

The Role of the threespot damselfish, *Stegastes planifrons*, in Contemporary Caribbean Reef Ecology

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Abstract

Caribbean reef ecosystems have undergone major ecological changes in the last 30 – 40 years, with the result that ecological systems once dominated by structurally complex *Acropora cervicornis* and *Montastraea annularis* corals now consist mainly of flattened carbonate substrates with macroalgal overgrowth. A need for greater understanding of coral reef ecosystems is imperative if we are to attempt to conserve them. The threespot damselfish, *Stegastes planifrons*, is herbivorous damselfish species ubiquitous to Caribbean reefs, where it has been termed a keystone species. Aggressive in nature, *S. planifrons* defends territories of around 70 cm in diameter from other roving herbivorous fish and urchins, in apparent effort to maintain the algal resources therein for its own use. The predilection of *Stegastes planifrons* for basing its territories on the now Critically Endangered staghorn coral, *Acropora cervicornis*, and the Endangered boulder coral *Montastraea annularis* is well known, however the likely ecological implications of this fact have not been investigated. Using a combination of experimental and observational methodologies we examine the ecological implications of coral microhabitat choice and use by *S. planifrons*. We also assess the magnitude of the direct and indirect effects of *S. planifrons*' territorial behaviour on macroalgal dynamics both within and outside of territory confines, at the reef-wide level.

We find that coral microhabitat is a more important determinant of algal community structure than damselfish presence, and that this can be explained by a previously unrecognised effect of coral microhabitat on the grazing behaviour of roving herbivorous fishes - on which *S. planifrons*' territorial behaviour has little effect. In a modification of the space availability hypothesis of Williams et al (2001) we suggest that *Acropora cervicornis* acts as a grazing fish 'exclusion zone', and we further hypothesise that the existence of large stands of this coral prior to the Caribbean 'phase shift' may have acted to concentrate the grazing pressure of excluded roving fish onto the remaining areas of the reef. We further hypothesise that the loss of such 'exclusion zones' and accompanied effective dilution of grazing pressure may have been on a scale large enough to have been a significant underlying factor in the proliferation of macroalgae seen on modern day Caribbean reefs.

In the absence of demonstrable direct or indirect effects on benthic algal communities we question the continued keystone status of *S. planifrons*, particularly since the status

was originally based on interference behaviour involving the important grazing urchin *Diadema antillarum*, which is now functionally absent from Caribbean reefs. Implications of the context-dependant nature of keystone status are also discussed. We find that the effect of *S. planifrons* on coral community may be more important than its effects on benthic algal community. In examining the factors involved in habitat coral choice we establish a significant preference for 100% live coral substrate over substrates with a supply of algal food. Territory selection was followed by a high rate of coral biting – a behaviour which has previously been shown to result in coral tissue death and the fast establishment of algal turf communities on which *S. planifrons* likes to feed (Kaufman 1977). We also demonstrate a novel and significant association between *S. planifrons* presence and disease incidence its primary habitat coral, the Critically Endangered staghorn coral *Acropora cervicornis*, and a significant correlation between areas of fish biting and the later onset of disease.

Changes to the overall role of damselfish on today's Caribbean reefs are discussed in light of these insights.

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I choose to remember the moon shadows. The jumping iguanas. The day of the dragonflies. The poor small, exhausted birds, and the hawk that killed them. The fish eagle. The day of the jellyfish. The Island crocodile. The silversides and the groupers; the giant salp; the garden eels. The celestial night dive. The dead sailors, and the one that swam ashore. The most incredible whale sharks and their beady eyes; the enormous glowing whirl of cuberra snapper. One Barrel Rum and coconut water. Rice and beans. Escabeche. ..And of course, the midnight parrotfish.

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CHAPTER 1

General Introduction.

THE STATUS OF CORAL REEFS

Worldwide trends

Coral reefs are under threat worldwide: it has been estimated that as much as 30% of the world's coral reefs are already lost or damaged, and as much as 60% may be lost by 2030 (Wilkinson 2004). In recent years such forecasts have promoted concern for the status of coral reef habitats in general (Bellwood et al. 2006, Carpenter et al. 2008, Hughes et al. 2010). In addition to localised problems of pollution and eutrophication, and unsustainable fishing practices (Lapointe et al. 2004, Mumby et al. 2007b, Wilkinson 2008), recent studies have predicted that coral bleaching and ocean acidification will cause rapid and severe losses of scleractinian corals from tropical ecosystems (Hoegh-Guldberg 1999, Hoegh-Guldberg et al. 2007, Carpenter et al. 2008, Donner 2009, Kiessling and Simpson 2011). Coral bleaching stemming from sea surface warming due to anthropogenic climate change is blamed for ecosystem-level losses of reef habitat complexity and biodiversity which have already occurred (Wild et al. 2011). It has been predicted that ocean acidification (decreasing seawater CO_3^{2-} ion concentrations resulting from increased atmospheric CO_2 concentrations) will increasingly degrade the ability of scleractinian corals to secrete their calcium carbonate skeletons, to the extent that rates of erosion may exceed rates of reef deposition in some areas within 40 to 100 years (Hoegh-Guldberg et al. 2007). Over the last two million years coral reefs globally have been subject to changing environmental conditions, but whilst changes in sea-level rise and ocean temperature have previously been experienced at rates similar to those being experienced today, the present rate of CO_2 rise is unprecedented (Pandolfi and Greenstein 2007). Although there is now a body of literature pointing towards imminent concerning threats to coral reef conservation (Wilkinson 2004 (Hoegh-Guldberg 1999, Bellwood et al. 2006, Hoegh-Guldberg et al. 2007, Carpenter et al. 2008, Donner 2009, Hughes et al. 2010, Kiessling and Simpson 2011) (Wilkinson 1999, Hughes et al. 2003, Pandolfi et al. 2003, Birkeland 2004, Hoegh-Guldberg et al. 2007, Wilkinson 2008, Sammarco 2009, Hoegh-Guldberg 2011a, Hoegh-Guldberg 2011b) a recent review of the evidence by one of the foremost experts in the field concludes that whilst major changes to coral reef ecosystems are occurring, large-scale changes may not be as homogeneous or as rapid as the decadal scales previously indicated by some authors (Pandolfi et al. 2011). It has also been projected that under reduced anthropogenic carbon emissions scenarios, adaptation will enable the

survival of some coral species, which would then proliferate to occupy space left by the former assemblage (Baskett et al. 2009). In such a scenario high coral cover may be able to persist, although the resemblance of reefs to the biodiverse and complex habitats of today would not (Pandolfi et al. 2011). Although management of the over-riding threat of climate change processes requires inter-governmental cooperation at the highest levels, there is also evidence that mitigation of localised stresses, such as overfishing (implicated macroalgae proliferation) can have significant local effects (Pandolfi et al. 2011). Whether reductions in carbon emissions significant enough to ameliorate the larger problems of climate change and ocean acidification will be achieved, will be determined by the extent to which society becomes informed, concerned, and reactive to the potential results of climate change; something which has yet to be seen.

Declines in live coral cover and the proliferation of macroalgae in the Caribbean

This study is based in the Caribbean, where the last 30 – 40 years has seen a massive decline in live coral cover, with reefs which were once structured by live Acroporid staghorn and elkhorn corals and massive *Montastraea* bolder corals now dominated by dead coral carbonate reef and macroalgal cover - in what has been termed an ecological ‘phase shift’ (Hughes 1994, McClanahan and Muthiga 1998, McClanahan et al. 1999, McCook 1999, Ostrander et al. 2000, Precht et al. 2002, Mumby 2006, Rogers and Miller 2006). The replacement of live coral reef with dead rubble and algae is a concerning trend due to associated effects such as loss of amenity value, and the deleterious consequences of reduced habitat complexity, including lower productivity fisheries and reduced species diversity (Roberts 1995). Primary underlying causes of the ‘phase shift’ now implicated through a multitude of regional studies are: coral disease - especially white diseases of acroporid corals, the loss of the keystone grazing urchin, *Diadema antillarum*, and coral bleaching; with reduced grazing by herbivorous fish due to overfishing further exacerbating the situation (Wilkinson, 2008).

The first of the large scale impacts on Caribbean reefs was a mass mortality in Acroporid species across the entire region, due to the combined effect of the Caribbean white band disease epizootics of the late 1970s and 1980s (Gladfelter 1982c, Bythell et al. 2000, Aronson and Precht 2001, Aronson et al. 2002a, Aronson et al. 2002b, Precht et al. 2002, Schutte et al. 2010). *Acropora cervicornis* reductions of 95% or more

occurred in many areas (Aronson and Precht 2001, Precht et al. 2002), resulting in a paucity of this once-dominant reef-building species unprecedented in the Caribbean in the last 3000 years (Aronson and Precht 1997b, Precht et al. 2002). As a consequence, *Acropora cervicornis* has now been added to the IUCN Red List where it is categorized as Critically Endangered (Aronson R et al. 2008). The result of this loss is that Caribbean reefs have seen a general decrease in three dimensional structure and complexity (Alvarez-Filip et al. 2009), and an opening up of dead carbonate substrates to algal colonisation and proliferation (Mumby et al. 2006, Williams and Polunin 2000, Williams et al. 2001). In combination with the increased space for algal growth, the loss of the voracious algae-grazing urchin *Diadema antillarum* in a region-wide epizootic in 1983 (Lessios et al. 1984) has contributed greatly to the Caribbean-wide proliferation of macroalgae, since the remaining herbivore community is unable consume enough to maintain reefs clear of large algal standing crops (Carpenter 1988, 1990b, a, Williams et al. 2001). As a result of these dramatic wide-scale changes it is apparent that an understanding of the processes governing coral-algal dynamics is important if we are to effectively manage reefs towards recovery of their former coral-rich state (Hughes 1994, McClanahan and Muthiga 1998, McClanahan et al. 1999, McCook 1999, Ostrander et al. 2000, Precht et al. 2002, Mumby 2006, Rogers and Miller 2006).

INTRODUCTION TO REEF SYSTEMS AND CORAL-ALGAL DYNAMICS

Coral reefs as biologically derived structures

Scleractinian or 'stony' corals (Phylum Cnidaria; Class Anthozoa; Order Scleractinia) are a diverse taxa of soft-bodied organisms that secrete a calcium carbonate endoskeleton, which by serial accumulation is responsible for the often complex structural network that forms the three dimensional basis of the coral reef ecosystem. Corals are colonial organisms; with individual units consisting of polyps they gain energy heterotrophically, by ingestion of particulate food captured by means of stinging nematocyst-laden tentacles, and in many cases also by absorption of sugars generated autotrophically by endogenous single-celled algae termed zooxanthellae (Birkeland 1997). Many scleractinian corals are functionally dependant on the presence of these

zooxanthellae symbionts, and can die when the symbiosis breaks down for any period of more than a few days – as is the case in sustained coral bleaching (Hoegh-Guldberg 1999, 2004, Hoegh-Guldberg et al. 2005, Wilkinson 2008, Hoegh-Guldberg 2009, Hoegh-Guldberg 2011b, Wild et al. 2011). The coral reef benthic community lives on the surface veneer of the reef structure which is composed of the previously secreted skeletons of scleractinian corals, space for colonisation and growth by sessile benthos – primarily algae, gorgonians, sponges, and the present generation of *Scleractinia* themselves, is ultimately limited by the total area of the underlying calcareous reef structure.

Competition between coral and algae for space on the reef.

Coral and algae are naturally in a state of competition for space on coral reefs (Lirman 2001, McCook 2001). Macroalgal presence has been shown to deleteriously affect live coral cover through, among other things: i) competition for benthic space - where macroalgal contact and overgrowth can have a negative effect on coral health (Rasher and Hay 2010), ii) transmission of coral disease (Nughes et al. 2004), and iii) effects on coral recruitment (Carpenter and Edmunds 2006, Rogers and Miller 2006, Birrell et al. 2008, Diaz-Pulido et al. 2010, Idjadi et al. 2010). In addition to being affected by macroalgal presence, coral recruitment is also known to be negatively affected by the presence of thick algal turfs (Birrell et al. 2005), including those found in damselfish territories (Arnold et al. 2010). Given the present live-coral-depauperate state of the Caribbean, successful coral recruitment is increasingly seen as a key underlying process enabling reef recovery (Birrell et al. 2008, Venera-Ponton et al. 2011). Since space is needed for coral recruit settlement and growth, the success of this process may often be mediated by the pre-existing algal community (Carpenter and Edmunds 2006, Rogers and Miller 2006, Birrell et al. 2008, Arnold et al. 2010, Diaz-Pulido et al. 2010, Idjadi et al. 2010). Although algal dominance is generally seen as deleterious to coral health, the outcome of spatial competition between corals and common algal groups is subject to complex dynamics (as reviewed by (McCook 2001)). Scleractinian corals have developed in spatial competition with algae and have evolved some defences against overgrowth (Lang 1973). Many scleractinia produce mucus secretions containing chemotoxins, and in some cases nematocyst stinging cells which are deleterious to competitors (Chadwick 1988). Other defences include specialist ‘sweeper’ tentacles that

passively sweep proximate surfaces, discharging stinging nematocysts when stimulated by foreign agents (Richardson et al. 1979, Wellington 1980, Sheppard 1981, Goldberg et al. 1990), and mesenterial filaments can also be capable of secretion of extracoelenteric digestive fluids, damaging or killing space competitors (Lang 1973, Wellington 1980). Although the dynamics of the relationship between corals and macroalgae are complex, processes such as herbivorous grazing that decrease algal abundance can be said to favour coral cover.

The importance of herbivory on Caribbean reefs

Algal standing stock is fundamentally a product of the offset of the rate of primary production against the rate of loss due to disturbance, where disturbance is any factor that has a deleterious effect on algal biomass (Hatcher and Larkum 1983, Carpenter 1986, Steneck 1988). Within coral reef ecosystems the major cause of disturbance-mediated algal loss is normally herbivory (Steneck 1988), which is recognised as an important mechanism for the removal of algae, and also structuring algal communities (Ogden and Lobel 1978, Carpenter 1986, Steneck 1988, Steneck and Dethier 1994). Herbivory is therefore seen as a key process affecting the long-term persistence of coral-rich reef ecosystems, because its role in reducing algal standing crop thereby favours the coral-dominant state (Hughes et al. 2003, Mumby and Harborne 2010, Edwards et al. 2011).

Key exponents of herbivory on coral reefs are urchins and grazing fish (Carpenter 1986). The grazing fish have previously been split behaviourally into two groups termed ‘Foragers’: “relatively mobile, schooling grazers, including the parrotfish and surgeonfish”, and ‘Farmers’: “highly site-attached, territorial species, primarily the damselfish” (Ceccarelli et al. 2005a). Historically, the voracious keystone herbivorous urchin, *Diadema antillarum*, played a large role in maintaining algal biomass at low levels on Caribbean reefs (Carpenter 1981) with their presence often denuded substrates occupied by crustose coralline algae (Carpenter 1986, Steneck 1988). However, since the 1983 – 1984 Caribbean-wide loss of *Diadema* due to an unidentified epizootic agent (Sammarco 1980, Lessios et al. 1984, Liddell and Ohlhorst 1986, Bauer and Agerter 1987, Williams and Williams 1987, Greenstein 1989) to the point of ‘functional extinction’ on present-day reefs (Mumby et al. 2006), ‘forager’ parrotfish (Scaridae and Sparisomidae) and surgeonfish (Acanthuridae) can now be said to be the key grazers of

functional importance to Caribbean reefs (Mumby 2006, Mumby et al. 2007a). Therefore, by virtue of the importance of algal reduction for coral recruitment and growth (as discussed above) (Nughes et al. 2004, Birrell et al. 2005, Carpenter and Edmunds 2006, Rogers and Miller 2006, Birrell et al. 2008, Arnold et al. 2010, Diaz-Pulido et al. 2010, Idjadi et al. 2010, Rasher and Hay 2010, Venera-Ponton et al. 2011), the foraging activity of these fish is now recognised as a process of fundamental importance to reef recovery in the Caribbean (Mumby 2006, Mumby et al. 2006, Mumby et al. 2007a). However, in addition to the ‘foraging’ parrotfish and surgeonfish there territorial ‘farmer’ damselfish (the subject of this study) are ubiquitous to the Caribbean and in some places can occupy up to 90% of the substrate (Robertson et al. 1981, Ebersole 1985). Although little-quantified, it has therefore been suggested that territorial damselfish may also exert significant control over algal dynamics, with the question of the relative ecological importance of roving ‘forager’ grazers relative to the site-attached damselfish requiring further clarification (Ceccarelli et al. 2001a, 2005a). A more detailed introduction to the ecology of territorial herbivorous damselfish is given below.

CORAL DISEASE – THE INCREASING IMPORTANCE OF AN EMERGING FIELD

The importance of coral disease

Alongside global sea temperature rise and associated bleaching, ocean acidification, and overfishing, coral disease has been listed as one of the major contributing factors to the global trend of coral reef decline (Wilkinson, 2008). It has been suggested that coral diseases are increasing in prevalence world-wide (Barber et al. 2001, Aronson and Precht 2006), with new diseases still emerging - or at least still being discovered (Goreau et al. 1998, Harvell et al. 1999). In addition, it has been shown that many diseases increase in both prevalence and pathogenicity with raised ambient temperatures (Harvell et al. 1999, Harvell et al. 2002, Rosenberg and Ben-Haim 2002, Harvell et al. 2007), provoking concern about potential increased outbreaks under predicted future global warming scenarios.

The most high-profile outbreak of coral disease so far documented was the unprecedented Caribbean white band disease epizootics of the late 1970s and 1980s which caused mass mortality in Acroporid species across the entire region (Gladfelter 1982c, Bythell et al. 2000, Aronson and Precht 2001, Aronson et al. 2002a, Aronson et al. 2002b, Precht et al. 2002, Schutte et al. 2010), with live coral cover reductions of 95% or more occurring in many areas (Aronson and Precht 2001, Precht et al. 2002). This has resulted in a paucity of the once-dominant reef-building species *Acropora cervicornis* and *A. palmata*, unprecedented in the Caribbean in the last 3000 years or more (Aronson and Precht 1997b, Precht et al. 2002), which continues to this day (Weil and Rogers 2011). As a consequence, these coral species have now been added to the IUCN Red List where they are categorized as Critically Endangered (Aronson R et al. 2008). Despite previous initial signs of a small-scale recovery at Dairy Bull reef in Jamaica, this has now faltered (Idjadi et al. 2006, Quinn and Kojis 2008), and today, more than two decades after the 1970 – 1990 epizootics, Caribbean reefs show few signs of recovery, and predictions are that reef regeneration will be slow - with no guarantee of a return to the previous Acroporid-dominated state (Aronson and Precht 2001, Schutte et al. 2010). The loss of these key species and associated three dimensional habitat complexity (Alvarez et al 2010) has fundamentally changed Caribbean reef structure, illustrating the potential of coral disease to cause profound ecosystem-level consequences across an entire eco-region (Aronson and Precht 2001). Although the study of Yakob and Mumby (2011) suggests (through epizootological modelling) that coral populations remaining after disease outbreaks will be less susceptible to disease in the future, this provides limited reassurance regarding coral reef resilience when, as seen in the Caribbean, the impacts of large-scale outbreaks can persist for many decades (Aronson and Precht 2001, Schutte et al. 2010).

At least 19 coral diseases have so far been identified, affecting more than 150 zooxanthellate species across the scleractinians, hydrozoans, and gorgonians; diseases have been associated with multiple pathogens including bacteria, fungi, protists, and cyanobacteria (Sutherland et al. 2004, Weil and Rogers 2011). Worldwide, more than three-quarters of known coral diseases have been reported from the Caribbean (Rosenberg and Loya 2004b), which has been termed a ‘disease hotspot’ (Richardson 1998). Although the high rates of diseases recorded in the Caribbean may be partly inflated by increased research effort focused here, it seems certain that there is also an

underlying trend of disease prevalence compared to other biogeographical regions (Sheppard et al. 2009 , Weil and Rogers 2011). However, despite generally low distribution and prevalence of disease in the Indo-Pacific (Willis et al. 2004), it has become apparent that here too rates are also increasing (Rosenberg and Loya 2004a). It seems safe to assume that coral diseases are not a new phenomenon in themselves, however there is evidence that in the Caribbean at least (where there has been some focus of research effort) such outbreaks are uncommon in recent history, since the 1970s – 1980s white band epizootic caused mortalities in colonies which were found to be more than 500 years old, and coring studies have revealed only two previous hiatuses in *Acropora palmata* accretion over the last few millennia – one around 800 years ago, and the over 3000 years ago (Hubbard et al. 2008). Although these pauses in growth and accretion cannot necessarily be ascribed to disease causation, their infrequency would suggest minimal time periods to the last potential prior epizootics. In addition to the increased frequency of coral disease outbreaks of the last twenty – thirty years, the Caribbean has also seen unprecedented epizootics of the grazing urchin *Diadema antillarum* (Lessios et al. 1984, Carpenter 1990a, b), as well as the sea fan *Gorgonia ventalina* (Smith et al. 1996, Smith and Weil 2004), although no similar scale epizootics have been recorded on Indo-Pacific reefs (Weil et al. 2006). Abiotic factors identified as possible stressors promoting increased disease include elevated seawater temperatures, pollution (and the introduction of human faecal bacteria), eutrophication, and sedimentation (Sutherland et al. 2004). The prevalence of such abiotic stressors would be expected to be relatively high in the Caribbean Sea, due to its relatively contained nature, bordered by land on two sides, with a prevalence of human settlements from the USA and other Central American countries.

The status of coral disease research

Research on coral disease is hindered by technical difficulties in both culturing and identifying pathogens, with the result that only 9 pathogens have been identified out of more than 19 reported diseases of corals and sea fans (Weil and Rogers 2011). In both epidemiology and epizootiology the accepted method of proof that a disease is the result of a biotic agent is the fulfilment of Koch's postulates (Koch 1982). These postulates stipulate that infectious biotic causation is demonstrated when: i) the putative pathogen

is found associated with every diseased individual , ii) the putative pathogen can be isolated from the diseased individual and grown in pure culture, and iii) the disease can then be induced in experimental organisms by inoculation with the isolated cultured pathogen (Koch 1982). Later there was an additional fourth postulate which required that the putative pathogen can also then be isolated again from the experimentally diseased organism, however Koch apparently did not stipulate that it was necessary to fulfil this later postulate (Sutherland et al. 2004). Attempts to isolate pathogens and prove coral disease causation through re-inoculation and the traditional application of Koch's Postulates are fraught with problems (Sutherland et al. 2004), not least because some diseases may be the result of a microbial consortium rather than a single agent (Antonius 1981b, a, Weil and Rogers 2011).

Modern molecular techniques are useful in examining the association between healthy or diseased coral states with particular bacterial community ribotypes (Ritchie et al. 2001, Bythell et al. 2002, Cooney et al. 2002, Frias-Lopez et al. 2002, Frias-Lopez et al. 2003, Frias-Lopez et al. 2004, Sekar et al. 2008, Mouchka et al. 2010), however such correlations do not demonstrate disease causation, and therefore cannot conclusively be used to identify pathogenic agents on their own (Sutherland et al. 2004, Weil and Rogers 2011). In view of these difficulties visual descriptions of disease signs and manifestation are in many cases still the only means by which diagnoses are made (Williams and Miller 2005) – although far from ideal, in many cases this is still the most practicable option in this emerging field (Work and Aeby 2006, Weil and Rogers 2011). One notable exception to this is the much-studied Red Sea coral *Oculina patagonica*, where surface mucous has been shown to be a site of attachment for the pathogen *Vibrio shalloi* - a demonstrated agent of temperature-mediated bleaching (Kushmaro et al. 1996, Kushmaro et al. 1997, Kushmaro et al. 1998)

Although Caribbean white band diseases are perhaps the most high profile of all the coral diseases, much still remains unknown about their aetiology. Two forms of the disease have so far been identified: WBD Type I (WBDI) - originally termed 'white band disease' (Gladfelter 1982a), which has been reported throughout the Caribbean (Antonius 1981b, 1982, Gladfelter 1982b, a, Bythell and Sheppard 1993); and WBD Type II (WBDII), which is so far only reported from the Bahamas (Ritchie and Smith 1998), and Puerto Rico (Gil-Agudelo et al. 2006). As yet, the pathogen for neither disease has been conclusively identified. In the case of WBDII, early studies indicated an apparent consistent association with *Vibrio charchariae* but Koch's postulates were

never fulfilled (Ritchie and Smith 1995a, Ritchie and Smith 1998). More recently inoculation studies of WBDII from Puerto Rican corals have fulfilled the first three of Koch's postulates and preliminary molecular analyses point toward the causative agent being a *Vibrio* species close to *Vibrio harveyi*, a close relation of *V. charchariae* (Gil-Agudelo et al. 2006). In the case of WBDI in *Acropora palmata* certain bacterial ribotypes have been found to be 'consistently' present in diseased colonies (n = 4), but not found in remotely located healthy corals (Pantos and Bythell 2006). This correlative result is consistent with much of the wider field of research into the bacterial communities of coral holobiont – where newly developed (or implemented) molecular techniques are increasingly revealing trends of altered surface bacterial consortia associated with diseased and non-diseased, or bleached versus non-bleached states (Mouchka et al. 2010); however, in most cases it remains unknown whether differences in microbial communities are the cause, or the consequence, of the unhealthy state (Pantos and Bythell 2006, Mouchka et al. 2010).

Coral disease descriptions in general have suffered from a lack of standardization (Work and Aeby 2006), and it seems that any white disease of *Acropora* has been termed either WBDI or WBDII, based on the supposition that any disease of *Acropora* must be one of these two (Williams and Miller 2005). There has not yet been enough investigation to know for certain whether such described diseases are in fact attributable to a the same pathogen in each case (Sutherland and Ritchie 2004). It also cannot yet be ruled out that some disease signs may actually be stress responses that are coral species-specific, rather than pathogen-specific, indeed Work and Aeby (Work and Aeby 2006) point out that in organisms such as corals which have a limited number of physiological responses, it is likely that different causal agents could elicit similar gross stress responses or lesions (Work and Aeby 2006). In addition, the term 'white band disease' was initially also used to describe a similar disease of massive corals such as the reef building *Montastraea* species, however the term 'white plague' is now commonly used for such diseases, although there is no obvious known study that distinguishes the two diseases (Bythell et al. 2004).

Taken together, it can be seen that there are many inconsistencies within the emerging field of coral disease - many due to practical limitations of current techniques and

methodologies. Unfortunately a robust and justifiable systemic classification of white band disease or other white diseases of Acroporid species has yet to be developed, and is beyond the scope of the present study, so in lieu of such a system of more precise disease determination the term ‘Acroporid white disease’ will be used in this study.

INTRODUCTION TO THE STUDY SPECIES: *STEGASTES PLANIFRONS* – A TERRITORIAL HERBIVOROUS DAMSELFISH

Territorial herbivorous damselfish are small fish usually less than 15 cm long, which typically maintain of ‘garden’ algal territories or ‘lawns’ of around 1m² in area, within which they are known to modify algal communities, and from which they have been said to derive most, if not all their dietary needs (Robertson et al. 1981, Ceccarelli et al. 2001a). Herbivorous damselfish are generally aggressive and known to act agonistically towards roving herbivorous ‘foragers’ in an apparent attempt to maintain the resources of the algal lawn for themselves (Ceccarelli et al. 2001a). Fine, filamentous algal ‘turfs’ are commonly held to be the desired end-product of damselfish gardening activities, with high turf cover commonly found within territory boundaries relative to the surrounding reef - as reviewed by Ceccarelli et al (2001a).

