrids (Chapter 2, this dissertation) and probably also by the sediment in the mats. Continued, unapproved removal of grouper and other larger carnivorous fishes keeps the predation pressure on the relatively high populations of territorial damselfish populations at low to negligible levels. The combined effects of bound sediment and exclusion from grazing, particularly within pomacentrids territories,

appears to have allowed TAS mats to increase in frequency, distribution and inevitable contact with, and displacement of, stony corals. An increase herbivory might therefore assert some control over the rates of TAS mat expansion. The key Caribbean herbivore, *Diadema antillarum*, is able to consume TAS mats (*pers. obs.*) but since the mass mortality in the 1980s (Lessios 1988), their populations have been very low. Research on *D. antillarum* population size and effect on the abundance of TAS mats would prove valuable and might also provide a management solution for areas with a prevalence of TAS mats.

In terms of local turf-algal species richness and distribution, worthy of note are the 15 new species previously unreported for the Western Caribbean region and 31 new depth records. Another important note is that encrusting cover estimates made in the field can be significantly lower (by more than 50%), than the true values.

My results have shown highly localized variations (on the order of decimeters), in the physical characteristics and turf algal composition of TAS mat communities. Although TAS mats as a whole can be stable and fairly resilient under a wide range of shading and burial by sediments, the differences in frequency of occurrence of some genera based on sediment load suggests that this is an appropriate level of distinction at which to consider the effect of sediment. Indeed, sediments appear to smother most algal genera (Figure 4.7 and Table 4.7). Given their higher frequencies of occurrence when sediment was removed, it also seems reasonable to suggest that genera like *Polysiphonia* and *Wurdemannia* are

less tolerant of shading and burial than their counterparts. That *Dichothrix* occurred at a higher frequency in both treatment types compared to controls is perhaps an indication that this genus fairs well in conditions of change or disturbance.

Polysiphonia and *Wurdemannia* may also be relatively important in aggressive TAS mat encroachment over stony corals, since TAS mats with less bound sediment appeared to outcompete corals more quickly than those with higher levels of sediment (*pers. obs.*). My study was not designed to test relationships such as these, but its results provide a launching point for further investigation at an appropriate level of inquiry.

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