The threespot damselfish *Stegastes planifrons* (Figure 1.1), is widely distributed over tropical west Atlantic and Caribbean reefs (Itzkowitz 1977a, Robertson et al. 1981, Ebersole 1985, Lirman 1994, Tolimieri 1995, McClanahan et al. 2002), where it can be one of the most abundant species (Robertson et al. 1981). Globally, the damselfish family (Pomacentridae) forms a widespread and diverse component of coral reef communities (Ceccarelli et al. 2001a), with nine species being found in the Caribbean alone (McCormick and Makey 1997). Without exception the Pomacentridae are territorial in nature (Ceccarelli et al. 2001a), although a minority of planktivorous species only exhibit this habit seasonally (Itzkowitz 1977a). *Stegastes planifrons* has a high affinity for basing its territories on the branching coral *Acropora cervicornis* (Brawley and Adey 1977b, Itzkowitz 1977a, 1977b, Robertson et al. 1981) (Figure 1.1), which is now a Critically Endangered species (Precht et al. 2002, Aronson et al. 2008). This coral is apparently also a desirable habitat for other damselfish species, but *S. planifrons* is the most aggressive of the Caribbean damselfish community and is able to

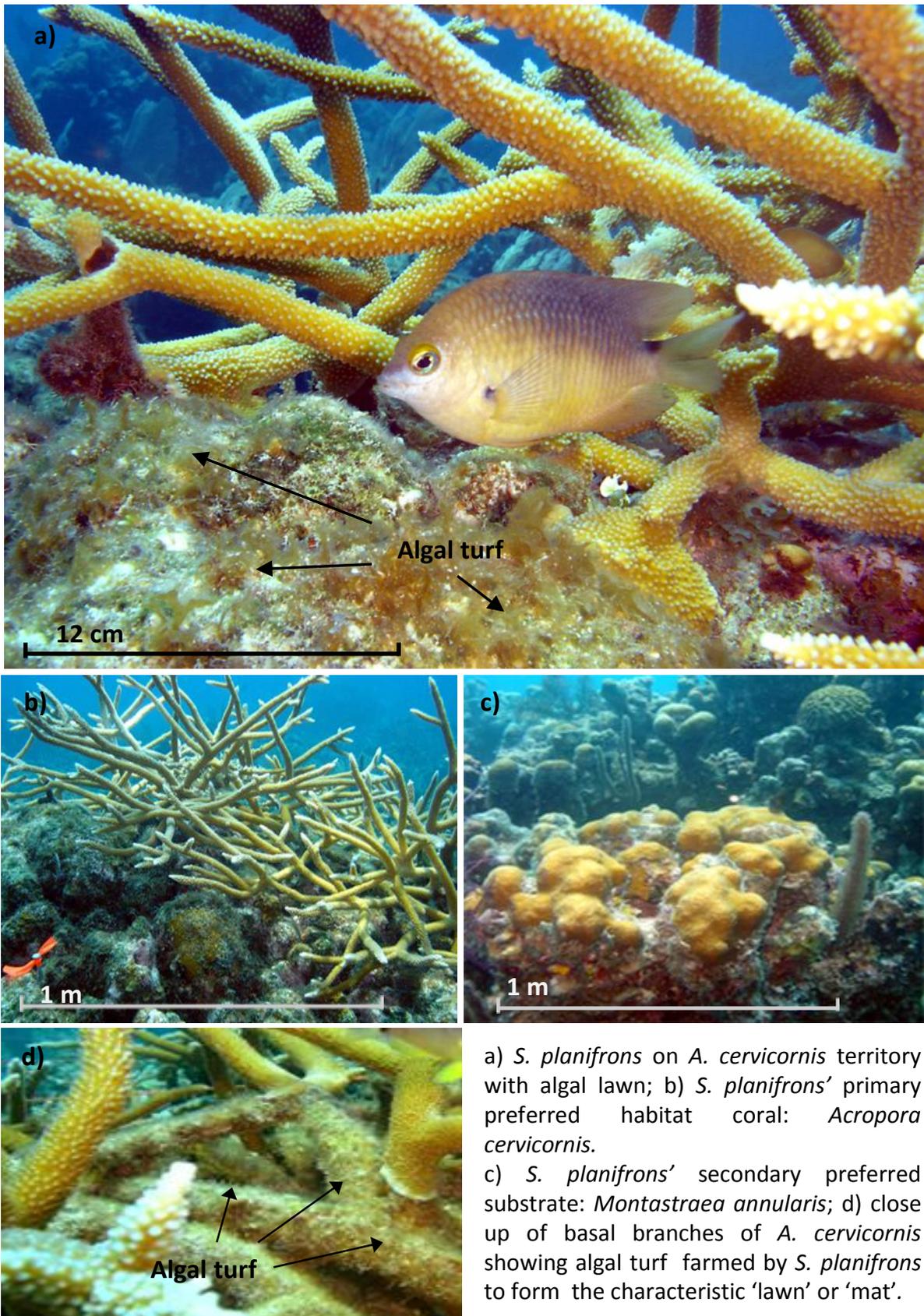


Figure 1.1 *Stegastes planifrons* and its habitat characteristics.

dominate the *A. cervicornis* habitat (Ebersole 1985). Other territory coral microhabitats such as *Montastraea annularis* (Tolimieri 1995), illustrated in Figure 1.1c, *Acropora palmata* (Brawley and Adey 1977b), *Agaricia spp* (Robertson et al. 1981, Lirman 1994), *Zoanthus* beds (Brawley and Adey 1977b), and various massive coral and rock substrates (Itzkowitz 1977a), are generally used only as a secondary or tertiary option.

High turf cover of damselfish territories has been attributed to one or a combination of the following effects, which a 'farmer' damselfish may exert within its territory confines: i) aggressive exclusion of roving herbivorous fish and urchins, resulting in reduced overall herbivory within the territory compared to the external reef (Brawley and Adey 1976, 1977b, Itzkowitz 1977b, Williams 1980a, 1981), ii) possible fertilisation effects of fish metabolic waste and by-products on territory algae (Klumpp et al. 1987), and iii) "gardening" or "farming" activities of the damselfish where weeding and /or constant cropping of the algae favours palatable turf species, and also maintains these algae in a fast growth phase, preventing community succession beyond the highly productive 'turf' phase, e.g. (Lassuy 1980, Sammarco 1983, Klumpp et al. 1987, Ferreira et al. 1998, Ceccarelli et al. 2001a). Like many of the other Pomacentridae (Ceccarelli et al. 2001a), the territories of *S. planifrons* have been much documented as clearly visible on the reef as distinct algal turf patches ("lawns", or "mats") of relatively dense algal growth (Figure 1.1), apparently defended from intruding macro-grazers by the resident damselfish (Itzkowitz 1977a, 1977b, Williams 1979, 1980a, Robertson et al. 1981, Williams et al. 1985). *S. planifrons* can derive all its dietary needs from within its territory (Robertson et al. 1981), and has been widely shown to manipulate benthic communities within its territory confines, ostensibly to promote growth of the algal turf mat. *S. planifrons* has also occasionally been shown to bite and kill areas and small colonies of both *Acropora* and *Montastraea* within its territories, thereby apparently extending the area of coral substrate under algal cultivation (Kaufman 1977, Robertson et al. 1981).

Individual *S. planifrons* mats are around 70 cm in diameter (Lobel 1980), and together they can be virtually contiguous on some shallow reefs (Robertson et al. 1981, Ebersole 1985), although they may be more widely spaced at deeper locations (Brawley and Adey 1977b). Due to the significant amounts of space that can be occupied, by

extrapolation it has therefore been suggested that due to the high algal biomass and modification of benthic communities within territories, and perceived exclusion of other important grazers, damselfish territories may play an important trophic role at the reef-wide scale (Ceccarelli et al. 2001a). The extent of their within-territory effects has led several damselfish to be allocated ‘keystone’ status (Ceccarelli et al. 2001a). *S. nigricans* has been called a ‘key ecosystem engineer’ (White and O’Donnell 2010), and the Hawaiian damselfish *Stegastes fasciolatus* has also been suggested to act as a ‘keystone species in reverse’ for the high algal diversity of its territories, which has been seen as a sign of intermediate disturbance mediated through the damselfishes direct actions on the algal turf, as well as the exclusion of other roving herbivorous fish (Hixon and Brostoff 1983a). Although sometimes referred to as a keystone species in general terms for its effects on benthic communities both inside and outside of its territories, the threespot damselfish was in fact initially given this status for its ability to mediate competitive interactions between two important grazers of Caribbean systems: the previously ubiquitous keystone urchin, *Diadema antillarum*, and the less voracious urchin *Echinometra viridis* (Williams 1980a, 1981). However, these studies were prior to the 1983 mass die-off of *Diadema antillarum* (Sammarco 1980, Lessios et al. 1984, Liddell and Ohlhorst 1986, Bauer and Agerter 1987, Williams and Williams 1987, Greenstein 1989). Despite the now “functional extinction” (Mumby et al. 2006) of *Diadema* from the Caribbean system, the keystone status of *S. planifrons* has never been revisited. A further and more detailed introduction to the keystone species concept is given next.

THE KEYSTONE SPECIES CONCEPT

The concept of a keystone species originated from work by Paine in the late 1960s (Paine 1966, 1969), who first used the term in relation to a situation where feeding by a predator (in this case the rocky shore starfish *Pisaster ochraceus*) prevented local competitive exclusions by its prey species, thereby indirectly maintaining a state of high diversity in the localised habitat. Paine stated that experimental removal of the carnivorous *Pisaster* starfish top predator was accompanied by local extinctions of several invertebrate and algal species, due to the loss of the moderating influence of the

top predator, which had previously prevented dominance by otherwise competitively superior species within the community (Paine 1966). Paine's original concept was that keystone species are those that exert 'influences on the associated assemblage, often including numerous indirect effects, out of proportion to the keystone's abundance or biomass'. The keystone species concept was readily adopted by the scientific community, mostly due to the perceived conservation value of the identification and preferential preservation of such species that are likely to exert large impacts or controls over a wider community level (Payton et al. 2003, Cottee-Jones and Whittaker 2012).

Whilst Paine's use of the word keystone referred conceptually to the keystone of an arch, and was used in relation to a species whose presence maintained or perpetuated a particular stable ecological state, this concept has since been extended widely, to include non-predatory species, and even inanimate objects such as logs in riverine systems, which have been termed 'keystone architects'; the main requisite 'keystone' attribute being that the animal or object has an impact on its community or ecosystem of a magnitude "disproportionately large relative to its abundance" (Power et al. 1996). The concept has been so readily adopted by the scientific community that Paine's original 1966 paper has now been cited at least 2509 times, with the term 'keystone species' featuring in the titles or topic descriptions of 1600 articles as of September 2012 (Cottee-Jones and Whittaker 2012). Indeed, the term has been used with such a variety of interpretations that, notwithstanding attempts to redefine the concept in the 1990s (Paine 1995, Power et al. 1996), there is now such significant disparity in its applications that it has been recently suggested that there is now "considerable confusion" over what exactly constitutes a keystone species (Cottee-Jones and Whittaker 2012), where no single definition now exists (Mills et al. 1993, Cottee-Jones and Whittaker 2012).

In the most recent attempt to review of the keystone species concept (Cottee-Jones and Whittaker 2012) the authors came to the conclusion that there were two options: i) "...formulate a specific definition of 'keystone', with testable quantitative thresholds, which would allow researchers to discard or include the wealth of species currently listed as keystones", or ii) "...use a general definition that encompasses the current interpretation of the keystone concept, which can be broadly applied, and which has no quantifiable thresholds or criteria". Despite the authors stated scientific preference for the former they concluded that the more practicable resolution would be to settle on the following definition: 'a keystone species is a species that is of demonstrable importance

for ecosystem function’, whilst noting that the generality of this definition may in reality just emphasise that the term has now become so vague that it has become a panchreston. For this reason in this thesis it has been chosen to adhere to an updated definition in the spirit keystone concept, that of a ‘species that exert influences on the associated assemblage, often including numerous indirect effects, out of proportion to the keystone’s abundance or biomass’ (Paine 1995).

OUTLINE OF THE PRESENT STUDY

Many of the classic studies of Caribbean damselfish ecology were conducted prior to the recent wide-scale ‘phase shift’ of Caribbean reefs (Thresher 1976b, Brawley and Adey 1977b, Kaufman 1977, Potts 1977, Itzkowitz 1977a, 1977b, Williams 1978, Irvine 1980, Williams 1980b, Hay 1981, Mahoney 1981, Robertson et al. 1981, Sammarco and Carleton 1981, Schmale 1981, Risk and Sammarco 1982, Sammarco and Williams 1982, Hixon and Brostoff 1983b, a). In the intervening time, Caribbean reefs have seen wide-scale losses of *S. planifrons*’ primary habitat, *Acropora cervicornis*, which is now designated a Critically Endangered species (Aronson et al. 2008). Additionally, *Diadema antillarum*, the critical urchin species that *S. planifrons* acted upon when it was first termed a keystone species (Williams 1979, 1980a) has now been termed “functionally extinct” in the Caribbean (Mumby et al. 2006). The alteration of benthic communities which has occurred since the *Diadema antillarum* mass mortality of 1983 could be expected to have had secondary effects on the composition of damselfish territories, as well as the wider reef (Hughes et al. 1985, Hughes 1994).

In addition to the possible changing relative role of *Stegastes planifrons* due to wider scale changes in Caribbean reef ecology, some fundamental attributes of its ecology have never been fully examined. Due to large amounts of space occupied by *S. planifrons* territories, it has been much speculated that effects of the exclusion of roving grazing fish from these areas may have important consequences at the reef-wide level; however no study has yet attempted to quantify such effects (Ceccarelli et al. 2001b, 2005a).

Here we set out to establish the role of the threespot damselfish *Stegastes planifrons* in contemporary Caribbean reef ecology, with specific attention to the following areas of focus as given in the chapter outlines below.

In Chapter 2, we examine the distribution of modern day *S. planifrons* populations in relation to the availability of different coral microhabitats at Glovers reefs, Belize. We then go on to experimentally examine habitat choice in the absence of competition and other extrinsic factors. Implications of the discrepancy between the two are then discussed in terms of habitat modification by *S. planifrons*.

Chapter 3 reveals a previously undocumented association between *S. planifrons* and incidence of white disease in its primary habitat coral, *Acropora cervicornis*. The current Critically Endangered status of *A. cervicornis* is due to previous Caribbean-wide mortalities due to a white disease (Aronson et al. 2008) with similar etiology to that observed here.

Chapter 4 examines the extent to which roving grazing fish are prevented from feeding within territories, as well as revealing a previously un-documented coral substrate effect on the grazing of roving herbivorous fish. These trends are examined in terms of ecological implications at the reef-wide level, as well as new insights into *S. planifrons* territory preferences and niche diversification within the damselfish community.

Chapter 5 goes on to examine the relative importance of damselfish territory presence versus coral substrate in determining algal functional communities on modern day Caribbean reefs. These findings are discussed in terms of the ecological implications for the wider reef, as well as the implications for *S. planifrons*' keystone status.

Chapter 6 comprises an overall assimilation and discussion of the principle findings of the experimental chapters and further examination of the validity of the keystone role of *S. planifrons* in contemporary Caribbean reef ecology, and the conservation implications of the study findings. There are concluding remarks in view of escalating rates of environmental change, and species extinctions.

This work has been conducted so that each analytical chapter presents a largely self-contained study, to be later submitted as an individual papers for publication. In the long term the resulting information from this thesis will be incorporated into large-scale predictive models investigating reef resilience, from which contemporary damselfish effects are currently lacking (Mumby and Dytham 2005). Such models enable the identification of important processes in reef ecology and the prediction of possible future ecological scenarios, and therefore will ultimately assist managers and policy makers by providing information necessary to the reef management decision making process.

This general introduction provides a contextual overview of the thesis, whilst a more specific review of the pertinent literature is given at the start of each chapter.

THE STUDY SITE: GLOVERS REEF ATOLL, BELIZE.

Glovers Reef atoll is a small island located 40 km offshore of the Central American country of Belize, in the Caribbean Sea (Figure 1.2). The atoll is located offshore from the Meso-American Barrier reef, which runs South from the Yucatan peninsula of Mexico through Belize, with its southern tip extending down to Honduras, and can be seen as an area of pale blue shallower reef in Figure 1.2b. Glovers reef is a large atoll with an enclosed relatively shallow inner lagoon composed of a largely sediment bottom studded with patch reefs. Outside the ring of islets and reef that make up the edge of the atoll the fore reef shelves to a drop-off and then to the ocean floor. Study sites were entirely located on the outer fore-reefs of the atoll, on both the east and west sides, whilst the research station was located at Middle Caye, on the eastern side of the atoll (Figure 1.2c).

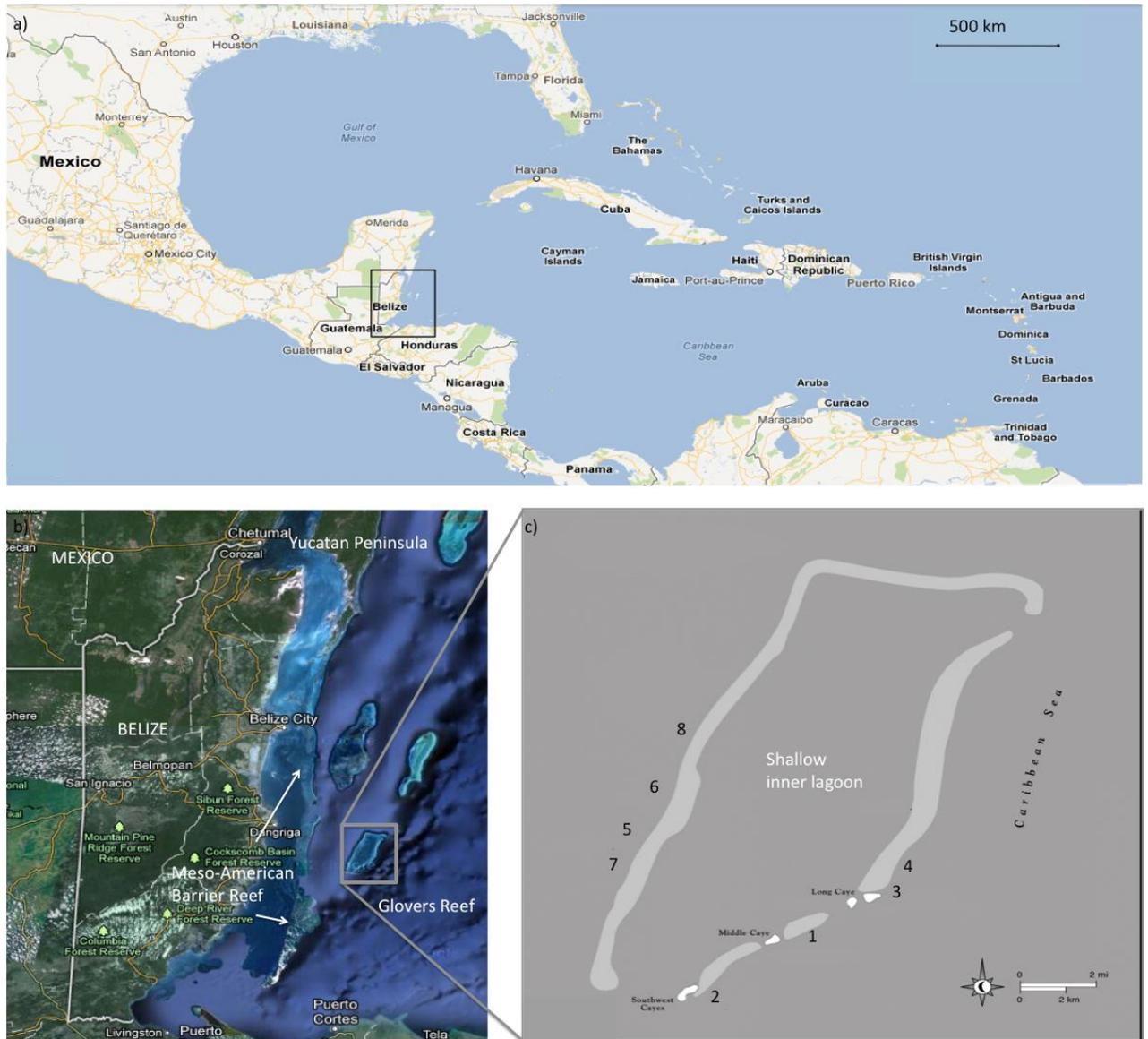


Figure 1.2 Location of Glovers Reef Atoll and study sites.

Location of Belize in Central America; b) Location of Glovers Reef atoll in Belize; c) Location of study sites at Glovers Reef atoll. Note that the research station was located on Middle Caye. Images courtesy of Google maps.

CHAPTER 2

*Habitat Choice in *Stegastes planifrons* on Contemporary Caribbean reefs*

ABSTRACT

Stegastes planifrons' predilection for basing its territories on the Critically Endangered staghorn coral, *Acropora cervicornis*, and secondarily the Endangered boulder coral *Montastraea annularis* is well known, however the likely ecological implications of this fact have not been investigated. Here we assess the coral microhabitat use of present day *S. planifrons* at Glovers Reef atoll (Belize), with particular attention to relative cover of live and dead corals within territories. On the basis of microhabitats preferentially used *in situ* we constructed replica artificial 'habitats' in a five-way choice pool experiment, in order to determine *S. planifrons* habitat preferences in the absence of competition or other confounding factors. Given the choice of uninhabited substrates reflective of those contained within *S. planifrons* territories on the fore-reef, fish spent significantly more time on H1 (100% live *Acropora*), than on any other habitat, including H2, which was designed to be reflective of the substrate they primarily based their territories upon on the reef (50% live *Acropora* and 50% dead carbonate branches with extant algal communities). Fish were then seen to bite at high rates (35 bites hr⁻¹) on corals which made up H1, but despite forays to other habitats in which fish fed significantly more on algae (13 bites hr⁻¹) than other possible food sources, fish rarely bit corals on other habitats at all. Bite rates totalled across all non-H1 corals were significantly lower (1.5 bites hr⁻¹; $p < 0.05$; glm) than those seen on H1, suggesting that this behaviour was not purely feeding behaviour, but was aimed at modification of the chosen habitat. Coral biting by *S. planifrons* has previously been documented as a method of killing coral to extend the algal mat (Kaufman 1977, Robertson et al. 1981) and the observation here of signs of necrosis and algal filaments appearing at biting spots by day 4 of the experiment suggests that this would have been the outcome over longer time-scales. The selection of a habitat with no algae present and the observed trend of coral biting in conjunction with the rapid growth of filamentous algae seen here, and elsewhere (Kaufman 1977, Robertson et al. 1981, Wellington 1982), suggests that damaged coral tissues may provide a better medium for the growth of turf algae than carbonate branches with pre-existing algal communities. These results imply a likely feedback process whereby *Acropora* loss (due for example to storms, disease, or bleaching) has implications beyond the initial reduction in live coral cover, since dispossessed resident *S. planifrons* populations are likely to adopt

healthy coral stands and begin biting coral tissues, rather than adopt previously degraded stands with pre-existing, but un-‘farmed’ algal communities.

KEY WORDS: Damselfish; *S. planifrons*; *Acropora cervicornis*; *Montastraea annularis*; coral biting.

INTRODUCTION

In common with all the Pomacentridae *Stegastes planifrons* is a territorial gardening fish, and maintains an algal territory, “lawn” or “mat”, for its own use by the exclusion of a high proportion of grazing fish and invertebrates from its territories (Brawley and Adey 1977b, Ceccarelli et al. 2001a). Individual mats of this species are around 70 cm in diameter (Lobel 1980), and together can be virtually contiguous on some shallow acroporid reefs (Robertson et al. 1981, Ebersole 1985), although they may be more widely spaced at deeper locations (Brawley and Adey 1977b). *S. planifrons* can derive all its dietary needs from within its territory (Robertson et al. 1981), and has been widely shown to manipulate benthic communities within its territory confines, ostensibly to promote growth of the algal mat, this is achieved by a variety of methods, including protection from roving grazers, and the selective ‘weeding’, and cropping of algal species (Brawley and Adey 1977b, Hinds and Ballantine 1987). *S. planifrons* has also previously been shown to bite and kill areas and small colonies of both *Acropora* and *Montastraea* within its territories, thereby extending the area under algal cultivation (Kaufman 1977, Robertson et al. 1981). Although Kaufman (1977) has previously suggested that the killing of the basal branches of *A. cervicornis* may allow access by boring organisms, ultimately weakening the internal carbonate matrix, and making these corals more susceptible to storm damage, the extent to which coral biting behaviour may impact on corals at the wider scale remains largely unknown. Further, it has never been established how the algal mat comes about when *S. planifrons* inhabits a new territory area, or if it is necessary for the damselfish to bite corals in order to establish an algal mat, or whether they will preferentially colonise corals which already have a high proportion of algal cover, as it might be postulated that a productive algal mat can then be established more quickly, and at a lower energetic cost to the damselfish.

Studies of territorial substrata indicate that the territorial damselfish *S. planifrons* has a high affinity for the branching staghorn coral *Acropora cervicornis*, which it uses as its primary preferred habitat (Brawley and Adey 1977b, Itzkowitz 1977a, 1977b, Robertson et al. 1981). *S. planifrons* is not limited to *Acropora*, however, and also commonly utilises *Montastraea annularis* as a secondary option (Itzkowitz 1977a, 1977b, Tolimieri 1995), and less commonly *Acropora palmata* (Brawley and Adey 1977b), *Agaricia* spp (Robertson et al. 1981, Lirman 1994), *Zoanthus* beds (Brawley and Adey 1977b), and various massive coral and rock substrates (Itzkowitz 1977a).

Over the last thirty years there has been a massive and widespread decline in the cover of *Acropora cervicornis* on Caribbean reefs, to the point that this once common reef building species is now listed as a Critically Endangered species (Aronson et al. 2008). The primary source of this decline was an outbreak of white band disease, which spread rapidly throughout the Caribbean in the late 1970s and early 1980s, causing mass mortality in acroporid species across the entire region (Gladfelter 1982c, Bythell et al. 2000, Aronson and Precht 2001, Aronson et al. 2002a, Aronson et al. 2002b, Precht et al. 2002, Schutte et al. 2010), with live cover reductions of 95% or more occurring in many areas (Aronson and Precht 2001, Precht et al. 2002). This initial loss has subsequently been further compounded by the effects of coral bleaching (Hughes 1994), as well as hurricanes, which have a particularly high impact on *Acropora cervicornis* in comparison to massive corals because of its branching thicket-like superstructure, combined with its habit of growing on relatively shallow reefs, where the effects of rough weather and storm surge are felt most intensely. Caribbean reefs have a history of periodic exposure to large scale disturbance events, and with the forecast of worldwide increases in both the prevalence and severity of extreme weather events under future climate change scenarios (Goldenberg et al. 2001), further disruptions to *A. cervicornis* populations are likely. By virtue of their effects on coral substrata such events have been shown to impact on habitat availability for damselfish territories (Knowlton et al. 1981, Kaufman 1983, Mumby 1999, Ostrander et al. 2000), When Hurricane Allen struck Jamaica in 1980, it caused severe destruction of branching Acroporid corals, the primary habitat of *Stegastes planifrons* (Kaufman 1983). Kaufman's account also details an immediate and widespread disruption of fish behaviour patterns, including altered feeding patterns, territoriality, and social and reproductive behaviour. More recently research has documented a possible shift of *S. planifrons* populations from the primary preferred *Acropora* substrate (Itzkowitz 1977a, 1977b) onto its secondary substrate, *Montastraea annularis* (Precht et al. 2010)

With large losses of *S. planifrons*' primary habitat, *Acropora cervicornis*, having occurred over the last 30 years and looking set to continue in future, this provokes the question of the likely short-term ecological outcomes of the dispossession of *S. planifrons* due to death or destruction of habitat corals (for example by disease, hurricanes or bleaching). One expectation is that the habitat choice of dispossessed fish would reflect the microhabitat associations of current of populations on the reef, both in terms of coral species and extent of live cover (where such substrates are still available).

The alternative hypothesis is that the territories are chosen for broad microhabitat characteristic, but then benthic composition is further modified to suit the needs of the fish.

Here, we examine habitat choice in *Stegastes planifrons*. We firstly identify the characteristics of extant *S. planifrons* territories with a survey of habitat composition of territories on the fore-reef of Glovers Reef Atoll (Belize). Secondly, by means of a five-way choice pool experiment we test the preference and avoidance of *S. planifrons* subjects to a selection of uninhabited substrates reflective of those microhabitats primarily utilised on the reef. Fish biting behaviour is recorded throughout the experiment to provide insight into the likely ecological consequences of habitat choice.

METHODS

Reef surveys

Stegastes planifrons densities and substrate utilisation surveys were conducted on the fore-reef of Glovers Reef atoll between June and August 2005. Damselfish densities were surveyed using belt transects of 2m wide x 20m in length; *S. planifrons* numbers were recorded along with the substrate occupied by each fish and percent live cover of this substrate. Percent live coral cover was estimated by eye, following several months in the field where accuracy of this technique had been checked with comparisons of visual estimates and photographic quadrats, revealing a mean agreement of +/- 5%. Thirty haphazardly located transects were completed between 4m and 15m depth (i.e. to the fore-reef drop-off at the study site), and over three different Cays: Middle Cay, Long Cay, and Southwest Cay.

Acropora cervicornis and *Montastraea* microhabitats were surveyed independently in order to record the proportion of live and dead cover of each species. Seventy *Acropora cervicornis* patches were surveyed at the same three cayes as the damselfish survey (Long Cay, Middle Cay, and Southwest Cay.) A one-hour underwater search was carried out at each location, and the relative proportion of live and dead cover was recorded for every structurally intact *Acropora* patch found. Dead corals were considered structurally intact when their height and three dimensional structure was visually similar to that of live *Acropora* on the reef, 40 cm used as a minimum height, reflecting the height of smaller healthy colonies. *Montastraea* percent live cover was calculated from photographs of haphazardly selected colonies within four survey sites on the east coast (n = 102 colonies); these sites were again from the same three cays, although two sites separated by 200m were located on Middle Cay, due to its expansive area.

Habitat choice Experiment

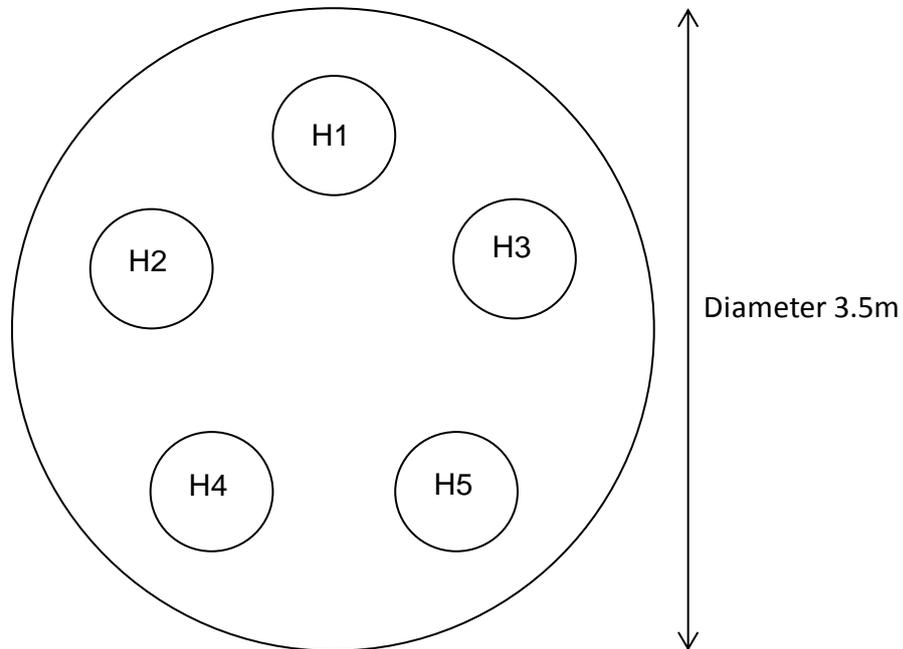
A five-way habitat choice experiment was conducted in order to examine what substrates *S. planifrons* would choose to establish territories on if presented with a

choice of uninhabited substrates representative of those they had been found to occupy on the reef.

Five different habitats were constructed inside a large 3.5 m diameter tank with a volume of approximately 7 m³. Habitat treatments were composed of live and dead corals (with their naturally occurring algal communities) were collected from 10 – 12m depth on Middle Cay reef under permit, with individual habitat treatment composition as described in Table 2.2. No 100% live *Montastraea* treatment was employed, since this habitat was very rarely available on the extant reef; and in addition the necessary amount of coral collection was deemed too destructive. Artificial habitats were constructed to match the observed characteristics of equivalent habitats on the reef – thus *Acropora* branches were arranged into upright thickets, and *Montastraea* ramets were arranged to replicate the subdivided surfaces of naturally occurring *Montastraea* colonies. Diameter of all habitats was 70 cm, reflecting average territory sizes recorded in the literature (Ebersole 1977, 1985). Habitats were positioned 40 cm from the perimeter of the pool and arranged equidistantly from each other (Figure 2.1). In order to avoid any potential confounding of the experiment by internal or external spatial factors the relative positions of habitats were randomized between replicates. In order to avoid possible confounding by differing availability of refugia, each habitat also had an underlying base of carbonate substrate pieces, arranged so as to provide cryptic refuges for treatment damselfish. These refuges were standardized between treatments and across replicates in terms of approximate diameter and height (relief), which were 60 cm 20 cm respectively. Carbonate substrates were originally of reef origin, but had been bleached in the sun for many months, then scrubbed thoroughly in fresh water prior to use. The tank was located outdoors but in full shade and was fed with reef water on a pumped flow-through system. All tank contents were changed between replicates.

S. planifrons experimental subjects were collected on SCUBA from depths of 8 – 10 m. Individuals were subdued underwater using clove oil so that two divers with aquarium nets were able to catch them, they were then each placed inside a ziplock bag which was rigidly filled with water and sealed. Fish were transported slowly to the surface in order to avoid injury by pressure change, once on land they were kept in individual holding

tanks for a recovery period of two to four days prior to experimental use. Different fish were used for each replicate of the experiment.



Habitat	Treatment	Algal cover
H1 (Habitat 1)	<i>Acropora cervicornis</i> : 100% live	0%
H2 (Habitat 2)	<i>Acropora cervicornis</i> : 50% live + 50% dead (structurally intact)	50%
H3 (Habitat 3)	<i>Acropora cervicornis</i> : 100% dead (structurally intact)	100%
H4 (Habitat 4)	<i>Montastraea annularis</i> : 50% live + 50% dead	50%
H5 (Habitat 5)	<i>Montastraea annularis</i> : 100% dead	100%

Figure 2.1 Planar diagrammatic representation of habitat arrangement in pool. H1 – H5 = habitats 1 – 5, with composition as detailed in the inset table. Relative positions of habitats were randomized between replicates.

Each replicate began at 08:00, when a single damselfish was introduced into the centre of the pool and allowed to swim freely. Observations began immediately and continued for thirty minutes; subsequent thirty minute observations periods were conducted at 12:30 and 16:30; these three observation periods were repeated each day until a total of eight observation periods was reached (three periods on days 1 and 2, and two on the final day.) Fish were monitored for five days in total for the first three replicates, but it was found that habitat use did not change after day two, so subsequent replicates were run for 8 observation periods with the aim of achieving a greater number of replicates within the available time for the experiment. Seven replicate experiments were run sequentially throughout August – September 2005, each with an entirely new s. Fish

behaviour was quantified in terms of time spent on different habitats and bites taken from coral, algae, and carbonate surface biofilms. The location of the fish was recorded at the start of each observation period, then habitat use was recorded in terms of fish arrival and departure from different habitats in real-time, with the last observation being the position of the fish at the end of the monitoring period. Although spent most of their time close to habitat substrates (less than 10 cm above surfaces), for analytical purposes fish were considered to be associated with a given habitat when they were within 15 cm of the artificial substrate. During periods when fish were not associated with a habitat a code was used to indicate either travelling directionally or hovering, however fish were rarely observed to spend time over open sand, except when travelling directionally from one habitat to another. Bites taken within habitats were allocated to coral, algae, or carbonate surface biofilm categories for that habitat.

Data treatment and statistical analyses

Analyses of field survey data were conducted using standard analysis of variance (ANOVA) and t-tests.

For the tank experiment a daily measure of % time spent at each habitat was calculated for each replicate fish by summing time spent at each habitat for all observation periods in a given day then converting to a percentage of observed time. Since there were 7 replicate fish this achieved $n=7$ independent values for % time spent at each habitat for each day of the experiment. On the basis that fish utilising habitats at random would be expected to spend 20% of their time at each habitat on average (being 5 habitat choices in total), the Student's t test was then used to test for significant differences between the time spent by replicate fish on each habitat, and 20%. Since it was hypothesised *a priori* that H2 would be the preferred habitat with fish spending significantly more time at H2 than would be expected at random a single tailed approach was used for this habitat. For the other habitats, since there was no *a priori* hypothesis specified of either significantly more, or significantly less time spent than would be expected if the fish split its time at random (i.e the test for significance could have indicated either more or less time spent at a given habitat), a single tailed test could not be justified, and a two-tailed test was used to detect any significant departure from random behaviour.

Count data relating to all fish bites observed on each feeding substrate type (coral, algae, or rock surface film) were summed for all observation periods over the duration

of the experiment for each replicate fish. Replicate 2 was omitted from fish biting behaviour analyses, because no bites were observed during the experiment, whereas bites from other replicates numbered in the hundreds.

Experimental bite count data were analysed using the software package, “R” to employ mixed models, using a quasi-poisson distribution. In all mixed models a result of $t > 2$ was taken to be significant at the $p < 0.05$ level, as given in Crawley, 2007. Models used were as follows:

Examination of total bite numbers by substrate:

```
FIT <-bites~substrate + (1 | Replicate)
```

Where: bites = total number of bites; substrate = coral, algae, or carbonate substrate biofilm. Distribution: quasi-poisson.

Examination of total feeding rates by substrate:

```
FIT2<-lmer(bites.hr~Substrate+(1|Replicate))
```

Where: bites.hr = feeding rate in bites per hour; substrate type = coral, algae, or carbonate substrate biofilm. Distribution: Gaussian.

RESULTS

RESULTS PART 1: Utilisation of fore-reef microhabitats at Glovers Reef by present day *Stegastes planifrons* populations.

Acropora cervicornis and *Montastraea annularis* were by far the main coral microhabitats utilised by *S. planifrons*, the population being split almost equally between the two substrates with around 47% of the population on each (Figure 2.2). On the basis of these results further investigations were confined to the use of these two predominant habitat substrates, *Acropora cervicornis* and *Montastraea annularis*.

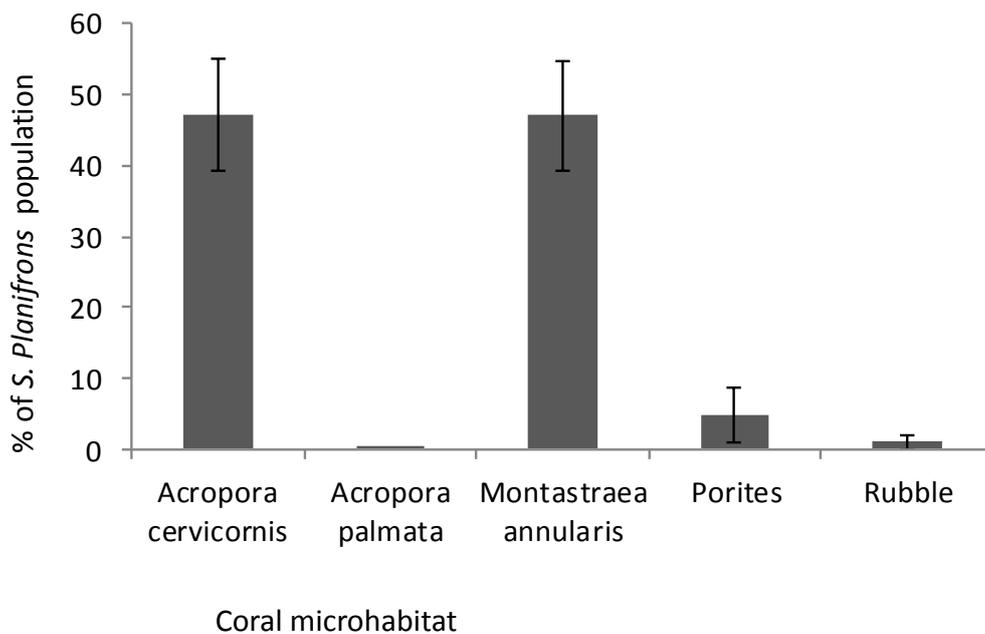


Figure 2.2. Distribution of *S. planifrons* populations by coral microhabitat (bars denote one standard error of the mean; n = 88 fish).

Density and relative use of *Stegastes planifrons* territories on *Acropora* and *Montastraea* microhabitats are illustrated in Figure 2.3. Densities of *M. annularis* and *A. cervicornis* territories were not significantly different at the reef wide level (Fig 2.3a), despite the availability of the *M. annularis* habitat being much higher (Fig 2.3b).

This reflected the increased saturation of the *Acropora* habitats relative to *Montastraea* habitats (Figure 2.3 a; b). Whilst *Stegastes planifrons* occupied almost all available live and dead (structurally intact) *Acropora* substrate, occupancy of the *Montastraea* microhabitat was generally lower, with a mean of approximately 45% of partially live corals (10 – 100% live cover) as opposed to around 35% of dead colonies (0 – 10% live cover) (Figure 2.3b). *Montastraea* was by far the more abundant of the two microhabitats, with a mean cover of around 45%; however this mainly consisted of dead coral cover, which occupied more than 40% of the reef. Live *Acropora cervicornis* occupied around 8% of the reef on average, with dead structurally intact cover accounting for a further 3% (Figure 2.3b).

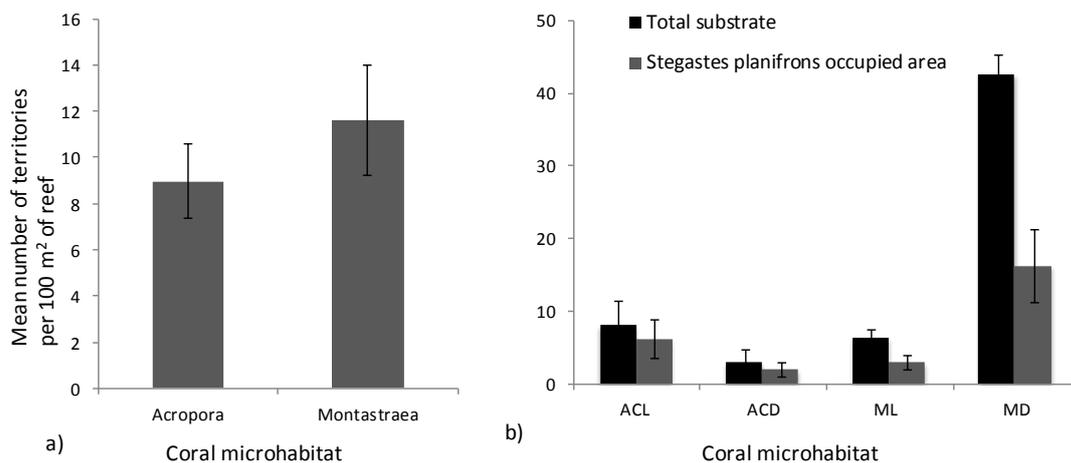


Figure 2.3 Density and distribution of fore-reef *Stegastes planifrons* territories on the fore-reef.

a) Density of *Acropora* and *Montastraea* *S. planifrons* territories obtained from 30 x 20 m random transects (no significant difference between treatments; $p > 0.05$; t test) ; b) Availability of *Acropora* and *Montastraea* microhabitats, and area occupied by *Stegastes planifrons*. ACL = *Acropora cervicornis* live (10-90% live cover); ACD = *A. cervicornis* dead (< 10% live cover); ML = *Montastraea annularis* live (colonies where live cover ranged from 10% - 90%); MD= *M. annularis* dead (colonies where live cover was less than 10%). Error bars denote one standard error of the mean.

Damselfish territory characteristics.

Mean live coral cover in *S. planifrons* *Acropora* territories was 35%, which was significantly lower than the 70% mean live cover found on *Acropora* patches at the reef-

wide level ($p < 0.0001$; ANOVA; Figure 2.4a; Table 2.1). Note that these figures apply only to *Acropora* which is structurally intact, and do not take into account areas of older, more degraded *Acropora* rubble. Analysis of data from a detailed survey of the territory characteristics of four replicate *S. planifrons* territories located on *Acropora cervicornis* carried out in the late 1970s reveals a very similar degree of live coral cover, with a mean live cover of $29\% \pm 10.9\%$ (Table 2.3). Overall the majority (70%) of damselfish territories were located on *Acropora* structures with less than 50% live coral cover (ie. corals which were more live than dead), and only around 18% of territories were located on *Acropora* with 91 - 100% live cover (Figure 2.4b). In contrast, *S. planifrons* territories on *Montastraea* contained significantly higher levels of mean live cover than was found at the reef wide level, with relative values of 24% within damselfish territories compared to 8% overall ($p < 0.01$ ANOVA; Figure 2.5 a; Table 2.2). This suggests that *S. planifrons* exhibited a preference for live coral cover on the *Montastraea* substrate, since this was not saturated with *S. planifrons* territories it is possible that high live coral areas were favoured (Figure 2.3). Again the majority of *S. planifrons* territories were on low live cover corals with 70% having less than half live cover, and only around 5% having 91 – 100% live cover.

Table 2.1 ANOVA table for comparison of percentage live cover of *Acropora* inside *S. planifrons* territories and live cover of randomly surveyed *Acropora* patches on the reef (i.e. *Acropora* survey at random, regardless of damselfish occupancy.) *** = $p < 0.0001$

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Treatment	1	36969	36969	34.94	3.4e-08 ***
Residuals	115	121659	1058		

Table 2.2 ANOVA table for comparison of percentage live cover of *Montastraea* inside *S. planifrons* territories and that of the wider reef. (ie *Montastraea* surveyed at random, regardless of damselfish occupancy.) ** = $p < 0.01$

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Treatment	1	4962	4961.6	7.06	0.008 **
Residuals	130	91291	702.2		

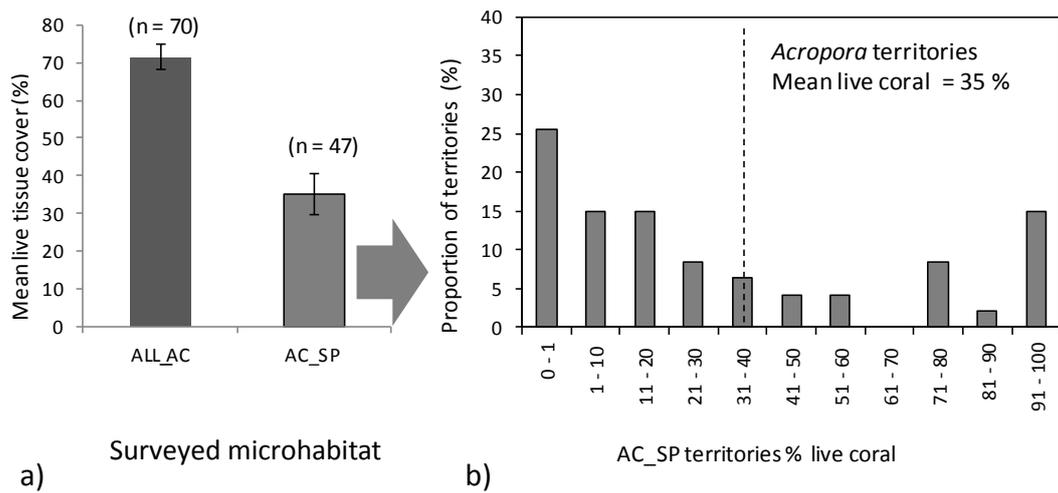


Figure 2.4 Relative abundance of live coral cover in randomly surveyed *Acropora* patches, compared to abundance of live cover in randomly surveyed *S. planifrons* territories. Coral cover was significantly different between treatments ($p < 0.05$; ANOVA). b) Distribution of *S. planifrons* territories on *Acropora* microhabitats in relation to % live coral cover; dotted line indicates the value of mean live coral cover across surveyed AC territories. ALL AC= Randomly surveyed *Acropora* patches; AC_SP = *Acropora cervicornis* inside *Stegastes planifrons* territories.

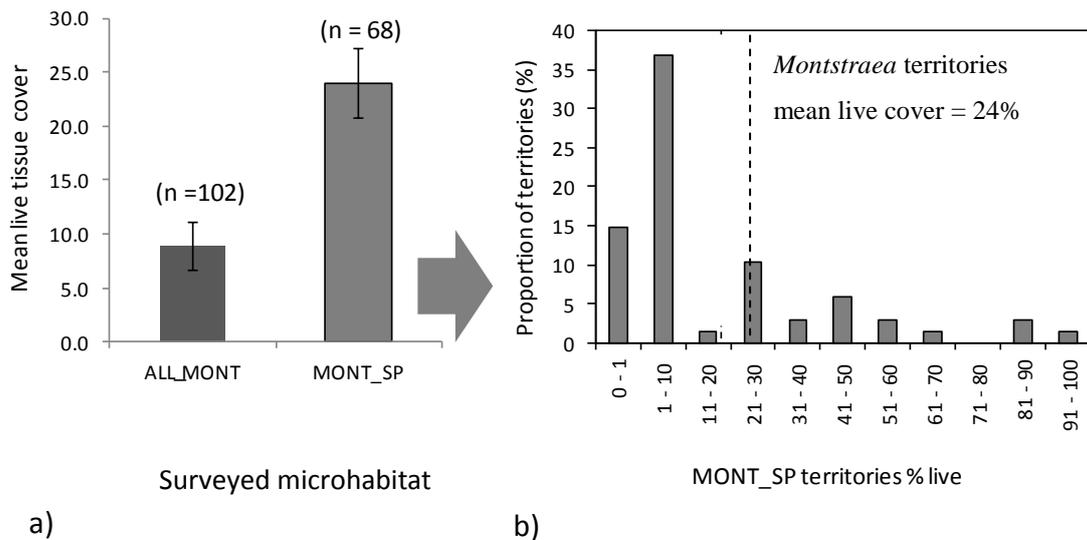


Figure 2.5 Relative abundance of live coral cover in randomly surveyed *Montastraea* colonies, compared to abundance of live cover in randomly surveyed *S. planifrons* territories. Coral cover was significantly different between treatments ($p < 0.05$; ANOVA) b) Distribution of *S. planifrons* territories on *Montastraea* microhabitats in relation to % live coral cover; dotted line indicates the value of mean live coral cover across surveyed MONT territories. ALL MONT = Randomly surveyed *Montastraea* colonies; MONT_SP = *Montastraea annularis* inside *Stegastes planifrons* territories. NOTE: Whilst mean live tissue cover in ALL_MONT is low, at less than 10%, higher values of live tissue within *S. planifrons* territories (MONT_SP) can be achieved by preferential occupation of high live tissue corals over low live cover corals. Figure b) does not contradict this since low availability of high live cover *Montastraea* in the environment overall can account for the low numbers of territories situated on these microhabitats.

Table 2.3 Live coral composition of *Stegastes planifrons* territories on *Acropora cervicornis* territories from the late 1970s.

Data from Lobel (1980). Grey box = original data. T1, T2, etc = territory replicates; AC = *Acropora cervicornis*.

	Area (m ²)				Mean	Standard Error
	T1	T2	T3	T4		
Dead AC with algal mat	0.1962	0.1277	0.1913			
Dead AC bare	0.0971	0.1284	0.1305	0.284		
Live AC	0.1346	0.3014	0.0712	0.0392		
Total AC	0.4279	0.5575	0.393	0.3232		
% live AC	31.5	54.1	18.1	12.1	28.1	10.7

In summary, modern day *S. planifrons* populations use corals with varying degrees of live cover on which to base their territories, but that the majority of territories are located on predominantly dead coral (< 50% live) substrates. It also appears from similar degree of live cover of *Acropora cervicornis* seen through analysis of data from Lobel (1980) (Table 2.3), and the current study that the overall mean live coral cover is likely a consistent feature of *S. planifrons* territories at around 30%.

RESULTS PART 2: Five way habitat choice pool experiment.

Habitat utilisation.

On release into the centre of the pool the majority of fish were observed to travel around the pool in a circular fashion, detouring to investigate the different habitats, but usually only lingering for a few seconds on each before moving on to the next. After several circuits, lasting between 5 – 10 minutes the fish tended to investigate the habitats more closely, often entering cryptic areas, and spending longer time periods on individual habitats.

Trends in habitat utilisation over the duration of the experiment are shown in figure 1. The Student's t test was used to examine the difference between the proportion of time fish spent at each habitat and 0.2, the proportion that would have been observed if fish split their time at random between the five habitats. The *a priori* hypothesis that fish

would favour habitat 2 (50% live *Acropora*, and 50% dead *Acropora* with algal cover) was rejected (Student's t test; $t = -2.822$, $df = 6$; $p \gg 0.05$). In fact fish were found to spend significantly more time at habitat 1 (AC 100% Live) than would be expected at random (two-tailed Student's t test; $t = 2.4253$, $df = 5$; $p < 0.05$), and were also found to spend significantly more time at H1 than any other habitat (glm; $p < 0.01$). In addition fish strongly avoided habitat 5 (100% dead *Montastraea*) (two-tailed test; $t = -13.35$, $df = 5$, $p < 0.01$). The two-tailed approach was used since this enabled a more robust test for a non-directional significant difference in use of the habitat to random, since this test was not based on an *a priori* hypothesis of fish avoidance of habitat 5 use of the one-tailed approach could not be justified. Habitats 3 and 4 were found to be neither significantly favoured nor avoided. With reference to Figure 1 it can be seen that the main trends in habitat utilisation were consistent from day one of the experiment, with fish spending significantly more time on H1 than would be expected at random, and strongly avoiding H5 consistently when utilisation was analysed on a daily basis. Use of habitat 2 was lower than random overall ($p < 0.05$; Student's t test).

Fish biting behaviour

A large degree of coral biting was observed in this experiment (Figure 2.7). Fish were found to bite significantly more on live coral substrates than on rock surface films ($t > 2$; linear mixed model; Table 2.4); but no significant difference was found in number of bites taken on coral and the number taken on algae, or between numbers of bites on algae and number taken on carbonate substrate biofilms (Figure 2.7).

Further examination of feeding behaviour was conducted within replicates where fish were considered to have adopted H1 as their primary habitat – i.e. replicates where fish spent significantly more time than expected at random on H1 ($n = 5$ out of 6 fish where feeding behaviour was observed). Within H1 fish biting rates were relatively high on coral with a mean of 35 bites hr^{-1} , but this rate was not found to be significantly different to feeding rates on rock surface films (mean of 16 bites hr^{-1} ; Figure 2.8; Table 2.1).

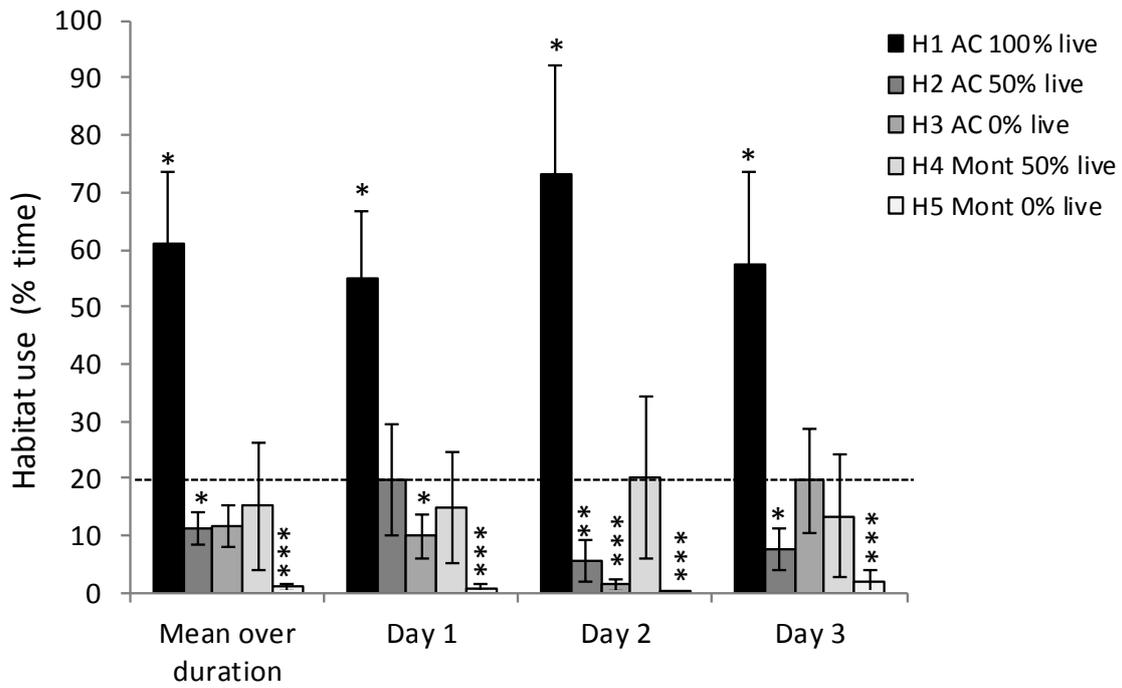


Figure 2.6 Mean % time spent by fish on each habitat over the course of the experiment, and by day.

Preference for habitat 1 was consistent from day 1, and throughout the experiment. H1, H2.. = habitat 1, habitat 2. etc. AC = *Acropora cervicornis*; Mont = *Montastraea*. Dotted line marks 20% level, i.e. the amount of time fish would spend at each habitat if they split their time randomly. Asterisks denote significant differences from 20% level using two tailed Student's t test for all habitats except habitat 2, where a-priori hypothesis that time spent would be higher than random allowed use of single tail approach (n=5): * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Error bars denote one standard error of the mean.

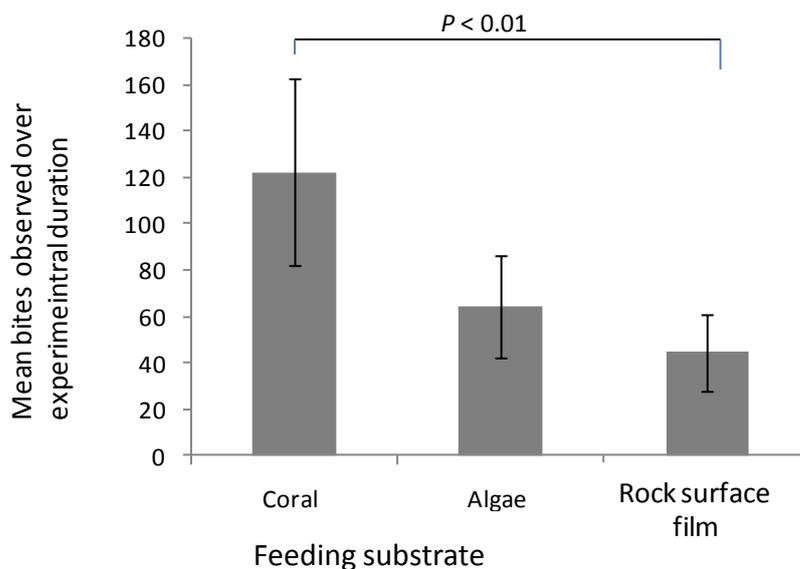


Figure 2.7 Mean of total bites observed on each substrate type across replicates where bites occurred

Bites observed over 8 x 30 minute periods over three days. Significantly more bites were taken on coral than on rock surfaces ($p < 0.01$; glm; n=7); no other differences were significant.

Table 2.4 Results of mixed model analysis of number of bites on coral substrates in comparison to those taken on algae and carbonate substrate biofilms.

Analysis using quasi-poisson distribution.

* = values of $t > 2$ are significant at a minimum of $p < 0.05$ (Crawley, 2007)

	Estimate	Std. Error	t value	Significance
Coral (Intercept)	3.77	5.5194	0.683	
Algae	-0.64	0.4304	-1.490	
Carbonate biofilm	1.01	0.4892	-2.064*	$p < 0.05$

Fixed effects:

Generalized linear mixed model fit by the Laplace approximation
 Formula: totalbites ~ substrate + (1 | Replicate)
 AIC BIC logLik deviance
 595.5 600.7 -292.7 585.5

Random effects:

Groups	Name	Variance	Std.Dev.
Replicate	(Intercept)	207.07	14.39
Residual		46.83	6.84

Number of obs: 21, groups: Replicate, 7

Table 2.5 ANOVA table for comparison of feeding rates (bites hr⁻¹) on habitat 1 coral in comparison to non-habitat 1 coral, algae, and carbonate biofilm substrates.

	Estimate	Standard error	t value	Pr(> t)
H1 Coral (Intercept)	35.04	7.89	4.44	0.0005
Non-H1 algae	-23.12	11.16	-2.07	0.05
Non-H1 coral	-34.40	11.16	-3.082	0.01
Non-H1 carbonate biofilm	-32.80	11.16	-2.939	0.01
H1 carbonate biofilm	-18.56	11.16	-1.663	0.11

Residual standard error: 17.65 on 20 degrees of freedom.
 F-statistic: 3.08 on 4 and 20 DF, p-value: 0.03961

Table 2.6 ANOVA results for comparison of feeding intensity (bites m² hr⁻¹) on habitat 1 coral and carbonate substrate biofilms.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Substrate	1	130089	130089	2.1254	0.183
Residuals	8	489647	61206		

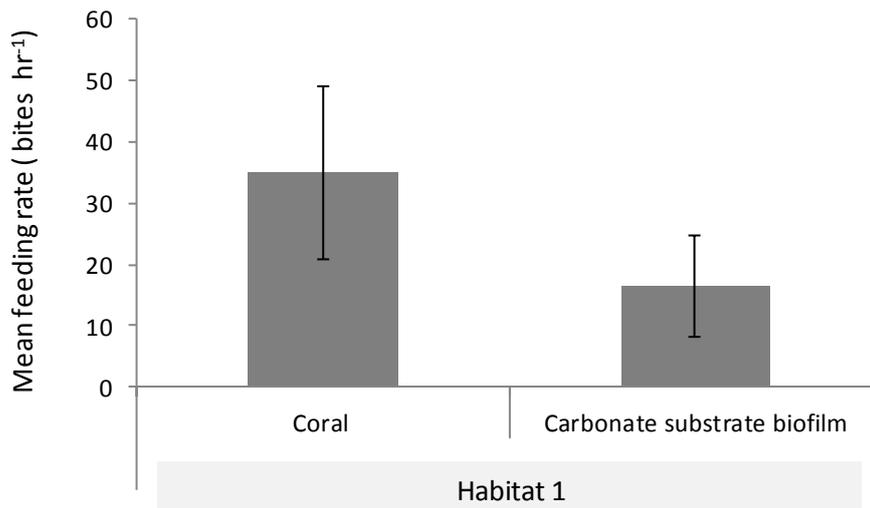


Figure 2.8 Feeding budget within Habitat 1 for fish that chose Habitat 1. No significant differences were found ($p > 0.05$; ANOVA). Error bars denote one standard error of the mean.

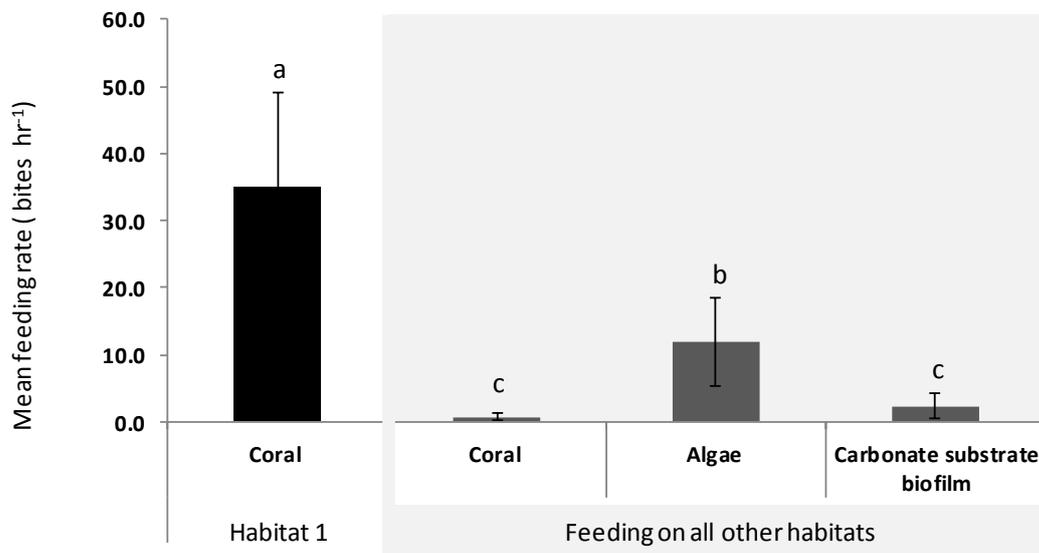


Figure 2.9 Feeding budget across habitats for fish that chose Habitat 1. Letters a, b, c denote groups found to be significantly different from each other ($p < 0.05$; ANOVA). Error bars denote one standard error of the mean. Fish fed on habitat 1 coral significantly more than on any other substrate, but when feeding on non-habitat 1 substrates they fed significantly more on algae than on other substrate types.

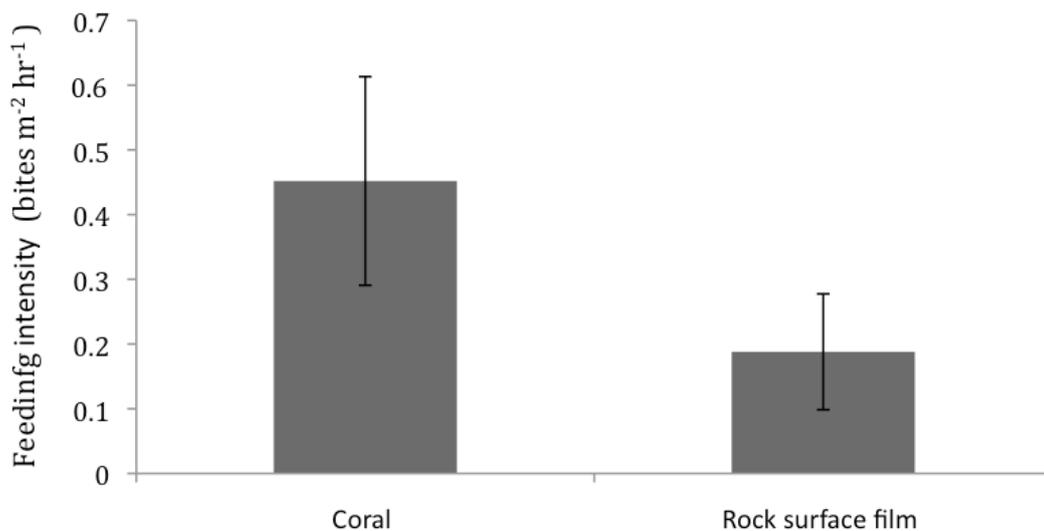


Figure 2.10 Feeding intensity on Habitat 1 substrates.

Feeding rates on H1 were also examined in relation to feeding rates on other substrates available on other habitats within the pool (Figure 2.9). Mean feeding rate on H1 corals was found to be significantly higher than on non-H1 substrates, with non-H1 algae ($p < 0.05$; ANOVA), as well as non-H1 corals, and rock surface films (both $p < 0.05$; ANOVA). Within non-H1 substrates fish feeding rates were significantly higher on algae than on both coral and rock substrates ($t > 2$; linear mixed model), indicating that when fish did choose to feed outside of their primary habitat they fed at a higher rate on algae than on the other available substrates. Within Habitat 1 a further investigation of feeding intensity revealed no significant difference in feeding intensity (bites m² h⁻¹) on live coral tissues compared to those on rock surface films (Figure 3; Table 2.6).

General observations

During the course of the experiment it was noted that fish tended to bite repetitively at the same locations, revisiting them at intermittent time intervals. By the end of the experiment (3 days) coral tissues at such bite spots often exhibited signs of tissue necrosis and bleaching, with very sparse algal filaments just visible, suggesting that the eventual result would have been tissue death at these locations. Unfortunately it was not possible to keep the corals for extended periods to determine whether coral death would have been the long term outcome, as this would have precluded sufficient replication of the experiment within the allotted field time.

DISCUSSION

*Characteristics of habitats used by *Stegastes planifrons* at Glovers Reef*

Reef surveys revealed that *S. planifrons* populations were almost entirely based on *Acropora* and *Montastraea*, with roughly 47% of the population on each, and few other microhabitats used. The use of these two corals is unsurprising since *Acropora cervicornis* and *Montastraea annularis* have previously been demonstrated to be the primary and secondary substrates of *S. planifrons* (Itzkowitz 1977a, 1977b). What is initially more surprising is the high use of *Montastraea*, which has been shown to be the secondary substrate (Itzkowitz 1977a, 1977b). However, whilst the *Acropora* habitat is virtually fully occupied by damselfish territories, less than 50% of available *Montastraea* is in use. This may well be explained by recent work suggesting that the low availability of *Acropora cervicornis* on modern day Caribbean reefs has forced the relocations of *S. planifrons* populations on to the *Montastraea* microhabitat (Precht et al. 2010).

The mean live cover of *A. cervicornis* within *S. planifrons* territories was 35%, which was half the 70% mean live cover found in *Acropora* patches on the wider reef. This reflected the incorporation of dead but structurally intact *Acropora* substrates into territories containing live coral stands. Analysis of data from Lobel (1980) revealed a very similar degree of live cover (29% +/- 10.9%; Table 2.3) to be present in territories surveyed in the late 1970s. Although this could be coincidence, the similarity of the results suggests that a value of around 30% live coral cover may be a consistent and inherent feature of *S. planifrons* territories. Caribbean reefs of the 1970s were very different to modern day reefs, with large stands of *Acropora cervicornis* occupying large tracts of reef (Lewis 1970, Gladfelter 1982a) as such there would have been far larger areas of healthy *A. cervicornis* to choose from, so it is unlikely that the low live cover of the territories surveyed by Lobel (Lobel 1980) would have been as a result of damselfish being forced onto degraded habitats. Further work should be done to investigate this hypothesis, potentially with further re-analysis of historical data, if it can be found. In contrast to those on *Acropora*, territories on *Montastraea* had

significantly higher live coral cover than the reef average, at 24% within territories compared to 8% on the wider reef. This suggests that *S. planifrons* exhibited a preference for live coral cover on this substrate, which was not saturated with *S. planifrons* territories.

In general *S. planifrons* utilised both *Montastraea* and *Acropora* with varying degrees of live coral cover, but the highest proportion of territories was found on structures where live cover was low, with less than 50% live coral cover. The presence of a significant proportion of dead carbonate substrate within the territory is in keeping with our knowledge that *S. planifrons*' maintains algal lawns, from which it derives much if not all its dietary needs (Robertson et al. 1981). Algal growth is not compatible with live coral surfaces, so the provision of dead carbonate surfaces could be seen as a vital quality of a serviceable territory.

Habitat choice by S. planifrons when presented with un-occupied substrates

On the basis of observed field trends in the extant territory characteristics outlined above, microhabitats were ranked in terms of their likely desirability as territory residences. This ranking was based on the observations that: i) *Acropora* was preferred over *Montastraea*, ii) within *Acropora* territories a mix of live and dead structural branches was typical iii) It is known from the literature and observed *in situ* that live *Acropora* could be modified by coral killing to enable a mat to grow, where not enough algal mat was available iii) dead *Acropora* substrates were also fully subscribed iv) within *Montastraea* territories live coral cover was significantly higher than it was on the wider reef, indicating that *S. planifrons* was utilising live cover within the *Montastraea* habitat at a significantly higher rate than random. The desirability of territories was ranked on this basis as follows: partially dead *Acropora* > totally live *Acropora* > dead (structurally intact *Acropora*) > live *Montastraea* > dead *Montastraea*. It was therefore hypothesised that in the absence of competition for habitat *S. planifrons* would choose partially dead *Acropora* as its primary preferred habitat during the habitat choice pool experiment. In a surprise result, fish favoured H1 (100% live *Acropora*) over H2 (50% live *Acropora* – 50 % *Acropora* structure with algae). We had expected fish to favour H2, because it was most closely matched the type of substrate association observed in the field, and it also had a supply of algal and dead substrates on which to

cultivate an algal lawn. Instead, fish consistently chose H1, spending more time there than would be expected at random ($p < 0.05$; two-tailed Student's t test), as well as significantly more there than on any other habitat ($p < 0.01$; glm). Fish also strongly avoided H5, the 100% dead *Montastraea* habitat (two-tailed t test; $p < 0.01$), spending less than 3% of their time there in each replicate. This result conformed to expectations from reef surveys on the basis of which *Montastraea* had been predicted to be the least preferred substrate. The almost complete lack of interest of the fish in H5 was nonetheless (subjectively) startling: during an initial 'prospecting' period at the start of each experiment fish were observed to circle the tank for several minutes, going from habitat to habitat; but whilst fish did generally investigate all other habitats, H5 was apparently dismissed almost immediately and fish would swim on their way. Whilst not formally quantified in the current study this trend was nonetheless notable, and could be investigated in future studies. Fish did not show the same complete lack of interest in H4 (50% live and 50% dead *Montastraea*), where time spent was not significantly different to that which would have been expected at random. These results were in keeping with the results of the reef survey which suggested that when basing their territories on *Montastraea* damselfish chose areas with higher live coral cover (as discussed above). Habitats 3 and 4 were neither significantly favoured or avoided, but surprisingly fish actually spent less time at H2 than would be expected at random.

Coral biting and feeding behaviour

Coral biting has previously been recorded for *S. planifrons* (Kaufman 1977) and another territorial damselfish *Stegastes acapulcoensis* (Wellington 1982); in both cases the activity was related to killing of coral colonies or areas of coral to extend territorial substrates for algal mats, rather than feeding behaviour. *S. planifrons* has previously been shown to kill both *Acropora* and *Montastraea* through the biting of live tissues, allowing algal mats to grow within one week (Kaufman 1977). In this study *S. planifrons* chose to adopt completely live *Acropora cervicornis* and immediately go about biting it, rather than adopt a habitat with an already established algal community.

This study does not determine whether fish biting behaviour had the purpose of feeding. However, when fish which had adopted H1 as their principle territory bit substrates

elsewhere they bit significantly more on algae than other substrates ($p < 0.05$; ANOVA; Figure 2.9), suggesting that forays may have been in order to specifically target algal food sources. Within fish that chose habitat 1 bite rates on non-H1 corals were extremely low (1 ± 0.7 bites hr^{-1}) in comparison to H1 corals (35 ± 13 bites hr^{-1}), and to non-H1 algae (13 ± 6 bites hr^{-1}) with each being significantly different ($p < 0.05$; ANOVA; Figure 2.9). Whilst the higher rates of biting seen on the algae illustrate that the fish was clearly able to feed outside its territory, the very low rates of biting on corals outside of the selected habitat are consistent with this behaviour being aimed at killing coral tissue in order to establish an algal mat, rather than for feeding. The repeated biting at the same spots recorded here is also typical of corallivory, according to Kaufman (1977), who documented that it being “necessary for the fish to bite experimental pieces day after day in the same exact spots, otherwise the corals could heal very quickly” but that caged corals experimentally injured at the outset of the experiment did not die but healed. A notable result in the current experiment was large number of bites taken on coral surfaces in comparison to those taken on algae or carbonate biofilms with the mean number of 120 observed bites on coral substrates compared to a mean of only 62 bites on algal substrates, and 42 on carbonate biofilms (Figure 2.7), however rates of coral biting could not be found from the literature for comparison. We do not demonstrate here that the outcome of coral biting was the establishment of a new algal lawn, but by the end of the experiment there was evidence of fine filamentous algae appearing around bite spots which exhibited signs of necrosis and bleaching. In view of the evidence from the literature where filaments were shown to establish between 2 – 3 days and lawns to follow (Kaufman 1977) we anticipate that this would have been the case in the present study had the experiment been run over longer time-scales.

In this study *S. planifrons* chose to adopt completely live *Acropora cervicornis* territory and begin biting coral, rather than adopt a habitat with an already established algal community. This behaviour suggests that when setting up a new territory it is more efficient for *S. planifrons* to bite and kill live coral as a surface for the growth of its algal mat, than it is for it to modify existing algal communities. Indeed, fast rates of algal growth on damages coral substrates have been seen within the present study (less than 4 days), and in the literature, where filaments have been shown to establish between 2 – 3 days (Kaufman 1977), and *S. planifrons* has been shown to be able to

convert an area of 1m² of *Montastraea* to algal lawn within a month. Although coral biting has previously been demonstrated by Kaufman this was mostly within territories, leading the authors to consider that this was a method of opening up additional space to algal colonisation when all carbonate substrates were already fully occupied. The results of this study were therefore a surprise i that *S. planifrons* preferentially chose to inhabit entirely live corals rather than occupy partially live corals and modify existing algal communities to achieve its desired algal lawn. It would seem from the fast rate of growth on injured corals that coral tissues are a particularly good substrate for algal growth, in contrast some algae are known to have chemical defences against other species, and it may well take longer for filamentous algae to establish in such conditions.

Ecological Implications

In this study *S. planifrons* chose to adopt completely live *Acropora cervicornis* and go about biting it, rather than adopt a habitat with an already established algal community. Coral biting by *S. planifrons* populations would be expected to result in partial mortality of whichever coral the fish chooses to base its mat upon. Given that *S. planifrons* territories surveyed on the reef had an average of 35% live coral compared to 70% live on surveyed patches generally, a number which was seen to be consistent when compared with territory data collected in the late 1970s (Table 2.3), this might suggest that the pristine coral inhabited by *S. planifrons* would deteriorate to a similar condition.

Kaufman (1977) suggests that dead basal areas of *Acropora cervicornis* (killed by damselfish) tend to become weakened by bio-eroders and boring organisms, making them more susceptible to storm damage. This suggests the possibility of a negative feedback loop: *S. planifrons*' inhabitation of *Acropora cervicornis* is associated with degradation of the habitat, pre-disposing the stand to storm damage and making the fish more likely to be dispossessed when a storm hits; now present results suggest that dispossessed fish are more likely to seek out pristine un-damaged *Acropora* colonies on which to establish new territories and begin the biting cycle again. Thus *S. planifrons*-inhabited corals are more likely to experience storm damage, and the extent of storm-induced damage extends beyond the loss of the original coral colony as *S. planifrons*

moves on to the next and begins to kill coral tissues. This model is corroborated by the observed consequences of Hurricane Allen in Jamaica in 1980, when dispossessed *S. planifrons* from demolished shallow water *Acropora* were observed to re-locate to deeper dead and ‘intact’ *Acropora* stands - where 10 days later significant secondary mortalities were seen to be due to *S. planifrons* inhabitation (Kaufman 1983). However, the Hurricane Allen study (Kaufman 1983) did not distinguish whether dead or ‘intact’ substrates were preferentially occupied.

Whilst it is unlikely that *S. planifrons* occupation of *Acropora* is a new phenomenon, and therefore such a cycle should not be new, *Acropora cervicornis* prevalence is currently at an all-time low unprecedented in the last 3000 years (Aronson and Precht 1997a, Aronson et al. 2004, Aronson et al. 2009). With both the frequency and severity of storms set to increase under future global warming scenarios, this cycle would therefore be expected to represent an additional stress to a coral population already pushed towards the margins of survival (Aronson et al. 2008). Whilst such processes may not previously have been a problem for the fast growing and prevalent *Acropora* stands of the past, with the expectation of increased frequency and severity of storm disturbance in the future (Goldenberg et al. 2001), processes affecting susceptibility may be more important, with any processes that weaken the *Acropora* framework being likely to further reduce resilience of this already severely diminished Caribbean coral.

The observation of the avoidance of the dead *Montastraea* habitat has interesting implications in the face of possible shifts of *S. planifrons* to the *Montastraea* microhabitat due to lower availability of their preferred *Acropora* microhabitat (Precht et al. 2010). Both our field and experimental results suggest that *S. planifrons* preferentially utilises higher live coral *Montastraea* over dead *Montastraea* with already established algal communities. If *S. planifrons* occupying the *Montastraea* microhabitat for the first time set about biting the coral to establish an algal lawn, it would be expected that such shifts would be detrimental to live *Montastraea*. In contrast to the multi-tiered *Acropora* microhabitat, which can sustain both algae and live coral within the same unit are of reef, the planar *Montastraea* substrate can only be one or the other, so *S. planifrons*’ mat is not compatible with on-going existence of live *Montastraea* cover (Kaufman 1977). In fact Kaufman (1977) suggested that the effects of *S.*

planifrons' coral killing behaviour may be worse for *Montastraea* than for *Acropora*, since although partial death of *Acropora* basal areas can lead to toppling, the main mode of *Acropora* proliferation is via fragmentation (Tunncliffe 1981), so remaining live portions of colonies may go on to survive and establish elsewhere. For *Montastraea* this is not the case and any toppling of colonies will normally result in death (Kaufman 1977). Kaufman (1977) recorded that *S. planifrons* was able to convert 1m² of live *Montastraea* to algal lawn within a month. On the *Montastraea*, the coexistence of algal lawn and live coral are not compatible within the same area due to the planar nature of the substrate, unlike *Acropora*, which can be viewed as a multi-tiered habitat, where algal-covered dead basal branches and live coral cover are compatible within the same unit area of reef, partly due to the three-dimensional superstructure of the coral, but also due to its fast growing nature away from basal algal covered areas (Idjadi et al. 2006) It has also previously been shown that *S. planifrons* territories exhibit decreased temporal persistence on alternative substrates such as *Montastraea*, in comparison to those located on *Acropora* (Itzkowitz 1977a), so it might be expected that serial territory establishment on this substrate could be even more damaging.

In evaluating the likely impacts of shifting *S. planifrons* populations further work needs to be done to establish what factors actually control population size. The recent observations of population shifts from one microhabitat and expansion into another (Precht et al. 2010) imply that populations are not presently controlled by habitat availability, as has also been recorded in the past (Robertson et al. 1981). Studies suggest that predation is also unlikely to be a major factor (Williams 1981, Precht et al. 2010), so it is possible that recruitment processes may play a role (Sale 1976b). A better understanding of the population dynamics of *S. planifrons* is therefore needed as the likely extent of the effects of such shifts will to be determined to a degree by the size of population that establishes on the new habitat.

In the next chapter of this thesis (Chapter 3) we document an association between *Stegastes planifrons* presence and biting of corals and the spread of a white coral disease, similar in etiology to 'white band disease', the major cause of *Acropora* reduction in the Caribbean of the last 30 years. This is concerning in view of the finding in the current chapter that *S. planifrons* chose to inhabit pristine healthy corals

and set about biting them (possibly to establish an algal lawn), rather than occupy other frequently available habitat types and utilise algal communities already present. In such a scenario disease could easily be spread by dispossessed fish looking for new coral hosts.

CONCLUSIONS

This study suggests that if *S. planifrons* individuals are dispossessed from their original habitat and face a choice of new substrates they are more likely to choose pristine healthy *Acropora* and set about biting coral tissues, than choose partially dead or degraded corals which already have a supply of algal matter.

Present-day *S. planifrons* territories *Acropora* territories at Glovers Reef (Belize) had an average of 35% live coral content, which compared very closely to a figure of 28 ± 10.7 % live content found from analysis of historical data from *S. planifrons* territories *Acropora* from Jamaican reefs of the 1970s, (Table 2.3). The similarity of these two results suggests that a figure of around 35% live cover is a common feature of *S. planifrons* territories on *Acropora*. The fact that the observed mean of independently surveyed *Acropora* colonies at Glovers reef was 70% further suggests that either damselfish modify their host coral to achieve a desired 35% level, or that they preferentially choose to locate their territories on already partially dead coral. Results of the five-way habitat choice experiment suggest that the former is the case. Given the choice of uninhabited substrates reflective of those contained within *S. planifrons* territories on the fore-reef fish spent significantly more time on H1 (100% live *Acropora*), than on any other habitat, including H2, which was designed to be reflective of the substrate they primarily based their territories upon on the reef (50% live *Acropora* and 50% dead carbonate branches with extant algal communities). Fish were then seen to bite at high rates on corals which made up H1, but hardly bit corals on other habitats at all, despite forays in which they bit significantly more on algae than other choices. Coral biting by *S. planifrons* has previously been documented as a method of killing coral to extend the algal mat (Kaufman 1977, Robertson et al. 1981) and the observation here of signs of necrosis and algal filaments appearing at biting spots by day 4 of the experiment suggests that this would have been the outcome had the experiment been run for longer. The selection of a habitat with no algae present and the observed trend of coral biting in conjunction with the rapid growth of filamentous algae seen here, and elsewhere (Kaufman 1977, Robertson et al. 1981, Wellington 1982), suggests that damaged coral tissues may provide a better medium for the growth of turf algae than carbonate branches with pre-existing algal communities. The rate of algal colonisation of damaged coral tissues versus bare carbonate branches, or scraped branches previously home to extant algal communities would provide an interesting

avenue for further research, since fast algal growth on damaged coral tissues could suggest a reason for *S. planifrons*' selection of live coral habitats, and subsequent biting behaviour.

This study suggests that dispossessed *S. planifrons* populations are likely to adopt healthy coral stands and begin biting coral tissues, rather than adopting previously degraded stands with pre-existing, but un-'farmed' algal communities. This means that secondary losses to *Acropora* populations would be expected to occur due to the relocation of the *S. planifrons* population. The observation of extreme avoidance of the dead *Montastraea* habitat has implications in the face of documented shifts of *S. planifrons* to this microhabitat, as a result of lower availability of their preferred *Acropora* microhabitat (Precht et al. 2010). Our field and experimental results suggest that faced with a choice of *Montastraea* substrates *S. planifrons* would pick higher live coral *Montastraea* over dead *Montastraea* with already established algal communities. If, again, the preference is to set about biting the coral to establish an algal lawn this suggests that shifting *S. planifrons* populations would be detrimental to live *Montastraea*. The shifting of populations from one microhabitat and expansion into another imply that populations are not presently controlled by habitat availability. In order to fully understand the dynamics of this system and the likely impacts of shifting *S. planifrons* populations further work needs to be done to establish what factors control population size.

CHAPTER 3

The association of Stegastes planifrons with the spread of white disease in staghorn corals.

ABSTRACT

Recent studies of coral disease have pointed toward a number of corallivorous vectors. However as yet those identified for Acroporid white diseases of the Caribbean have been limited to short range vectors such as the corallivorous snail *Coralliophila abbreviata*. Given the rapid spread of white band disease across the Caribbean during the 1977 and 1982 epizootics, there is scope for a larger scale more mobile vector, or vectors. In this study a possible role of the territorial damselfish *Stegastes planifrons* in the spread of a white band disease II-like disease of *Acropora cervicornis* is investigated. Using flow-through tanks and artificially constructed habitats of *Stegastes planifrons* preferred host coral, *Acropora cervicornis*, experiments were conducted at two scales of analysis. At the macro scale, there was a significant positive association between the presence of *S. planifrons*, and the occurrence of white disease on the host coral habitat ($p < 0.05$). A more detailed mechanistic approach then revealed a highly significant correlation between fish biting locations and later disease onset, with patches that later became diseased experiencing significantly more bites (whilst tissues were still brown and apparently healthy) than would be expected if bites were distributed at random over the colony surface (Chi squared test; $p < 0.001$). In addition, there was a high level of coral biting by this so-called herbivorous species, and intensive feeding on white tissues after disease emergence was coupled with ongoing biting on apparently healthy brown tissues. Given prior demonstration of the effectiveness of corallivore vectors in coral disease transmission, this feeding pattern coupled with the ubiquitous association with *Acropora cervicornis* suggests that *S. planifrons* would be likely candidate to serve as a possible vector of white Acroporid diseases, such as white band disease.

KEYWORDS: *Coral disease; white band disease; Stegastes planifrons; Acropora cervicornis; vector.*

INTRODUCTION

Coral disease has been listed as one of the major contributing factors to worldwide coral reef decline (Wilkinson, 2008). The capacity for coral disease outbreaks to degrade reefs at the ecosystem level has already been seen with the Caribbean white band disease epizootics of the late 1970s and 1980s, which resulted in the mass mortality of former key reef-building Acroporid species across the entire region (Gladfelter 1982c, Bythell et al. 2000, Aronson and Precht 2001, Aronson et al. 2002a, Aronson et al. 2002b, Precht et al. 2002, Schutte et al. 2010). Despite being the most high profile of all the coral diseases, much still remains unknown about the aetiology of the Caribbean white band diseases. So far, two forms of the disease have been identified: WBD Type I (originally ‘white band disease’) (Gladfelter 1982a), which has been reported throughout the Caribbean (Antonius 1981b, 1982, Gladfelter 1982b, a, Bythell and Sheppard 1993); and WBD Type II (WBDII), which is so far only reported from the Bahamas (Ritchie and Smith 1998), and Puerto Rico (Gil-Agudelo et al. 2006). As yet, the pathogen for neither disease has been conclusively identified, although - as with some other coral diseases, some studies do seemingly point towards an association with a strain of *Vibrio* (Ritchie and Smith 1995a, Ritchie and Smith 1998). The field of coral disease research is hampered by technical and methodological difficulties in pathogen isolation and identification – a topic which has been examined in more depth in the overall introduction to this thesis, along with an overview of the emerging importance of this field. At present, a robust and justifiable systemic classification of white band disease or other white diseases of Acroporid species has yet to be developed, and disease classification has been generally based on signs and patterns of manifestation (Work and Aeby 2006).

Coral disease transmission and the potential role of vectors

The dominant modes and mechanisms of Acroporid white disease spread and transmission are unclear. To-date, one short-range vector, the corallivorous snail *Coralliophila abbreviata*, has been identified, but the disease has been shown to be surprisingly hard to transmit using more passive, non-penetrative mechanisms (Williams and Miller 2005). Although Williams and Miller highlight that it cannot be known for certain that the disease they were working with was either WBDI or WBDII

(due in part to lack of identification of the causative pathogens, as discussed above), the general signs are similar, and in the past all diseases of Acroporids have been termed white band diseases (Work and Aeby 2006). In field experiments on sections of *Acropora cervicornis* Williams and Miller (2005) found that the disease did not transmit by indirect contact by vigorously swabbing the diseased corals then healthy corals with a latex-gloved hand, to the point where slight tissue damage occurred. This lack of indirect transfer, even in the presence of damaged tissues and likely high pathogen concentrations on the glove that had previously swabbed on the diseased tissue, would suggest that still more passive indirect disease transfer via the water column is still less likely - even if the coral tissues are already damaged. Early studies of white band disease were unable to elicit disease infection by direct contact between diseased and healthy corals Antonius (1981). In the study of Williams and Miller (2005) first attempts at disease transmission by direct contact also failed, and it was found that the margin of diseased tissue progressed along the source branch and away from contact with healthy coral before disease onset occurred, however, in a second experiment direct transfer of disease was achieved but required ongoing re-positioning of the actively diseased margin so it was in constant contact with the healthy test corals in order to achieve infection. In comparison to the direct and indirect modes of transmission attempted by Williams and Miller (2005), allowing the experimental snail vector to feed first on diseased tissues then on healthy test corals led to both higher rates of disease emergence, and a much more rapid onset, leading the authors to suggest that this was the most effective mode of disease transmission. Whilst the discovery that this disease can be transferred by vector is extremely interesting, the likely short range of movement of the snail vector does not provide a likely mechanistic explanation for the very rapid spread of white band disease across the Caribbean seen in the past epizootics (Hughes 1994). However, given the lack of easy direct indirect transfer described above (even in the presence of tissue damage) it seems unlikely that the disease would have moved this fast unaided. Taken together this evidence suggests a likely role for as yet unidentified, and more mobile vector(s) in the rapid transmission of the Caribbean WBD disease outbreaks.

To-date the only other empirically identified vectors of disease in addition to *Coralliophila abbreviata* are also small-range organisms, such as the Red Sea polychaete worm, *Hermodice carunculata*, which has been shown to act as a reservoir

for the *Oculina patagonica* bleaching pathogen *Vibrio shiloi* (Sussman et al. 2003), and potentially one corallivorous nudibranch species (Dalton and Godwin 2006). Increased numbers of the corallivorous snail *Drupella cornus* have also been coincident with outbreaks of disease in Red Sea Acroporid corals, although it is entirely untested as to whether these events are causally linked (Antonius and Riegl 1998). In the Indo-Pacific, however, recent studies have pointed towards corallivorous fish as having a likely role in the transmission of the diseases prevalent there. In correlative studies of Philippines and Great Barrier Reef corals, disease prevalence rates were found to be significantly negatively correlated to fish taxonomic diversity, with chaetodonts (butterfly fish) being the only family where a significant relationship could be seen when taxonomic groups were examined separately at high coral cover sites (Raymundo et al. 2009). Whilst chaetodont densities as a whole were significantly positively associated with rates of disease, it was found that within the chaetodont family obligate corallivores explained more of the trend than facultative corallivores, but perhaps counter-intuitively that non-corallivores were still weakly associated. Further studies of Great Barrier Reef Acroporids aimed at determining the likely pool of fish that could act as coral disease vectors identified twenty five different species from five different fish families which were seen to feed on naturally occurring disease lesions (Chong-Seng et al. 2011). Of these 25 species 17 were seen to feed preferentially on or adjacent to either black band or brown band diseased tissues, rather than healthy tissue, including several species of Chaetodonts, two Pomacentrids and the ‘herbivorous’ damselfish *Stegastes apicalis*.

Although much remains to be investigated, it is reasonable to hypothesise that other organisms whose ecology brings them into close and invasive contact with disease-infected corals (for example through feeding on coral tissues) would be likely suspects as disease vectors (Chong-Seng et al. 2011). In addition to chaetodonts, such potential vectors could include certain damselfishes and potentially parrotfishes, as previously suggested by Mumby (2009). Here experiments are described that examine the association of *Stegastes planifrons* territory establishment with subsequent white disease outbreaks, providing new insight into a potential role of this ubiquitous species in facilitating the spread of disease in its host coral habitat on Caribbean reefs.

METHODS

Experimental set up.

A series of round tanks were set up at Glovers Reef atoll (Belize, Central America) using a flow-through system. All tanks were located outdoors but in full shade. Tanks were kept aerated and had a good flow or volume of water, each tank had a direct water supply from the lagoon and overflowed waste-water was sunk into the ground. Tanks were filled at the start of each replicate using a high-pressure pump and hose, with water intake from an area of the lagoon near to the reef crest which was constantly supplied by fresh oceanic water. Both hose and pumps were newly installed at the start of the experiment, so it is unlikely that water oxygenation would have been affected by internal marine flora or fauna and water pressure was such that there was large degree of foaming and mixing, which would have delivered the water in an oxygen-rich state. Initially, replicates were sequential using a 3.5 m diameter tank, with a volume of approximately 7m³; in view of the small size of the fish (around 10 cm) this was thought to be a large enough to offer dilution of any waste products as well as a large reservoir of dissolved oxygen. As the experiment continued, a further eight replicates were set up and run simultaneously in smaller 1m diameter tanks. Although smaller in volume, these tanks were fed with a proportionally larger flow-through supply, so that the entire water volume was replaced every 24 hours. In every case there was a full water change between each replicate, when tanks were also scrubbed and all contents were changed.

Acropora cervicornis branches were collected from depths of 7 – 12 m on the fore-reef of the east coast of Glover Reef Atoll, and used to construct artificial damselfish habitats in the flow-through tanks. Coral colonies were visually checked for the absence of signs of disease before branches were collected. For each replicate a collection of coral fragments was positioned on top of a base of rubble rocks in such a way as to simulate a small *A. cervicornis* colony growing on top of reef substrate. The rocks were coral rubble in origin but were collected from the dry supralittoral zone of the island, and had not been submerged in water for some years. *Stegastes planifrons* were specifically collected from territories where there were signs of WBD-like disease. Individuals were subdued underwater using clove oil so that two divers with aquarium

nets were able to catch them. They were then each placed inside a ziplock bag which was rigidly filled with water and sealed. Fish were transported slowly to the surface in order to avoid injury by pressure change, once on land they were kept in individual holding tanks for a maximum of five days before use in an experiment.

Habitat selection and coral biting experiments

Two scales of analysis were carried out to investigate the potential roles of *Stegastes planifrons* in the spread of coral disease. At the *A. cervicornis* colony scale investigated whether the presence or absence of damselfish influenced the probability that disease would establish. Fourteen replicates were run using tanks ranging in diameter from 1 – 3.5m, as described above. Each tank contained several pieces of coral rubble to serve as a refuge for the fish, as well as several *Acropora cervicornis* branches. *A. cervicornis* branches were not from the same original colony. In each tank two pieces of coral rubble were included which had naturally occurring algal communities found on the fore-reef, these were provided as source of algal food material, but were not permitted to contact the *Acropora*. With the exception of the presence or absence of damselfish, all tank contents were otherwise identical for all replicates. There were 10 tanks with fish treatment present and 4 tanks with no fish treatment. A new damselfish was used in each replicate. The experiment was run for a period of five days, at the end of which the presence or absence of disease was scored for each tank /coral habitat. Ten further additional replicates (including more no-damselfish treatment replicates) were planned and commenced, however these experiments were interrupted when the entire field season was prematurely terminated by the evacuation of the author from the island. Unfortunately molecular examination of the microbial community was not possible, as swabs taken from fish mouth parts and diseased and healthy coral tissues prior to commencement and during the experiment were lost during a freezer malfunction in the Biological sciences department of Exeter University.

In a sub-sample of 5 of the replicates a more detailed investigation was employed to provide more mechanistic evidence by asking whether the emergence of disease was associated with the density distribution of damselfish bites. At the start of each replicate a new damselfish was introduced into the 3.5 m tank and allowed to settle on

to an artificially constructed *Acropora* 'habitat'. Fish biting behaviour was observed for three 30 minute periods daily, at approximately 08:00, 12:30, and 16:30 each day, until a total of 8 observation periods was reached (beginning at 08:00 hrs on day 1, and finishing at the end of the 12:30 observation period on day 3); the experiment was then run until day 5 with no further bite monitoring, but corals were re-photographed at the end of day 5. The exact locations of individual bites on coral substrates were logged on printed photographs of the coral 'habitat' and given a unique numerical identifier; associated data relating to the time of the biting episode, number of bites taken, and the colour of the coral tissue at the time of biting (i.e. brown healthy coral, or white diseased tissue) were then recorded against the same unique location number on a separate data sheet. Coral colonies were photographed twice a day to track the temporal emergence of disease until the end of the experiment on day 5.

Data extraction and statistical analyses

Scaled photographic images of the coral colonies were used to calculate surface areas of diseased and non-diseased tissues at the end of each day (pictures taken at 16:30 hrs daily). Surface area calculations were based on the assumption that the coral is composed of open ended cylindrical sections with a surface area equal to πdh , where $\pi = 3.142$; d = branch subsection diameter; h = branch subsection length.

Because of the unbalanced design of the experiment (fish treatment $n = 10$, no fish treatment $n = 4$) a binomial analysis (Crawley 2007) was used to examine the association between fish presence or absence and the presence or absence of coral disease. The binomial test for significance was based on the likelihood of disease presence rates seen in the smaller sample ($n = 4$) being observed if this sample had come from a population with the same rates of disease as recorded in the larger sample ($n = 10$). In order to exclude the possibility of an effect of tank size on the disease outcome a binomial test was also conducted to compare rates of disease emergence in fish treatments between the 1 m diameter and 3.5 m diameter tank replicates.

At the finer scale Chi Squared analysis (Crawley 2007) was used to compare the observed number of bites taken on diseased areas of coral to the number of bites that would be expected if bites had been distributed at random over the surface of the coral. Two forms of this analysis were used. Firstly, the number of 'brown bites' – bites taken on brown, apparently healthy tissues, were examined in relation to the observed

numbers recorded on areas of coral that later manifested disease by the end of the experiment, in comparison to the number that would have been expected if these bites had been distributed randomly over the entire area of the coral colony. The aim of this analysis was to investigate any significant relationship between the location and density of bites taken on apparently un-diseased tissues and the location of later patches of disease onset.

RESULTS

Description of disease manifestation.

As illustrated in Figure 3.1, disease manifested on the corals in the form of the appearance of bleached white tissue that was similar in appearance to photographic illustrations of ‘white band disease’ in other studies (Precht et al. 2002, Williams and Miller 2005, Weil et al. 2006, Weil and Rogers 2011). Bleached patches of tissue often emerged on day 2 or 3 (Table 3.1), usually, but not exclusively from basal portions of the coral (Figure 3.1), and then proceeded to spread along branches at rates of between 0 and 3 cm per day. There were often multiple disease starting points on a single coral habitat (artificially assembled from multiple single branches.)

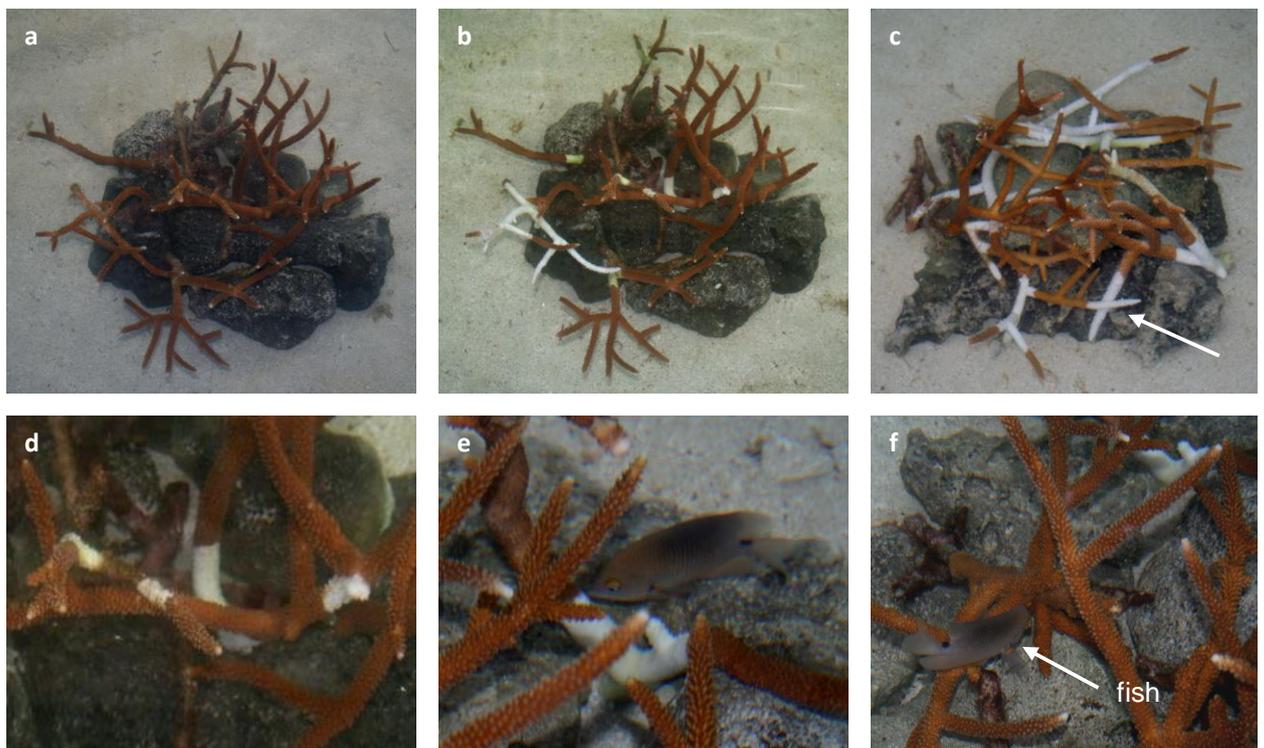


Figure 3.1 Examples of artificial ‘habitats’ used in the pool experiment.

a: Example of artificially constructed *Acropora cervicornis* damselfish ‘habitat’; b, c: stages of progression of WBD-like disease; d: disease originates at basal and mid-branch locations; e: damselfish biting white coral tissue; f: damselfish continues to bite brown tissue when white tissue is available.

Did fish presence increase the probability of disease occurrence?

By day five of the experiment 6 out of 10 coral colonies in the damselfish treatment category developed WBD-like disease as described above, whereas none of the four no-fish treatments developed disease. A binomial test was used to examine the likelihood that no disease would result in the smaller sample given the binomial probability of disease emergence found in the larger sample, where the incidence rate was 6/10. The binomial probability of achieving the rate of zero disease outcome in four replicates by chance was 0.026, and was therefore significant at $p < 0.05$ level. This supports the rejection of the null hypothesis and acceptance of the hypothesis that the presence of the damselfish increases the probability of the disease occurring. In order to exclude the possibility of an effect of tank size on the disease outcome a binomial test was also conducted to compare rates of disease emergence in fish treatments between the 1m and 3.5m tank replicates, which was found to be not significantly different (binomial Pr = 0.23.)

Is the location of biting activity associated with the onset or emergence of WBD?

Fish normally began biting corals on day 1 or 2 of the experiment. Fish biting behaviour often tended to focus around particular spots, which they returned to repetitively over the course of the experiment, with forays of 1 – 6 bites. In order to examine the association between damselfish biting activity and the locations of later disease patch emergence, the density of 'brown bites' (bites recorded on healthy brown coral tissue, as opposed to bleached white tissue) was compared between areas which did and did not manifest coral disease by the end of the experiment. Only replicates where disease emerged within the five days of the experiment were included in these analyses. Chi Square tests were carried out with the addition of the Yates' correction whereby a value of 0.5 is subtracted from the absolute value of each O-E value, to allow the test to be applied to data with only 1 degree of freedom (Crawley 2007). In all four cases where disease emerged, Chi Square analyses revealed significantly more 'brown bites' on areas that later developed disease than would be expected if bites were distributed at random over the entire coral area ($p \ll 0.001$; Fig 3.2). Bites on white coral were excluded from these analyses in an attempt to look at biting prior to disease emergence. However, if they are included the statistical significance of the results increases still because a higher proportion of bites are then located on diseased tissue ($p \ll 0.001$; Chi Square test).

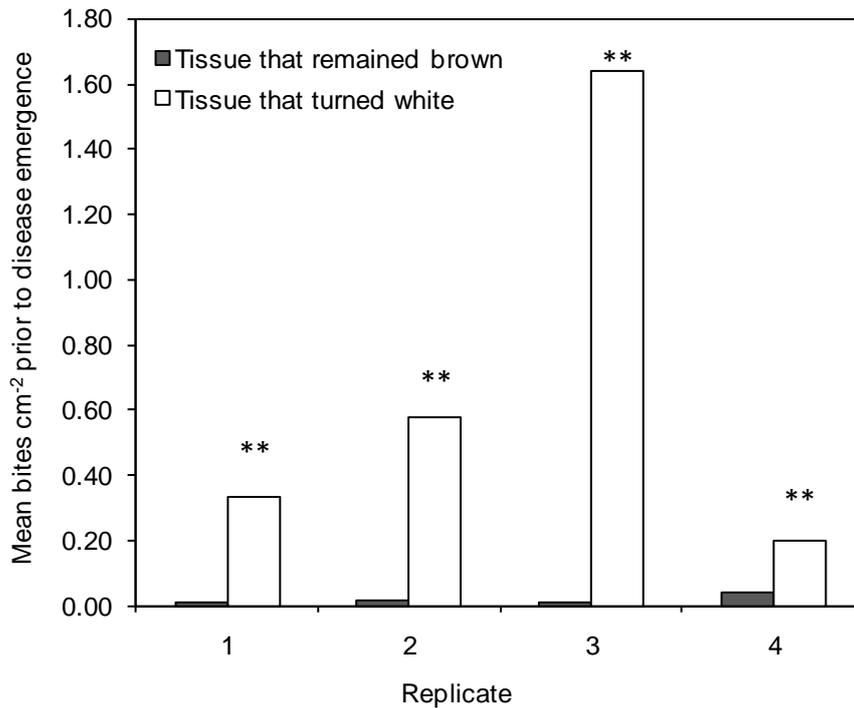


Figure.3.2. Mean bite densities on *A. cervicornis* tissues prior to visual manifestation of disease.

In each replicate bites density prior to visual manifestation of disease was significantly higher on tissues that later developed the disease (turning white) than would be expected if fish bit at random over the entire coral area (**Chi Squared test; $p < 0.001$.)

Across all replicates the average rate of biting observed on live coral tissue as a function of the time the fish spent on the coral habitat was 37 bites h^{-1} . Even after disease emergence fish continued to bite on both brown and white coral tissue (Fig 3.3), and over the duration of the experiment the number of bites taken on brown and white tissue were roughly equal, despite the diseased coral area being much smaller (Fig 3.4)

Despite the significant association of fish biting locations and later disease manifestation, it should be noted that disease emergence appeared erratic overall, with the link between fish biting and disease emergence not being absolute. In replicate 6 a substantial number of bites were recorded on the coral substrate, yet no disease emerged during the experimental period. Conversely, in replicate 2 no bites were recorded at all yet disease still emerged - although since monitoring was not continuous it is possible that fish could have bitten the coral unobserved during the course of the experiment.

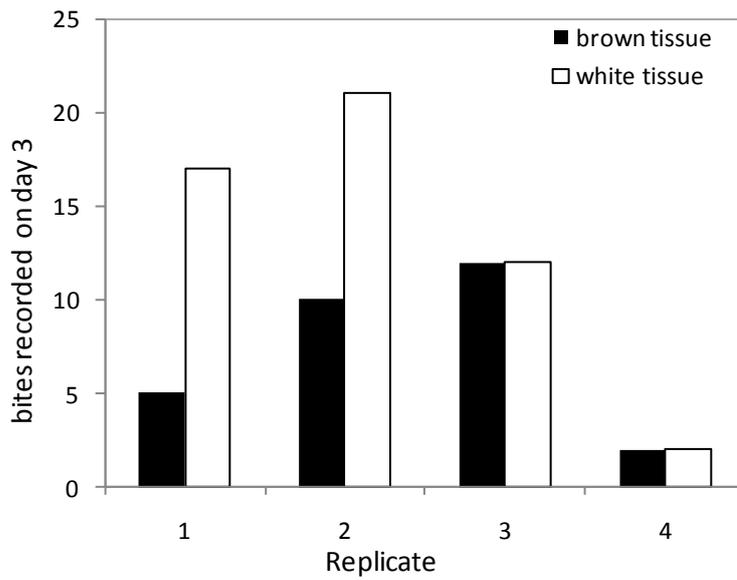


Figure 3.3 Total number of bites recorded on brown and white tissues on day three for each replicate (60 minutes total observation period).

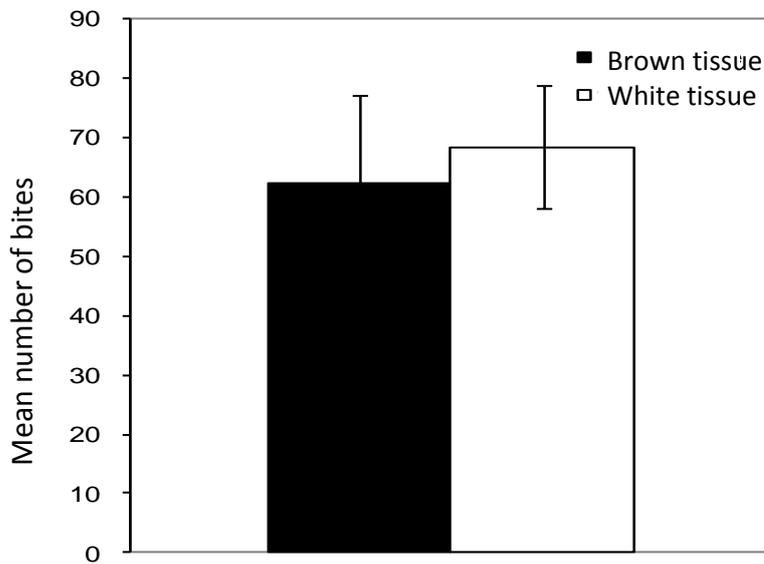


Figure 3.4 Total number of bites recorded on brown and white tissues over duration of the experiment (mean of 4 replicates +/- 1 STE.)

DISCUSSION

Was the observed bleaching due to white band disease?

The sudden appearance of abruptly demarcated bright white patches of coral tissue (Figure 3.1) is characteristic of previous descriptions and photographs of coral disease (Aronson and Precht 1997a, Williams and Miller 2005), rather than generalised coral bleaching (for example due to elevated temperature), where the colonies tend to pale more gradually and uniformly before becoming white. Sadly no molecular analysis was possible since swabs were lost during a freezer malfunction. However, as previously discussed, and highlighted by Work and Aeby (2006) at the time of working there was still difficulty in identifying the causative agent(s), even had I been able to analyse samples. There is a generally accepted need, therefore, to identify diseases based on their visible signs and aetiology (Williams and Miller 2005, Work and Aeby 2006)

Only four diseases are known to affect *Acropora cervicornis*: shut-down reaction (SDR), white band diseases I and II (Antonius 1977), and in the Pacific white band syndrome (Ainsworth et al. 2007). Although SDR is a known risk for corals under abiotic aquarium stress, and can be brought on by physical contact and/or lesions, the characteristic symptoms of SDR described by Antonius (Antonius 1977) were not observed here. Notably, there was no observation of the rapid tissue disintegration and “sloughing from the skeleton in strands or blobs” reported by Antonius, and in the current experiment the rate of disease progression of 0 – 3 cm per day was much slower than the characteristically speedy SDR rate of 10 cm h⁻¹ reported by Antonius. In addition there has been no other reported case of SDR documented in the literature since Antonius’ description.

The pattern of emergence and spread of the disease and its general appearance documented here are characteristic of previous descriptions of Acroporid white band diseases. Both WBD I and II are reportedly similar in signs of their manifestation, with the progression along coral branches of a band of diseased white tissue, with a characteristic abrupt demarcation between the diseased area and healthy-looking brown

tissue (Gladfelter 1982a, Ritchie and Smith 1998). Both diseases develop rapidly, but lesion progression rates have only been reported for WBDII, where a range of 0.2 – 2 cm per day has been found in *Acropora palmata* (Antonius 1981a, Gladfelter 1982a); these rates are similar to those observed in this study. The observation of bleached areas emerging at distal as well as basal areas of coral branches (Fig.3.1) would tend to support WBDII being the causative agent, as would the observation of this disease exhibiting a variable-width band of bleached tissue preceding the band of tissue loss as the disease spreads (Ritchie and Smith 1998); WBDI has no bleached band and just leaves a denuded coral skeleton in its wake (Gladfelter 1982b, Bythell et al. 2004) – a pattern not observed here. It should be noted, however, that at the present time WBDII has only ever previously been reported from the Bahamas, and Puerto Rico (Ritchie and Smith 1998, Gil-Agudelo et al. 2006), but it is possible that there may be some confusion of this issue, as it seems that any Acroporid disease was labelled as WBDI until the discovery of WBDII in 1988 (Ritchie & Smith 1988). Indeed, since the state of the field still does not allow for conclusive identification of the disease involved I am choosing to term the disease found in this study a WBII-like disease.

Was fish biting the cause of elevated disease incidence?

The presence of *S. planifrons* was found to be significantly associated with increased probability of corals developing the diseased state. Although disease did not occur in all replicates where fish were present it has previously been demonstrated that there is a low level of natural white disease resistance which occurs in 6% of Acroporid coral genotypes (Vollmer and Kline 2008), so it is possible that variation in host susceptibility could have contributed to this result. There are two possible mechanistic explanations for the disease onset pattern observed: i) direct fish effects: interactions between the fish and the coral promoted the increased disease incidence rate, and ii) indirect fish effects: the very presence of the fish in the tank indirectly promoted the onset of the disease. In view of the strong link found between fish bite location and the later onset of WBD, direct effects would seem the most likely explanation –in the form of an effect of fish biting on coral tissues. Areas that developed WBD by the end of the experiment experienced vastly more bites prior to disease emergence than would be expected if bites had been distributed at random over the coral area (Chi square test, $p < 0.001$). In view of the apparent lack of ease of transmission of white Acroporid diseases

demonstrated by Williams and Miller (Williams and Miller 2005), where the penetrative feeding on coral tissues of the corallivorous snail, *Coralliophila abbreviata*, presented a far more effective mode of disease transfer than even direct and prolonged contact of diseased tissues, the direct action of fish biting provides a compelling mechanism by which to explain the increasing disease incidence rates associated with fish presence. Indeed, early experiments on putative WBD found the disease impossible to transmit by direct contact (Antonius 1981a), leading the authors to suggest that the disease was not of bacterial origin, however the potential role of vectors was not examined in the study. However, despite the fact that bites were observed prior to any visual signs of disease, it cannot be ruled out that fish were attracted to bite in the areas by a possible unseen third-party agent or localised tissue change relating to a latent onset of the diseased state. Disease did also occur in areas where no bites were observed, however it is possible that bites could have occurred in these areas without being witnessed, since biting was only intermittently monitored. Recent field observations of black and brown band diseased corals in the Pacific revealed that fish fed preferentially on visually discerned disease lesions with significantly higher bite densities on diseased tissues than would be expected if fish fed randomly according to tissue availability (Chong-Seng et al. 2011). Twenty five fish species, from five different families, were recorded to bite on diseased areas, and of these 17 bit significantly more than randomly. Although the majority of these fish were known corallivores they also included normally planktivorous Pomacentrids and one species of ‘herbivorous’ damselfish *Stegastes apicalis*. A Pacific congener of *S. planifrons*, *S. apicalis* was observed to selectively feed on brown band diseased tissues and also at the disease ‘margin’ – an area defined as a 1cm wide band of live tissue adjacent to diseased tissue. It is impossible to know if fish were visually attracted to this apparently healthy looking band of tissue by the nearby presence of the observable disease margins, or if attraction was due to some latent change in these tissues which was detectable by the fish, but not visible to the authors. The situation described by Chong-Seng et al (2011) is differs from the current study where bites were recorded prior to any visual sign of disease presence, although the possibility that fish in the current study were attracted by latent diseased tissue needs further investigation. Future experiments could include localised swabs of areas of apparently healthy tissue when fish first begin biting, in order to determine any signs of altered microbial communities at this point. However, tissue-level changes would be hard to evaluate, as any kind of biopsy could be expected to compromise the experiment by stressing the coral and also providing a potential route for pathogens into coral

tissue. Designs for further experimental work to establish conclusively whether fish biting is necessary for disease onset to occur are given at the end of this chapter.

Since this experiment does not directly link cause and effect in terms of fish biting and disease onset it does remain possible that the very presence of the fish somehow causes increased disease incidence via one or more indirect effects. In another aquarium study, the presence of the corallivore butterfly fish *Chaetodaon capistratus* was found to increase incidence rates of black band disease in *Montastraea faveolata*, regardless of whether the fish was able to access and bite the corals; no infection occurred in the no-fish treatments (Aeby and Santavy 2006). These results lead the authors to speculate as to whether the fish might be transferring the pathogen onto the coral by deposition of faeces containing ingested pathogens. However, a separate experiment, reported in the same paper, found that in tanks with no fish, the BBD agent *Phormidium corallyticum* was only able to invade experimentally-injured *M. faveolata* fragments, with no disease occurring in healthy un-injured corals, even when the black band mat was placed directly on the corals. These results superficially appear contradictory so the experiment suggests in the case of BBD, at least, the situation may be more complex. There is at least one proven case of fish transferring coral disease via the faecal route, although this was trematode rather than bacterial disease. The Hawaiian corallivore *Chaetodaon multicinctus* is one of three hosts of a trematode pathogen of *Porites* corals, it has been shown to ingest the worms whilst feeding on *Porites* polyps, and then acts a vector by later excreting the eggs of the worm in its faeces during its travels over the reef (Aeby 2002). Whilst this may be the case for trematode and nematode diseases to be spread by animal oral-faecal route, there is no direct evidence of coral bacterial diseases being spread in this manner. Fish presence could also theoretically be associated with increased oxygen demand and waste product concentration (e.g. ammonia) in the tank, although no measurements were taken during the experiment a large excess of water volume and /or flow through system was used in order to minimise these potential effects, as described above.

Mechanisms by which fish biting could have enhanced disease rates

Possible mechanisms by which fish biting could have promoted the onset of coral disease include: i) the fish acting as a true vector of the disease by directly inoculating

coral tissues with the pathogenic agent, ii) the penetration of the surface mucous layer (SML), and /or the lesions created by fish provided a route for pathogens in the aquarium system to access coral tissue, iii) fish biting caused increased localised coral tissue stress which promoted increased susceptibility to a pathogen already present within the coral tissue or aquarium system.

Regarding mechanism i), although fish were deliberately chosen from corals that were exhibiting signs of white disease and coral branches were deliberately chosen from colonies that were not, without molecular analysis it is not possible to conclude for certain whether the fish were the original source of the disease in these experiments. Fish mouths were swabbed on collection but these swabs were lost in the freezer malfunction. Even so, it is hard to imagine that disease would not be spread by the biting behaviour of the fish which still continued to bite on brown apparently healthy tissues in between intensively bouts of feeding on actively diseased lesions (Fig 3.1; Fig 3.4). Regarding mechanism ii), previous experiments on black band disease showed that artificially induced tissue lesions enabled coral infection, whilst undamaged corals did not succumb to infection (Aeby and Santavy 2006). In addition to tissue defences, the SML acts both as a physicochemical barrier to coral infection (as reviewed by Brown and Bythell (2005)), and the mucous of the *A. cervicornis* congener, *A. palmata*, has been shown to be able to inhibit growth of potentially harmful microbes up to 10-fold, while 20% of the culturable bacterial from the SML were found to have some degree of antibiotic activity (Ritchie 2006). In this study it is mechanistically possible that fish bite lesions acted initially as merely a route for external pathogens to get past the coral SML or tissue defences. However once the disease had manifested it seems unlikely that free-floating pathogens in the tank system would be at higher concentrations, or more active, than those on the mouthparts or face of fish that have been feeding on actively diseased tissues immediately prior to biting on the coral. In this study, therefore, it would seem likely that if tissue /SML transgression by fish biting was enough to allow pathogens in passively from the surrounding water it would be even more likely to allow infection to be spread via fish mouthparts. It also remains possible that the stress represented by sustained fish biting could have increase diseased susceptibility to pathogens already present in coral tissues. In both cases further study is needed, for example by caging fish away from corals, but artificially inducing lesions with a sterile tool.

S. planifrons’ as a vector of coral disease

Regardless of whether disease outbreaks in this study were first initiated by *S. planifrons*, the sustained and intensive biting on diseased tissues as well as apparently healthy tissues (Figure 3. 1e, f; Fig. 3.3.) suggests that this fish could be a candidate to act as a vector of coral disease as it goes between the healthy and diseased tissues. Disease has been shown to be more effectively transferred between fragments of *Acropora cervicornis* by the biting of a corallivorous snail vector (*Coralliophila abbreviata*), than by direct contact of actively infected coral tissues, with both average times to disease emergence and rates of infection being greater with the snail vector (Williams and Miller 2005). To date other organisms implicated as coral bacteriological disease vectors are either corallivores or live within coral tissues (Kushmaro et al. 1996, Kushmaro et al. 1997, Williams and Miller 2005, Raymundo et al. 2009). Given the apparent lack of ease of transfer of the white disease demonstrated by Williams and Miller (Williams and Miller 2005), the rapidness of the spread of the 1970 – 1990 white disease epizootic throughout the Caribbean would seem to point towards the existence of a larger scale vector than the previously identified snail. *S. planifrons* is highly plausible as a vector of WBD or WBD-like diseases due to its predilection for Acroporid species on which to base its territories, particularly *A. cervicornis* ((Itzkowitz 1977a, 1977b). In view of the high rates of coral biting reported here, the potential for damselfish to spread disease may be larger than might previously have been thought.

Unlike previously discovered vectors *S. planifrons* is quite mobile and therefore has the potential to spread disease over longer distances and at much faster rates. This is particularly concerning due to the propensity for *S. planifrons* to choose the endangered coral *A. cervicornis* as its primary habitat, in many cases occupying more than 90% of available live cover in this study (Chapter 2). Although it might be imagined that the majority of *S. planifrons* biting and disease transference would be within its own coral territory, prior studies have shown that they do also visit the territories of others, and it has been demonstrated in this thesis that when choosing a new habitat *S. planifrons* prefers to inhabit live and healthy corals and begin biting them, rather than modify existing algal communities (Chapter 2). Another study also showed that when threespot damselfish were dispossessed from their territories (in that case by storms) that the

damsel fish roamed over the reef for a short period until they found new unoccupied *A. cervicornis* on which to set up territories (Kaufman 1983). Given this situation the negative feedback model proposed by Williams and Miller (Williams and Miller 2005) (fig 3.5) could equally be applied to damselfish – whereby death of host corals due to disease would cause the damselfish to move on to remaining available *Acropora cervicornis* habitats, taking the disease with them in a stepwise feedback loop. Even if all *A. cervicornis* habitats are saturated at the time of disease outbreak this loop would still be expected to occur, since previous studies have shown that there is competition between damselfish for good quality territories, and when larger fish are introduced to a new area they will push smaller fish out of the most desirable territories or increase territory density (Robertson et al. 1981). It can therefore be suggested that the presence of *S. planifrons* on modern day reefs may retard recovery by possible increased incidences of coral disease. In comparison to the snail vectors, the increased mobility of a species like *S. planifrons* operating in such a loop would be expected to be far more devastating to Acroporid species. In Chapter 2 a situation was simulated whereby the fish had to adopt a new territory on the reef; when presented with a healthy stand of *Acropora cervicornis* the fish took up residence and normally started to bite the coral within 24 hrs. Disease then began to appear on day 2 - 3, and was in an advanced state by day 5 (Figure 3.2) Although rates of disease progress on the reef might be somewhat different this still suggests a rapid mechanism by which Acroporid diseases could be spread between corals.

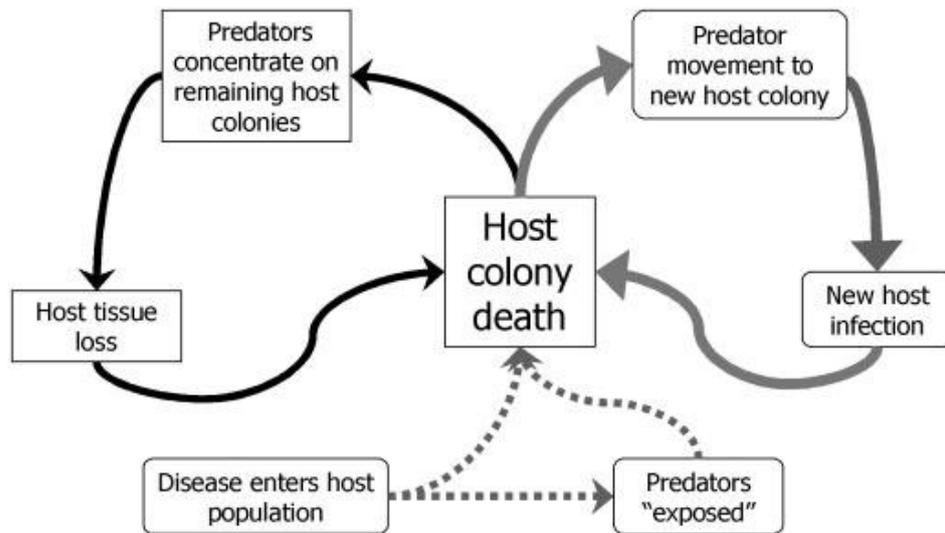


Figure 3.5 Williams and Miller's figure of potential negative feedback loop associated with corallivores

(Williams and Miller 2005). The model demonstrates the mode by which coral disease might be spread to different coral colonies when vectors are dispossessed from the original colony by host death. This model could easily be applied to *Stegastes planifrons*, if able to act as a vector, whereby the effects would be expected to be a more rapid and devastating spread of disease due to the increased mobility of this fish compared to the snail vector described by Williams and Miller, coupled with the propensity for *S planifrons* for *Acropora cervicornis*.

Plans for further experimental work to test the potential vector role of S. planifrons

Figure 3.6 outlines an experimental design to empirically test whether *S. planifrons* can act as a vector of Acroporid white disease. The experiment should be replicated a minimum of three times, but preferably more. In the absence of molecular identification of Acroporid white disease pathogens signs of disease manifested on diseases host corals from which fish were collected should be recorded and used to compare to signs of disease in experimental corals in order to provide evidence that the two diseases are the same (Work and Aeby 2006). Under this experimental design it could be concluded that *S. planifrons* is a vector of Acroporid white disease if treatment i) corals developed white disease whilst all other corals remained healthy. Treatment ii) has been included in order to control for the possibility that some aspect of the injury caused by *S. planifrons* coral biting promotes the onset of disease when the fish itself is not the source of the pathogen (i.e. if the pathogen is already contained within the system, for example bacteria present on coral surfaces). Treatment ii) is similar to treatment vi) in that it allows investigation of whether the disease can occur without the fish being the

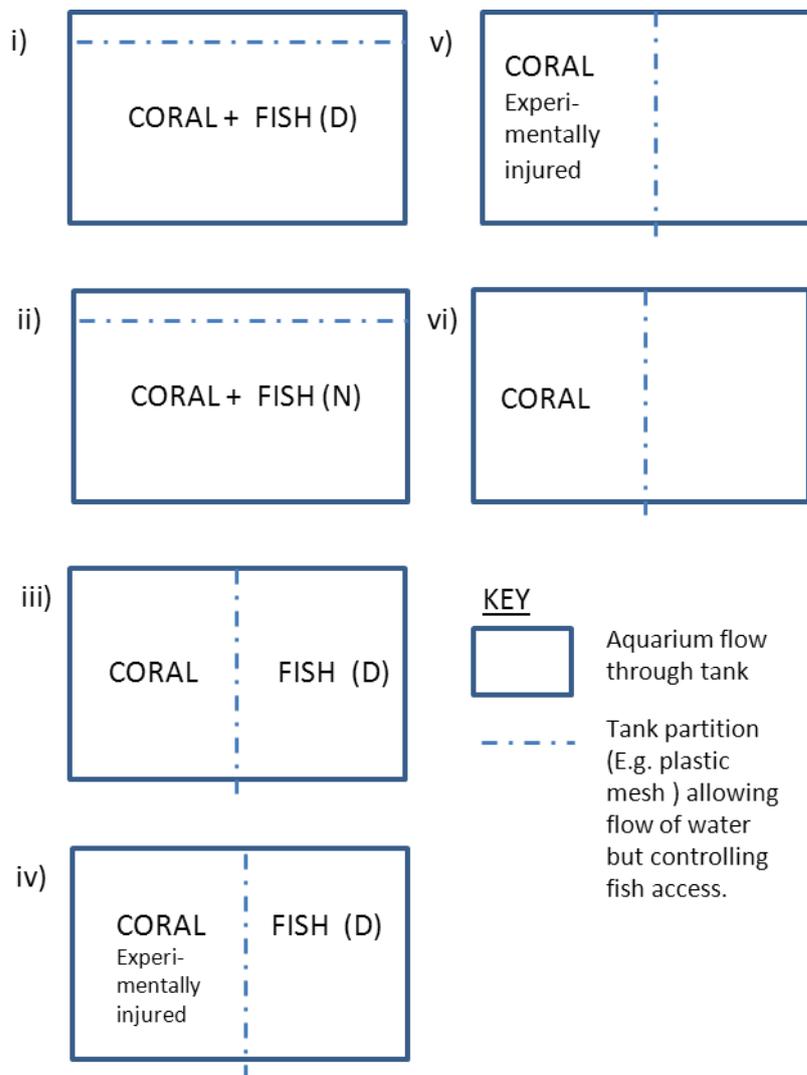


Figure 3.6 Plan view of proposed experimental design to empirically test the potential role of *S. planifrons* as a vector of Acroporid white disease

Tanks to be sterilised at the start of each replicate and filled with sterilised artificial sea water. Where: CORAL = branch of *Acropora cervicornis*, and FISH = individual *Stegastes planifrons*, collected from (D) = corals exhibiting signs of extensive Acroporid white disease infection, or (N) = corals appearing totally free of disease. Individuals used for the FISH (N) treatment would be kept in holding tanks with non-diseased corals for a period of 10 days prior to commencing the experiment and only used if disease infestation did not occur. Therefore FISH (N) denotes a fish not carrying the disease. Experimental injury of test corals to be carried out using sterilised dissecting needle so as to replicate the puncturing of coral tissues by fish biting. Treatments: i) Both fish and coral are present, the fish (from a diseased coral host) is able to access and bite the coral; ii) Both fish and coral are present, the fish (from a non-diseased coral host) is able to access and bite the coral; iii) both fish and coral are present, but the fish (from a diseased coral host) is not able to directly access or bite the coral; iv) both fish and coral are present, the fish (from a diseased coral host) is not able to directly access or bite the coral, but the coral has been experimentally injured to replicate puncturing effect of fish biting, v) coral is present but no fish, coral has been artificially injured; vi) Coral is present but no fish. All treatments incorporate the tank partition material, for purposes of control.

source of the disease. However, the inclusion of treatment vi) would allow elucidation of whether simply puncturing coral tissues is enough for the disease to occur, or whether there is something particular to the injuries caused by fish biting which promote disease onset. The implications of further informative outcomes are given below.

Outcome	Implications
1 Treatment vi) coral develops disease	Control coral has disease, the experiment is unable to determine mode of disease transfer.
2 Treatment v) coral develops disease. Treatment vi) coral does not develop disease .	Artificial injury of coral is enough to allow disease infection. This suggests that the disease is present within the system, since water and tank are sterile this suggests that coral tissue surfaces or mucous layer are the source of the disease and that puncturing of coral surfaces is enough to allow disease infection.
3 Treatment ii) coral develops disease. Treatment v) and vi) corals do not develop disease .	This suggests that injury by fish biting specifically (rather than other artificial injury) facilitates disease infection by a disease already within the system. As for outcome 3 this would suggest the coral surfaces as a possible source of the disease pathogen.
4 Treatment iii) coral develops disease. Treatment v) and vi) corals do	This suggests that the fish is the source of the disease pathogen, but that it is not necessary for direct contact between the

not develop disease .

fish and coral for infection to occur.

- 5 Treatment iv) coral develops disease.
Treatment iii), v) and vi) corals do not develop disease .
- This suggests that the fish is the source of the disease pathogen, but while it is not necessary for direct contact between the fish and coral for infection to occur, puncturing of coral tissues is necessary.
- 6 Treatment i) coral develops disease.
All other treatment corals remain disease free.
- This suggests that the fish is acting as a vector and that not only is the fish the source of the disease, but direct contact and biting of the coral by the fish is necessary for the disease to occur.

CONCLUSIONS

This study provides correlative evidence for a role of the ubiquitous Caribbean damselfish, *Stegastes planifrons* in the spread of Acroporid white disease; however cause and effect of fish biting and later emergence of disease cannot be concluded. Nevertheless, given prior demonstration of the effectiveness of corallivore vectors in the transmission of white Acroporid disease (which otherwise seems not to be easily transferable by either direct or indirect non-invasive contact) the results presented here strongly suggest that *S. planifrons* could act as an Acroporid white disease vector. Even if fish were not the original source of infection of coral tissues in this experiment, the sustained and repetitive biting of both white diseased tissues and apparently healthy brown tissues seen here suggests that disease would likely be transferred from one to the other. Given the rapid spread of the putative white band diseases across the Caribbean in the 1970s and 80s, there is scope for the role of a more mobile vector, or vectors, than the snail that is so far identified. Further work is needed to investigate conclusively whether *S. planifrons* may fulfil this role.

CHAPTER 4

The importance of coral substrate and damselfish territoriality in structuring parrotfish and surgeonfish grazing on Caribbean reefs:

*New implications of the loss of the staghorn coral, *Acropora cervicornis*, from Caribbean systems?*

ABSTRACT

This study sought to extend the ‘Space-Availability Hypothesis’ of Williams *et al* by positing that the grazing activity of herbivorous fish excluded from damselfish territories would thereby be concentrated on the remaining non-territory areas of the reef. The implications of such an effect are interesting because of the widespread loss of the common damselfish habitat *Acropora cervicornis* from Caribbean reefs. Reef substrates were viewed as coral-damselfish complexes according to the coral microhabitat and damselfish territory present. More than 5000 fish bites were recorded across six sites, and planar grazing intensity (bites m⁻² hr⁻¹) of roving herbivorous fish (parrotfish and surgeonfish) were calculated for commonly occurring coral-damselfish complexes. Mixed models were used in a nested analysis to test for significant differences between these complexes. In a surprise result few incidences of significant reductions of grazing within *Stegastes planifrons* territories were found, but instead there was a large and significant reduction in both parrotfish and surgeonfish grazing intensity associated with the Caribbean staghorn coral *Acropora cervicornis* microhabitat, compared to the common reef-building coral *Montastraea annularis*. Thus, in an unexpected extension to the ‘Space-Availability Hypothesis’ it is suggested that the grazing activity of fish excluded from the *Acropora cervicornis* habitat would thereby be concentrated on the remaining areas of the reef. Grazing rates on the commonly-occurring *Acropora-S. planifrons* complex were also significantly lower than those on possible alternative non-territory *Montastraea* or the *Montastraea-S. planifrons* complexes. It is hypothesised that the scale of *Acropora* loss from the Caribbean may have been large enough for the loss of *Acropora*-associated low grazing areas to have resulted in a net dilution of fish grazing pressure, potentially large enough to contribute to Caribbean ‘phase shifts’ towards macro-algal domination. In addition it is suggested that the low grazing pressure seen in *Acropora cervicornis* habitat presents a plausible explanation of the predilection of *Stegastes planifrons* for this substrate, and contributes to a possible new explanation of the niche diversification between *S. planifrons* and *S. fuscus*, which has never been fully explained.

Key words: *Stegastes planifrons*; *Stegastes fuscus*; herbivory; *Acropora cervicornis*; *Montastraea*; parrotfish; surgeonfish; Caribbean; phase shift; mixed models; lme4.

INTRODUCTION

Herbivory is seen as an important process affecting the long-term persistence of coral-rich reef ecosystems (Hughes et al. 2003, Mumby and Harborne 2010, Edwards et al. 2011) because of its role is the removal of algae, which has been shown to be deleterious to coral health and survival (Nughes et al. 2004, Rasher and Hay 2010) (Birrell et al. 2005, Carpenter and Edmunds 2006, Rogers and Miller 2006, Birrell et al. 2008, Arnold et al. 2010, Diaz-Pulido et al. 2010, Idjadi et al. 2010). Coral-algal dynamics are of particular interest in the Caribbean due to the large-scale ‘phase shift’ over the last 30 – 40 years and transformation from previously live-coral dominated system to one which is dominated by dead and macroalgae covered substrates (Hughes 1994, McClanahan and Muthiga 1998, McClanahan et al. 1999, McCook 1999, Ostrander et al. 2000, Precht et al. 2002, Mumby 2006, Rogers and Miller 2006).

Termed the ‘Space-Availability Hypothesis’, Williams et al (2001) have previously shown that the occupation of reef area by un-grazeable substrates can cause the feeding activity of roving herbivorous fish to be condensed into the remaining space – leading to an intensified grazing pressure on these areas. When antifoul-coated PVC tile ‘pseudo-corals’ were attached to the reef to simulate an increased live coral cover (and proportionate decrease in carbonate substrates available for algal growth), fish grazing was condensed on to the remaining carbonate substrate algal community. The result was a reduction of algal biomass proportional to the space removed by the tiles. In the Caribbean, territorial herbivorous damselfish have long been recognised to aggressively exclude roving herbivorous fish from their territories (Myrberg and Thresher 1974, Brawley and Adey 1977a, Itzkowitz 1977b), which they have been said to guard as a resource for their own needs (Robertson et al. 1981, Ceccarelli et al. 2001a). It is generally assumed that the net effect of these exclusions is a reduced grazing pressure inside the territories in comparison to that on the external reef – as apparently evidenced by the comparatively high internal algal biomass (Brawley and Adey 1977b, Sammarco 1983, Ferreira et al. 1998, Ceccarelli et al. 2001a). (Although it should also be noted that there good evidence for increased primary productivity within damselfish territories (Brawley and Adey 1977b, Klumpp et al. 1987).) Due to such documented grazer-exclusion it is therefore reasonable to attempt to extend the ‘Space-Availability Hypothesis’ of Williams *et al* (2001) and posit that the grazing activity of such excluded fish would thereby be concentrated on the remaining non-territory areas of the reef.

Since the territories of aggressive and ubiquitous damselfish species such as *Stegastes planifrons* can inhabit up to 50% of the Caribbean reef substrate, with algal mats virtually contiguous in some areas. (Brawley and Adey 1977b, Robertson et al. 1981, Sammarco and Williams 1982, Wellington 1982, Ebersole 1985), such grazer-exclusion and concomitant concentration could have an important effect at the reef-wide level. In addition, different species of damselfish have been shown to favour different coral microhabitats on which to base their territories (Itzkowitz 1977a), meaning that the degree to which damselfish affect grazing may be coral substrate-specific, and could have altered concurrently with changes to Caribbean coral assemblages. In order to examine the macro-level effects of damselfish on grazing, coral substrate must therefore be taken into account.

The association of damselfish with coral substrate is of particular interest on Caribbean reefs, where the ubiquitous and highly territorial threespot damselfish utilises the staghorn coral, *Acropora cervicornis*, as its primary habitat substrate (Brawley and Adey 1977b, Itzkowitz 1977a, Ebersole 1985). Formerly one of the main reef-building species of the Caribbean, *Acropora cervicornis* has seen large-scale declines in cover since the 1970s, to the point that it is now an endangered species (Hughes 1994, Greenstein et al. 1998, Ostrander et al. 2000, Aronson and Precht 2001, Precht et al. 2002, Aronson et al. 2008, Alvarez-Filip et al. 2009). The loss of the habitat has opened up more low-relief habitats, in particular there has been shift to greater dominance of relatively planar dead *Montastraea* carbonate habitats (Alvarez-Filip et al. 2009), habitats which may naturally underlie *Acropora* thickets. Recently, some authors have shown that the loss of the *Acropora* habitat may have led to the relocation of some *S. planifrons* populations to *Montastraea* substrates (Precht et al. 2010). In view of the highly aggressive and territorial grazer-exclusion behaviour of *S. planifrons*, and its strong association with the *Acropora* microhabitat (both outlined above), it is interesting to consider the net impact on grazing dynamics of the loss of this coral and the associated coral-damselfish complex, and its subsequent replacement with alternative substrates, such as underlying dead *Montastraea*, and /or a shift of the previously resident *S. planifrons* populations to the *Montastraea* microhabitat.

Since the mass die-off of the voracious grazing urchin, *Diadema antillarum*, parrotfish (Scaridae and Sparisomidae) and surgeonfish (Acanthuridae) can now be said to be the key grazers of functional importance to Caribbean reefs (Mumby 2006, Mumby et al. 2007a). Here the relative roles of coral substrate and damselfish territoriality in

structuring parrotfish and surgeonfish grazing on Caribbean reefs are examined, as well as the implications of the loss of the *Acropora cervicornis*-*Stegastes planifrons* complex for grazing at the reef-wide level. Particular attention has been directed at the following specific questions:

1. Does coral microhabitat (*A. cervicornis* versus *M. annularis*) have an effect on fish grazing behaviour?
2. Within and between coral microhabitats do damselfish territories act as grazer exclusion zones, with the ipso-facto concentration of grazing intensity on substrates external to territory boundaries?
3. What are the implications of the loss of *Acropora cervicornis* and the associated *Acropora cervicornis*-*Stegastes planifrons* complex for grazing intensity at the reef-wide level?

In order to address these parrotfish and surgeonfish feeding behaviour was surveyed in relation to coral microhabitat and damselfish territory presence. Two scales of analysis were conducted, firstly six 10m x 10m plots were used to examine questions of reef-level effects of microhabitat on grazing intensity, and secondly a fine-scale analysis was performed on a subsection of observations in order to examine potential within-territory effects within coral microhabitats.

METHODS

Study sites

Fish grazing behaviour was quantified in six replicate plots measuring 10 m x 10 m, four of which were located on Glovers Reef east coast (Long Cay and Middle Cay), and two on the west coast. Plot locations were chosen using a stratified random sampling method. Larger plots were used in order to encompass a range of microhabitats at each site, thereby reducing the possibility of any site-specific differences in ambient fish grazing levels being auto-correlated with microhabitat. Plots were spaced a minimum of 200 m apart and were semi-permanently marked in order to allow repetitive sampling.

At each site a collapsible 6m x 6m quadrat was used as a guide for marking out the 10m x 10m area, using galvanised nails as reef markers. The quadrat had two-meter cross strings and was composed of 6m lengths of PVC pipe that were assembled into a square by two divers underwater; the quadrat was then re-deployed in an overlapping manner to allow the 10m square to be delineated accurately. Subsequently the perimeter of each site was strung out with taught nylon string, and cross strings attached at 2m intervals creating a grid of twenty five 2m x 2m squares, which was left in place (Figure 4.1). Each 2m square was photographed individually from above in plan view using a 7 megapixel digital camera at maximum resolution. Images were trimmed in Photoshop and assembled to form a photographic base-map of each site, consisting of one large mosaic of the entire 10m x 10m plot (Figure 4. 2). This was printed onto thin card and laminated for use underwater, where it could be marked temporarily with a chinagraph pencil, enabling spatially explicit data collection (a cheap black make up pencil made a good locally available substitute when supplies ran out). This innovative benthic base-map system enabled the collection of data on fish feeding behaviour, damselfish territoriality, and coral microhabitat in a novel and a spatially integrated manner.

Mapping of damselfish territories

Damselfish territory positions (*S. planifrons* and *S. fuscus*) were recorded directly onto the photographic base map at each site, enabling this information to later be interrelated to substrate composition and fish grazing behaviour. Each 2m x 2m square was observed individually and the

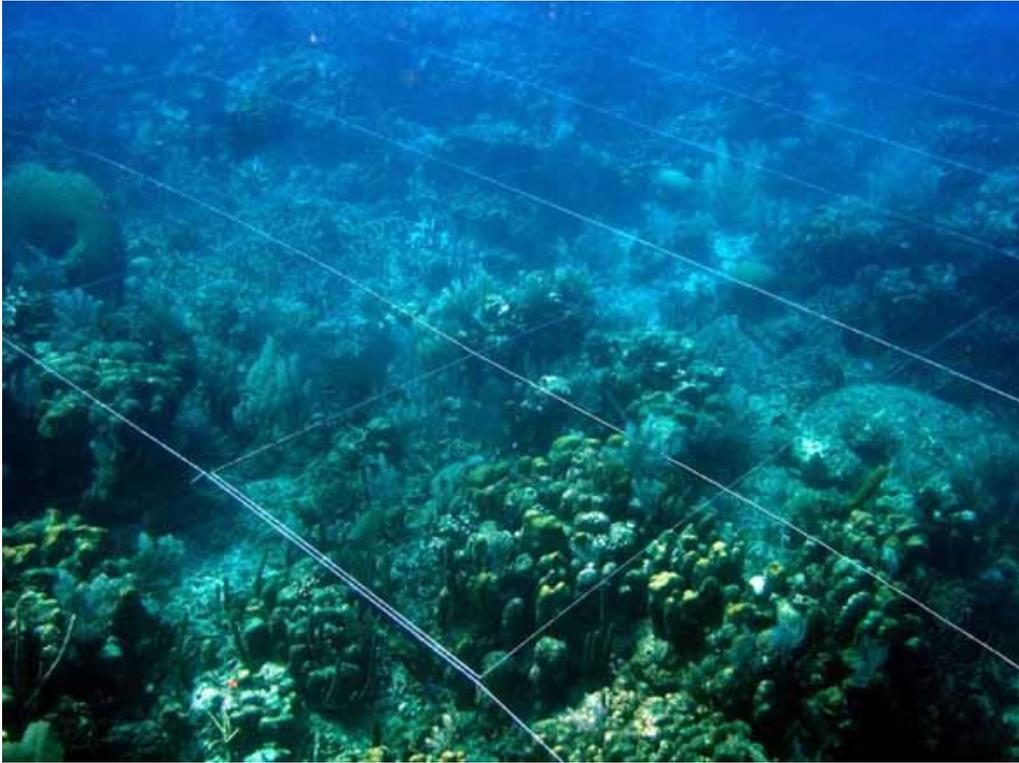


Figure 4.1 Overview of an experimental plot on the east coast of Glovers Atoll showing the 10m x 10m string grid composed of 2m x 2m squares.

changing positions of damselfish marked on the laminated substrate base map each time the fish moved to a new position. Divers hovered statically above the substrate at a minimum distance of 3m so as not to disturb fish behaviour. Fish were monitored for a minimum of ten minutes, or until fish movements did not extend the area of general movement for any fish for at least two minutes. Dots were then connected to denote the extent of the fish's movements and demarcate individual territories, and a species code was recorded. Where a damselfish territory overlapped the edge of a 2m x 2m square the movements were marked in the appropriate position on the adjacent square on the base map. Once back on land these territory boundaries were exactly transcribed onto printed copies of the base map, and the laminated copy was wiped clean for use in fish grazing observations. This process was repeated for each site 3 months later in order to check for consistency of territory locations, it was found that there was little observable difference in territory positions.

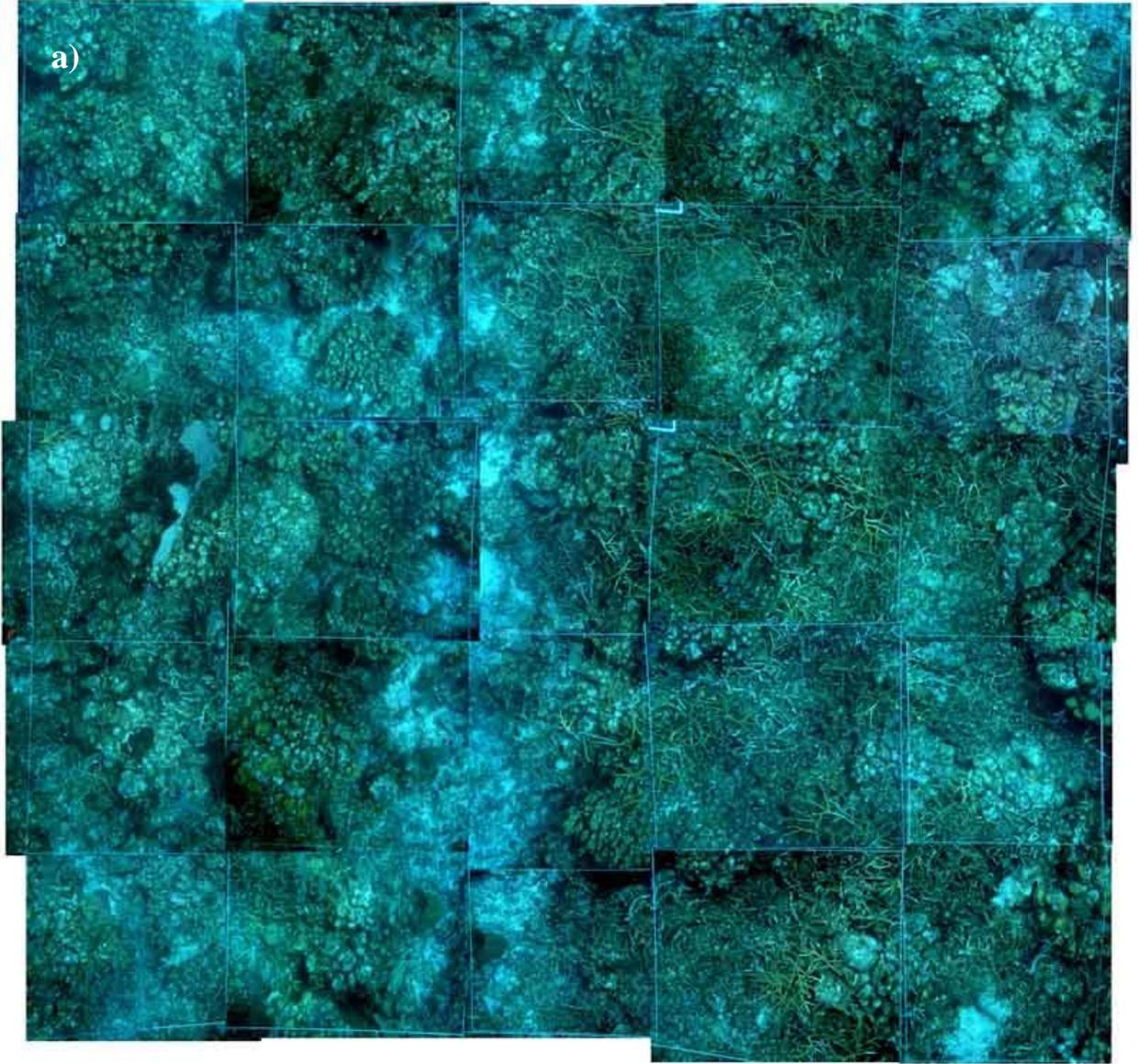
Quantification of fish grazing behaviour

Parrot and surgeonfish biting positions were recorded directly to the laminate base map independently of any information on damselfish territories. In a similar manner to the damselfish observations, individual 2m x 2m squares were watched from above (static

hovering above the substrate at a minimum distance of 3m) for individual observation periods of 3 mins. This 3 minute observation period allowed all 25 squares at each site to be surveyed by two divers during a single observation period, being a single dive. Exact (within 5cm) feeding locations of herbivorous fish were noted on the base map using a unique observation number. The observation number was concurrently recorded onto a data sheet, along with a code for fish species, phase, length, and number of bites taken. When multiple fish fed at the same spot new records were made against the same observation number – thus the observation number related to a position on the reef substrate. This process was repeated for each of the 25 squares at each site so that on aggregate the whole 100m² of the site was watched for three minutes; taken together this data was considered as a single site replicate. Site observation replicates were conducted over a period of four months, with sets of observations in the morning, middle of the day, and afternoon to allow for diel variation in fish grazing behaviour, although at three sites only two observation sets were possible due to an unexpected need to cut the fieldwork short. As explained in more detail later, the positional observation number of the fish biting behaviour on the habitat base-map was later used to relate the position of individual fish bites to coral substrate and mapped damselfish territory positions.

Quantification of benthic cover

Benthic cover categories used in this study are defined in Table 4.1, along with abbreviations used. For analytical purposes substrates were considered in terms of coral-damselfish complexes, and data was extracted from the photographic base-maps on this basis. As an example the coral-damselfish complex ACL_SP denoted an area of reef composed of a live stand of *Acropora cervicornis* which was also an *S. planifrons* territory; for ease of reference a key to the full list of these complexes is found in Table 4.2. This gave a total of 12 possible coral-damselfish complexes on which data was collected at each site. Using the substrate information from the photographic base-map in conjunction with the damselfish territory boundaries recorded on the same map, individual coral-damselfish substrate complexes were delineated. The computer program Vidana (<http://www.marinespatialecologylab.org/resources/vidana/>) was then used to calculate percent cover of each complex for each 2m x 2m square individually.



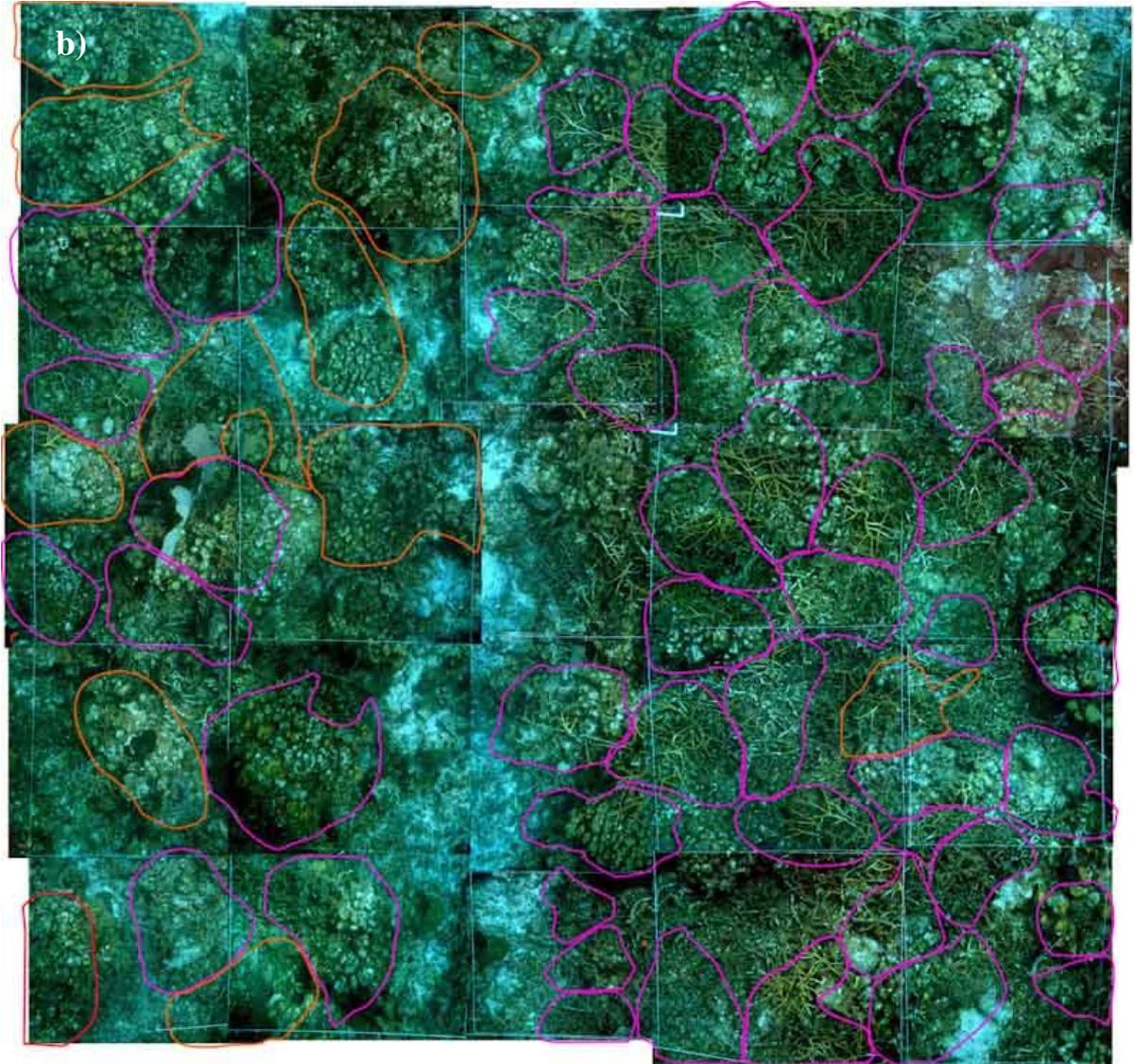


Figure 4.2 Example of photographic base-map mosaic of a single experimental plot.

Each smaller square measures 2m x 2m, and 25 squares make up the total plot size of 100m². Base maps were printed onto card, laminated and taken underwater so data could be recorded spatially in relation to the substrate (more details given in methods). a) base map mosaic b) example of mosaic with damselfish territory boundaries mapped onto it.

Table 4.1 Benthic cover categories defined in this study.

Cover type	Abbreviation	Description
<u>Coral microhabitat cover types:</u>		
<i>Acropora cervicornis</i> live	ACL	Live stands of <i>A. cervicornis</i>
<i>Acropora cervicornis</i> dead	ACD	Dead stands of structurally intact <i>A. cervicornis</i>
<i>Acropora cervicornis</i> rubble	AR	Dead lower relief rubble of <i>A. cervicornis</i> origin
<i>Montastraea annularis</i> dead	MD	Dead <i>Montastraea annularis</i>
<u>Damselfish territory cover types:</u>		
Non-territory area	N	Reef areas uninhabited by damselfish
<i>Stegastes planifrons</i> territory	SP	Mapped territories of <i>S. planifrons</i>
<i>Stegastes fuscus</i> territory	SF	Mapped territories of <i>S. fuscus</i>

Table 4.2 Key to substrate-damselfish complexes used in this study.

Substrate-damselfish complex	Coral microhabitat	Damselfish species
ACL_SP	<i>Acropora cervicornis</i> live	<i>Stegastes planifrons</i> territory
ACL_SF	<i>Acropora cervicornis</i> live	<i>Stegastes fuscus</i> territory
ACL_N	<i>Acropora cervicornis</i> live	Non territory area
ACD_SP	<i>Acropora cervicornis</i> dead	<i>Stegastes planifrons</i> territory
ACD_SF	<i>Acropora cervicornis</i> dead	<i>Stegastes fuscus</i> territory
ACD_N	<i>Acropora cervicornis</i> dead	Non territory area
AR_SP	<i>Acropora cervicornis</i> rubble	<i>Stegastes planifrons</i> territory
AR_SF	<i>Acropora cervicornis</i> rubble	<i>Stegastes fuscus</i> territory
AR_N	<i>Acropora cervicornis</i> rubble	Non territory area
MD_SP	<i>Montastraea annularis</i> dead	<i>Stegastes planifrons</i> territory
MD_SF	<i>Montastraea annularis</i> dead	<i>Stegastes fuscus</i> territory
MD_N	<i>Montastraea annularis</i> dead	Non territory area

Values for each square were then summed to reach a figure for total availability for each coral-damselfish complex at each site. Live *Montastraea* cover was excluded from the analysis since this did not represent a surface for algal growth or fish grazing therefore the only *Montastraea* category used is MD (*Montastraea annularis*_dead.) Since live cover only represented about 7% of the *Montastraea* microhabitat area this was not a great loss. In contrast live stands of *Acropora* had dead basal branches which represented a substrate for algal growth and fish grazing, so a category of ACL (*Acropora cervicornis*_live).

*Examination of specific ecological scenarios associated with the loss of *Acropora cervicornis* complexes from Caribbean reefs.*

In order to answer the ecological questions set out in the introduction differences in fish grazing intensities between non-territory coral microhabitats were tested, as were differences between territory and non-territory areas within coral microhabitat. In order to examine possible impacts of the loss of the live *Acropora* habitat on grazing ecology at the reef-wide level the differences in grazing intensity between this and other prevalent coral-damselfish complexes which might replace it were also tested. The following specific were tested :

Loss of ACL_N complex and replacement with ACD_N or MD_N

Loss of ACL_SP complex and replacement with ACD_N, or MD_N

Loss of ACL_SP complex and replacement with ACD_SP, or MD_SP

The first scenario considers the possible impact on fish grazing of the loss of non-territory live *Acropora* (ACL_N), being replaced with other non-territory coral complexes. The second scenario considers the impact of the loss of the prevalent live *Acropora-Stegastes planifrons* (ACL_SP) complex and subsequent replacement with non-territory coral complexes, and the third considers the loss of this the ACL_SP complex and possible shift of the resident damselfish population to other substrates, or the expansion of the *Stegastes fuscus* niche on increasingly available *Montastraea* habitat (which has been shown to be their primary substrate (Itzkowitz 1977a).

Statistical methods

Assessing feeding intensity is complicated by the need to take appropriate account of relative food source availability – particularly in cases where they are not fed upon. Simple calculations of feeding rates per unit of area of cover type are not appropriate, since a value of zero bites taken from a large area achieves the same weighting as a value of zero bites taken from a small source. Electivity indices have commonly been used as a solution to this problem, however a recent examination of two prominent electivity indices (including Vanderploeg and Scandia's E, which was initially used in data exploration for this study) revealed that these are flawed and can be highly unreliable in their assessment of non-random feeding patterns (Tokeshi and Daud

2011). In order to avoid the possibility of erroneous interpretation of data other analytical approaches were employed.

To address reef-scale questions about grazing behaviour mixed models (Crawley 2007) were used with the lme4 package with the free software “R” (<http://www.r-project.org/>). This approach enabled the effects of coral substrate and fish to be examined together and separately, as well as allowing for the nested experimental design. Fixed effects were substrate (ACL, ACD, AR, or MD) and damselfish (N, SP, or SF), with response variable as number of parrotfish or surgeonfish bites, or area grazed. Area of the substrate-damselfish complex was included as an offset term, and the random effects were coast (east or west), site (1 – 6), and ‘Set’ being the term use for temporal replicates within site. Tests of the model revealed that coast did not have a significant effect so this was removed. The reason area was incorporated as an offset term was to allow the availability substrate of a particular type to be factored into the analysis, but to avoid bite data effectively being treated as rates by the analysis (example: 5 bites m⁻² hr⁻²). Bite rates were not appropriate since there since this caused problems in that

Bite data was analysed using a Poisson distribution, with the offset term logged in order to take account of the log-link function used in this distribution; an additional observation-level random effect was also incorporated into the model to adjust for over-dispersion, since quasi-poisson distribution is not compatible with the lme4 package. Residuals were plotted to confirm the fit to the model. Mean bite intensities were subsequently extracted by back transformation. The code used was as follows:

```
FIT<-lmer(FishBites~Damsel*Substrate+(1|Site)+(1|Set)+(1|Obs),  
offset=log(CM2_COVER), family=poisson,data=dat)
```

Where: FIT is the name of the model; FishBites = number of parrot or surgeonfish bites (depending which analysis was being performed); Damsel = damselfish species; Substrate = coral microhabitat. Site= site name; Set = within site replicate; Obs = observation level unique variable; CM2_COVER = area of coral-damselfish complex.

In order to examine area grazed by parrotfish a different version of the model was used which employed a Gaussian distribution, and the observation-level effect was omitted. Residuals were plotted to confirm the fit to the model. Mean bite intensities were subsequently extracted by back transformation. The code used was as follows:

```
FIT <-lmer(ParrotGrazingCM2~Damsel*Substrate+ (1|Site)+(1|Set),
```

```
offset=log(CM2_COVER),data=dat)
```

Where: FIT is the name of the model; ParrotGrazingCM2 = parrotfish grazed area in cm^2 ; Damsel = damselfish species; Substrate = coral microhabitat. Site= site name; Set = within site replicate; CM2_COVER = area of coral-damselfish complex.

In light of the fact that several factors in the results attained probability values of between 0.05 and 0.054 specific p values are provided in the results but an overt decision is made to adopt a critical value of α of 0.054.

RESULTS

Analyses of fish feeding behaviour

A total of over 5000 individual fish bites, consisting of 2199 Acanthurid bites, and 2948 parrotfish bites were recorded across the six replicate sites. Since it was found that *Stegastes fuscus* territories were almost solely concentrated on the *Montastraea* microhabitat and very rarely occurred on *Acropora cervicornis* (< 1% of substrata on average) this substrate complex was omitted from further analyses.

Significant differences were found in planar grazing rates (biting intensity) of parrotfish and surgeonfish at all treatment levels, with differences between coral substrates unoccupied by damselfish, between damselfish species within corals, and between coral-damselfish complex comparisons relating to the possible effects of loss of *Acropora* from the Caribbean reef system (Figure 4.3, and summarized in Table 4.3). Whilst in some cases damselfish presence did have a significant effect on fish grazing, these effects were not always consistent across coral substrates or across grazing fish family (parrotfish or surgeonfish), and in fact damselfish presence often served to increase grazing intensity, rather than reduce it. In addition fine-scale significant differences in parrot and surgeonfish feeding behaviour were found at the sub-territory level. A more detailed examination of specific questions of ecological interest is presented below. Parrotfish and surgeonfish results are analysed separately due to fundamental difference in their feeding mechanisms, and likely impacts on benthic communities. Coral-damselfish complex abbreviations are used, as outlined in Table 4.2.

EFFECTS OF CORAL SUBSTRATE AND DAMSELFISH TERRITORIALITY ON ROVING HERBIVORE GRAZING.

Effect of coral microhabitat (A. cervicornis versus M. annularis) on fish grazing behaviour, in the absence of damselfish territories.

The most striking result of the analysis of grazing intensities is the low rates of grazing seen on non-territory *Acropora* substrates (ACL_N) in comparison to non-territory

Montastraea substrates (MD_N) (Figure 4. 3; Table 4.3). For both parrotfish and surgeonfish mean feeding intensities on ACL_N was the lowest seen on any habitat complex, with feeding rates of less than 3 bites m⁻² hr⁻¹ and 2 bites m⁻² hr⁻¹ respectively. In contrast the feeding rate on non-territory *Montastraea* (MD_N) was one of the highest for both groups of fish, being eight times higher for parrotfish at 24 bites m⁻² hr⁻¹, and nearly thirty times higher for surgeonfish, where mean feeding rates approached 60 bites m⁻² hr⁻¹. These rates were found to be significantly different between the *Acropora* and *Montastraea* complexes for both groups of fish ($p < 0.001$; glm; Figure 4. 3; Table 4.3).

An examination of feeding rates on ACL_N compared to those on non-territory dead *Acropora* (ACD_N) revealed a similar but less significant trend to that seen in the ACL_N to ACD_N comparison. Parrotfish feeding rate on ACD_N was almost three times higher than that on ACL_N, and again surgeonfish feeding intensity differences were larger still with mean grazing intensities of 23 bites m⁻² hr⁻¹ compared to 2 bites m⁻² hr⁻¹ respectively, these difference were again significant ($p < 0.05$ and $p < 0.01$ respectively; glm; Figure 4. 3; Table 4.3.)

Differences between ACD_N and MD_N were not significant, although for both fish families calculated mean grazing intensities on the former were about half those on the latter; however standard errors of the mean were high so this difference was not significant.

These results reveal that for both surgeonfish and parrotfish the live *Acropora* habitat represents a zone of very low grazing intensity in comparison to other prevalent microhabitats. Given the higher bite rates seen on the MD_N substrate for surgeonfish the low bite rates seen on ACL_N are particularly striking.

Effects of damselfish territories within and between coral microhabitats: do damselfish territories act as grazer exclusion zones?

In contrast to acting as grazer exclusion zones, parrotfish grazing rates were actually found to be significantly higher in *S. planifrons* *Acropora* territories than on non-territory *Acropora*, with mean values of 7 bites m⁻¹ hr⁻¹ versus less than 2 bites m⁻¹ hr⁻¹ respectively ($p < 0.05$; Figure 4.3; Table 4.3). Again, rather than repelling surgeonfish

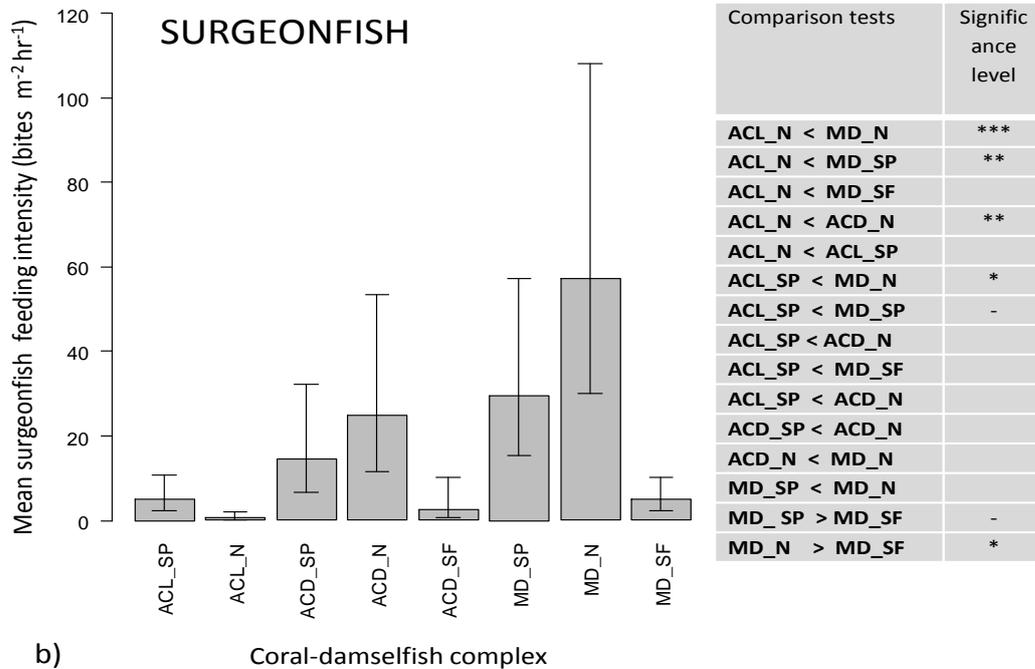
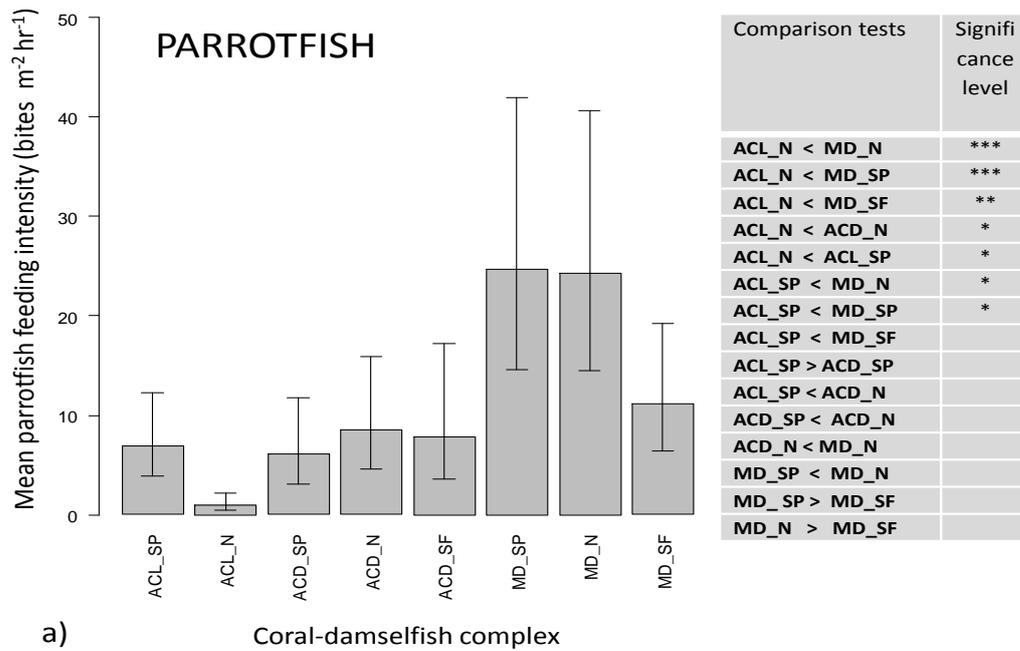


Figure 4.3 Differences in mean parrotfish and surgeonfish feeding intensities according to coral-damselfish complex.

Bars denote one standard error of the mean, note that the upper portion of the bar is slightly longer than the lower due to the log-link term used in the linear model. Panel gives a summary of the results of pairwise comparisons between grazing intensity; a more detailed explanation of these comparisons is found in Table 4.3. Substrate codes are as explained in Table 4.2: ACL = *Acropora cervicornis*(live); ACD = *Acropora cervicornis*(dead); MD = *Montastraea annularis*(dead); N = no damselfish territory; SP = *Stegastes planifrons*; SF = *Stegastes fuscus*. . Significance codes: '***' $p < 0.001$; '**' $p < 0.01$ '*' $p < 0.05$ '-' $p < 0.8$; no significance code means that tests were not significant.

Table 4.3 Summary of feeding intensity differences between coral-damselfish complex pairs. Analysis of bites m⁻² hr⁻¹. Parrotfish and surgeonfish results are given separately. Refer to Figure 4. 3 for mean feeding intensity values. Significance codes: ‘***’ $p < 0.001$; ‘**’ $p < 0.01$ ‘*’ $p < 0.054$ ‘.’ $p < 0.8$.

Coral-damselfish complex 1	Coral-damselfish complex 1	Direction of grazing differential	Significance level	P
PARROTFISH FEEDING				
<i>Acropora</i> Live – Non territory	<i>Montastraea</i> Dead – Non territory	ACL_N < MD_N	***	0.0002
<i>Acropora</i> Live – Non territory	<i>Montastraea</i> Dead – <i>S. planifrons</i>	ACL_N < MD_SP	***	0.0002
<i>Acropora</i> Live – Non territory	<i>Montastraea</i> Dead – <i>S. fuscus</i>	ACL_N < MD_SF	**	0.0053
<i>Acropora</i> Live – Non territory	<i>Acropora</i> Dead – Non territory	ACL_N < ACD_N	*	0.0187
<i>Acropora</i> Live – Non territory	<i>Acropora</i> Live – <i>S. planifrons</i>	ACL_N < ACL_SP	*	0.0276
<i>Acropora</i> Live – <i>S. planifrons</i>	<i>Montastraea</i> Dead – Non territory	ACL_SP < MD_N	*	0.0512
<i>Acropora</i> Live – <i>S. planifrons</i>	<i>Montastraea</i> Dead – <i>S. planifrons</i>	ACL_SP < MD_SP	*	0.0522
<i>Acropora</i> Live – <i>S. planifrons</i>	<i>Acropora</i> Dead – <i>S. planifrons</i>	ACL_SP > ACD_SP		
<i>Acropora</i> Live – <i>S. planifrons</i>	<i>Montastraea</i> Dead – <i>S. fuscus</i>	ACL_SP < MD_SF		
<i>Acropora</i> Live – <i>S. planifrons</i>	<i>Acropora</i> Dead – Non territory	ACL_SP < ACD_N		
<i>Acropora</i> Dead – <i>S. planifrons</i>	<i>Acropora</i> Dead – Non territory	ACD_SP < ACD_N		
<i>Acropora</i> Dead – Non territory	<i>Montastraea</i> Dead – Non territory	ACD_N < MD_N		
<i>Montastraea</i> Dead – <i>S. planifrons</i>	<i>Montastraea</i> Dead – Non territory	MD_SP < MD_N		
<i>Montastraea</i> Dead – <i>S. planifrons</i>	<i>Montastraea</i> Dead – <i>S. fuscus</i>	MD_SP > MD_SF		
<i>Montastraea</i> Dead – Non territory	<i>Montastraea</i> Dead – <i>S. fuscus</i>	MD_N > MD_SF		
SURGEONFISH FEEDING				
<i>Acropora</i> Live – Non territory	<i>Montastraea</i> Dead – Non territory	ACL_N < MD_N	***	0.0004
<i>Acropora</i> Live – Non territory	<i>Montastraea</i> Dead – <i>S. planifrons</i>	ACL_N < MD_SP	**	0.0028
<i>Acropora</i> Live – Non territory	<i>Acropora</i> Live – <i>S. fuscus</i>	ACL_N < MD_SF		
<i>Acropora</i> Live – Non territory	<i>Acropora</i> Dead – Non territory	ACL_N < ACD_N	**	0.0065
<i>Acropora</i> Live – Non territory	<i>Acropora</i> Live – <i>S. planifrons</i>	ACL_N < ACL_SP		
<i>Acropora</i> Live – <i>S. planifrons</i>	<i>Montastraea</i> Dead – Non territory	ACL_SP < MD_N	*	0.0137
<i>Acropora</i> Live – <i>S. planifrons</i>	<i>Montastraea</i> Dead – <i>S. planifrons</i>	ACL_SP < MD_SP	.	0.0768
<i>Acropora</i> Live – <i>S. planifrons</i>	<i>Acropora</i> Dead – <i>S. planifrons</i>	ACL_SP > ACD_SP		
<i>Acropora</i> Live – <i>S. planifrons</i>	<i>Montastraea</i> Dead – <i>S. fuscus</i>	ACL_SP < MD_SF		
<i>Acropora</i> Live – <i>S. planifrons</i>	<i>Acropora</i> Dead – Non territory	ACL_SP < ACD_N		
<i>Acropora</i> Dead – <i>S. planifrons</i>	<i>Acropora</i> Dead – Non territory	ACD_SP < ACD_N		
<i>Acropora</i> Dead – Non territory	<i>Montastraea</i> Dead – Non territory	ACD_N < MD_N		
<i>Montastraea</i> Dead – <i>S. planifrons</i>	<i>Montastraea</i> Dead – Non territory	MD_SP < MD_N		
<i>Montastraea</i> Dead – <i>S. planifrons</i>	<i>Montastraea</i> Dead – <i>S. fuscus</i>	MD_SP > MD_SF	.	0.0700
<i>Montastraea</i> Dead – Non territory	<i>Montastraea</i> Dead – <i>S. fuscus</i>	MD_N > MD_SF	*	0.0120

Acropora - *S. planifrons* territories were associated with increased grazing intensity with a mean of 30 bites m⁻² hr⁻¹ inside territories compared to a non-territory mean of 6 bites m⁻² hr⁻¹ ($p < 0.01$; Figure 4. 3; Tables 4.3.) The effect of *S. planifrons* territory presence on *Montastraea* was different, but there was still no pronounced reduction in roving herbivore grazing beyond ambient non-territory levels. No significant difference was found in parrotfish feeding rates on *S. planifrons* territories and uninhabited

substrates, which were similarly high at around 24 bites $m^{-2} hr^{-1}$. Despite large standard errors, the closeness of the means and the high p value given in Table 4.3 suggest this result was unlikely to be a type II error. For surgeonfish grazing although mean grazing intensity on MD_SP was around half that on MD_N this was not found to be significant in the current analysis ($p = 0.47$; glm). In comparisons of ACD_SP to ACD_N mean feeding rates were broadly the same on both substrates for parrotfish, whilst for surgeonfish mean grazing intensity was slightly lower on ACD_SP, but the difference was not significant ($p = 0.630$, Table 4. 3; Figure 4.3). Again there was no pronounced grazing reduction by the presence of *S. planifrons* compared to ambient grazing levels on this coral microhabitat.

As previously stated the *S. fuscus*- *Acropora*_live complex accounted for less than 1 % of substrates, so this was omitted from these analyses. In the case of *S. fuscus* on *Montastraea*, although mean parrotfish grazing rate was lower within territories than on non-territory areas with values of 11 bites $m^{-1} hr^{-1}$ and 24 bites $m^{-2} hr^{-1}$ respectively, the difference was not significant ($p = 0.209$; Figure 4. 3; Table 4. 3). In this case the difference in the means was fairly large but so are the standard errors, so it is possible that with more sampling this difference would become significant. Surgeonfish were apparently more affected by *S. fuscus* presence than parrotfish, with a large reduction in grazing in these *Montastraea* territories ($p < 0.05$; Figure 4. 3 b). In addition for surgeonfish mean grazing on MD_SF was about half that on MD_SP; this result was marginally significant with a p-value of 0.07 (Table 4.3). Although mean parrotfish grazing rate on MD_SF was less than half that on MD_SP, again standard errors were large, and the difference was not found to be significant.

Taken together, these results demonstrate not only that (in the case of *S. planifrons* at least) damselfish territories do not necessarily represent zones of low grazing intensity, but can actually be associated with significantly *increased* grazing rates compared to ambient grazing intensity on the same substrate. In addition, damselfish territory effect can be microhabitat-specific. *S. fuscus* was at times associated with reduced grazing within its territories, and it appears that *S. fuscus* territory presence on *Montastraea* is associated with a reduction in surgeonfish grazing, which is greater than that associated with *S. planifrons* presence (Figure 4. 3). *S. fuscus*' exclusion of surgeonfish must therefore concentrate their grazing elsewhere. Overall, surgeonfish trends tend to be

slightly more significant than parrotfish trends, but this may be due to the higher numbers of surgeonfish bites giving more power to the analysis.

EXAMINATION OF THE GRAZING ECOLOGY IMPLICATIONS OF THE LOSS OF ACROPORA CERVICORNIS, AND THE ACROPORA CERVICORNIS-STEGASTES PLANIFRONS COMPLEX

Grazing differences between Acropora and Montastraea substrate complexes: Implications of the loss of Acropora cervicornis, and dispossession of associated Stegastes planifrons communities.

In view of the Caribbean-wide decline of the *Acropora cervicornis* microhabitat (Aronson et al. 2008, Alvarez-Filip et al. 2009) (Hughes 1994, Greenstein et al. 1998, Ostrander et al. 2000, Aronson and Precht 2001, Precht et al. 2002, Aronson et al. 2008, Alvarez-Filip et al. 2009), and the shift towards dominance of low relief substrates and *Montastraea* (Alvarez-Filip et al. 2009) comparisons were also made of grazing intensity across coral-damselfish complexes occurring on *Acropora* and *Montastraea* substrates. In this study live *Acropora* presence was associated with low grazing intensity: in all comparisons between coral-damselfish complexes where significant differences were seen the live *Acropora* coral-damselfish complex had the lower grazing rate (Figure 4. 3). With reference to the rationale set out in the methods section, the following specific scenarios were examined for effects on grazing intensity:

Scenario 1: Loss of ACL_N complex and replacement with ACD_N or MD_N. This scenario considers the impact on fish grazing of the loss of non-territory live *Acropora*, being replaced with one of two other non-territory coral complexes: ACD_N or MD_N. A more detailed examination of these results has already been presented above in the section '*Effect of coral microhabitat..*' and will not be repeated here, except to reiterated the main trends in the ecological context of the loss of the ACL_N substrate complex. For both parrotfish and surgeonfish the lowest grazing intensities observed were on the ACL_N complex (Figure 4. 3). In the case of the ACL_N to MD_N comparison, mean grazing intensities were eight and twenty times higher on the MD_N habitat for parrotfish and surgeonfish respectively. For ACD_N the feeding rate

was three times higher than on the live *Acropora* for parrotfish, and more than ten times higher for surgeonfish. Therefore in this ecological scenario loss of the *Acropora* habitat and replacement with *Montastraea* represents the loss of a zone of very low grazing intensity, and replacement with one where fish grazing is not subject to the same restrictions.

Scenario 2: Loss of ACL_SP complex and replacement with ACD_N, or MD_N. This scenario considers the impact of the loss of the prevalent *Acropora-Stegastes planifrons* complex if it is replaced with other commonly occurring non-territory complexes, - i.e. if the loss of this complex is associated with a loss of the resident *S. planifrons* population, rather than a relocation. For both parrotfish and surgeonfish, grazing intensity was significantly lower on ACL_SP than on MD_N ($p < 0.05$; Figure 4. 3; Table 4.3), however there was no significant difference in the grazing rate on ACD_N complexes (parrotfish: $p = 0.776$, Figure 4. 3, Table 4.3; surgeonfish: $p = 0.629$, Figure 4. 3, Table 4.3). The loss of the ACL_SP complex and replacement with MD_N represents the loss of a zone of low grazing intensity and replacement with one where grazing has the potential to be high. This is not the case when ACL_SP is replaced with ACD_N, where differences were not significant.

Scenario 3: Loss of ACL_SP complex and replacement with ACD_SP, or MD_SP. This scenario considers the impact of the loss of the prevalent *Acropora-Stegastes planifrons* complex if the loss results in a relocation of resident *Stegastes planifrons* populations to alternative replacement coral substrates. Mean parrotfish grazing intensity was significantly lower on ACL_SP than on MD_SP, where feeding rates were more than double ($p < 0.054$; Figure 4. 3; Table 4.3), but whilst a similar trend was seen for surgeonfish the result was only weakly significant ($p = 0.076$). In addition, there was no significant difference in parrotfish or surgeonfish grazing intensity between ACL_SP and ACD_SP ($p = 0.865$ and 0.337 respectively; Table 4.3).

DISCUSSION

EFFECTS OF CORAL SUBSTRATE AND DAMSELFISH TERRITORIALITY ON ROVING HERBIVORE GRAZING.

Effect of coral microhabitat (Acropora cervicornis versus Montastraea annularis) on fish grazing behaviour: Acropora as a herbivore-exclusion zone?

Despite the large-scale changes in benthic composition Caribbean coral reefs (Hughes 1994, Alvarez-Filip et al. 2009), potential effects of coral substrate on fish grazing behaviour has received very little attention in the literature (Bruggemann et al. 1994a, Bennett et al. 2010). These results reveal a significantly different and much reduced grazing intensity of both parrotfish and surgeonfish associated with the non-territory live *Acropora* microhabitat, compared to either the widely abundant non-territory *Montastraea* habitat, or the non-territory dead *Acropora* habitat (Figure 4. 3). In fact, mean feeding rate on non-territory *Acropora* was the lowest seen on any habitat complex, with parrotfish and surgeonfish feeding rates of less than 3 bites m⁻² hr⁻¹ and 2 bites m⁻² hr⁻¹ respectively. In contrast the feeding rates on non-territory *Montastraea* were some of the highest for both groups of fish, being eight times higher for parrotfish, and nearly thirty times higher for surgeonfish. Parrotfish feeding rate on non-territory dead *Acropora* was almost three times higher than that on non-territory live *Acropora*, and again surgeonfish feeding differences were larger still, with mean grazing intensities of 23 bites m⁻² hr⁻¹ compared to 2 bites m⁻² hr⁻¹ respectively. These extremely low rates of grazing on non-territory live *Acropora* in comparison to other widely available microhabitats suggest that fish were avoiding this microhabitat. Although planar grazing is specifically examined in this study, the actual grazing per unit area of carbonate substrate in the *Acropora* microhabitat could be expected to effectively be lower still, due to the highly branched nature of basal areas, with high surface area available for algal growth. This means that if anything it would be expected that planar grazing to be higher on this habitat if it was proportionate to substrate areal availability.

Although correlation cannot prove cause and effect between patterns of fish grazing intensity and coral-microhabitat, it is hard to imagine any plausible third-party factors to which this result could be attributed. Plots were large enough for different microhabitats to be available at the same site, and microhabitats were also replicated between plots, so any possible site-specific effects on fish grazing intensity should not be auto-correlated with microhabitat. Further, the nested structure of the linear mixed model (Crawley 2007) should account for any such differences, and random effects were not found to be significant. In the absence of any alternative explanation, it is therefore considered that the significant differences in grazing intensity seen here are linked to coral-microhabitat treatment, and that *Acropora cervicornis* is acting as a zone of grazer exclusion /avoidance, although the mechanistic process by which this occurs is as yet undetermined. This finding is substantiated by a recent result from a study of roving fish grazing at the Keppel Islands on the Great Barrier Reef, where substantially lower grazing was recorded in branching (primarily Acroporid) coral habitats compared to low relief substrates (Bennett et al. 2010). Combined planar parrotfish and surgeonfish grazing on *Lobophora* and endolithic algal communities were respectively found to be more than 20 and 10 times lower in the coral thickets, which were 90% composed of the Pacific staghorn coral *Acropora formosa*, a congener of the Caribbean staghorn coral, *Acropora cervicornis* (Bennett et al. 2010). Since there was a significant difference between grazing in both live and dead (but structurally-intact) thickets compared to the planar reef, these authors considered three dimensional complexity to be the likely cause of grazer exclusion. As three-dimensional topographic complexity is often said to favour *increased* fish herbivory (Lewis and Wainwright 1985, Beukers and Jones 1997, Verges et al. 2011), Bennet and Verges suggest their novel findings may be due to the marginal nature of Keppel Islands reefs. Contrary to this notion, the current finding of similar trends in another branching acroporid coral in an entirely different eco-region, suggests that reduced grazing may be a more widespread phenomenon and a feature of highly branched *Acropora* thickets in general. Indeed, some of the studies cited by Bennet and Verges (2010) linking habitat complexity to increased herbivory actually related to urchins and herbivorous damselfish numbers (Beukers and Jones 1997, Almany 2004), and are therefore not relevant to the current debate. Although there are additional studies do show that increased habitat complexity may offer refuges from predation, supporting enhanced numbers of grazing fish in general, they do not document where the grazing of these fish is focused (Lewis and Wainwright 1985). Where reefs are composed of patchy habitat matrices there is no reason to presume that

roving fish feeding is spread evenly over the substrate, so such studies should not in fact be considered contrary to the present finding of locally decreased grazing in the *Acropora* complex.

There are few obvious explanations from the literature for the observed grazing trends. It has previously been found that the stoplight parrotfish, *Sparisoma viridae* has a preference for feeding on lower density *Montastraea* substrates in comparison to higher density substrates, of which the *Acropora cervicornis* skeletal density was the highest (Bruggemann et al. 1994a, Bruggemann et al. 1994b). In addition these authors also showed that as a result of the low density of *Montastraea* skeletal material *S. viridae* was able to take larger bites from this substrate, thereby extracting a higher net yield of energy per bite (Bruggemann et al. 1994a). Although this may well be a factor for excavating herbivores such as *S. viridae*, the density of underlying carbonate substrates would not be expected to be as important for parrotfish species which employ a more superficial scraping mechanism, and should be of little relevance for browsing herbivores such as the Acanthurids (Francini et al. 2010). Although the area requires further investigation it seems likely that *Acropora* three-dimensional geometry could have a role in deterring or excluding grazers from areas where it is present. Whilst mechanistic explanations for grazing trends are not investigated, it could be suggested that in comparison to the open surfaces of *Montastraea*, dense *Acropora* thickets may not be an enticing prospect for larger herbivorous fishes. Firstly, a large parrotfish or surgeonfish feeding head-down in a thicket of branches may well be susceptible to predation, since peripheral vision will almost certainly be impeded and there is little room to manoeuvre, with routes of egress limited or non-existent (forward exits may be blocked by branches so fish may have to "reverse out" of a thicket). Secondly, grazing within *Acropora* thickets may also be less effective for larger fish, since certain parts of the substrate will simply be inaccessible. If three-dimensional structure is important it could also be expected that ACD_N would have similar but less extreme effects on reducing fish grazing intensity, since although the structure of the ACD habitat is more degraded than the live *Acropora* it still represents a thicket-like structure, and is far more complex than the MD structure. The observation of significantly higher grazing intensities on ACD_N than that on ACL_N ($p < 0.05$ and 0.01 for parrot and surgeonfish respectively; Figure 4. 3) would support this notion. However, the other fundamental difference between ACL_N and ACD_N is the live nature of the former.

Whilst completely untested it is possible that potential grazing by jagged and sharp skeletons of live *Acropora*, along with potentially bacteria-laden mucosal coverings (Ceh et al. 2011), could provide an additional deterrent for fish entering this microhabitat, as it can be imagined that grazing against this substrate could provide routes for infection (as many softer-skinned human snorkelers have found). Although the presence of live tissue was not significant in the case of the effect of *A. formosa* on grazing (Bennett et al. 2010). These results provide scope for further manipulative work to evaluate the effects of habitat structure on grazing rate, in particular whether roving grazers tend to avoid highly branched coral ‘thickets’. However, in functional terms, for the Caribbean at least, since *Acropora cervicornis* is the only coral with such a complex and high-relief structure (although *Acropora palmata* is potentially similar in nature, but forms less dense thickets, and dead *Acropora* is by nature a transient microhabitat (Alvarez-Filip et al. 2009)), for practical and management considerations the association of the live *Acropora* habitat with low grazing intensity is the main point of interest.

Do damselfish territories act as grazer exclusion zones?

*Effects of *Stegastes planifrons* territories on grazing intensity*

Due to the prevalence of literature documenting *Stegastes planifrons*' aggressive attacks and repulsion of fish (Thresher 1976b, Brawley and Adey 1977b, Williams 1978, Robertson et al. 1981, Sammarco and Carleton 1981, Meadows 1995), it was originally thought that their territories would act as exclusion zones, with significantly lower grazing than external reef substrates. A surprising result was that rather than being zones of low grazing intensity, *S. planifrons* territories on live *Acropora* (ACL_SP complex) had significantly higher grazing intensities than non-territory areas, with mean rates at least three times higher inside the damselfish territories for both parrotfish and surgeonfish ($p < 0.05$; glm; Table 4.3; Figure 4. 3). In addition, parrotfish grazing on *Montastraea* was not significantly reduced below ambient levels by *S. planifrons*, and the rate of feeding in territory and non-territory areas was similar and not significantly different ($p = 0.97$; glm; Table 4. 3; Figure 4. 3). In the case of surgeonfish, however, the mean grazing intensity inside territories was about half that outside of territories, however standard errors were large and the difference was still not significant (Figure 4. 3; Table 4. 3). Whilst it could be argued that the lack of significance between surgeonfish grazing inside and outside of territories on *Montastraea* may be the result of

a type II error, and that with further data collection this might have become significant, the finding of significantly *more* grazing inside territories for both parrotfish and surgeonfish on live *Acropora* could hardly be subject to this argument. There is also nothing to suggest type II errors for parrotfish biting on *Montastraea*, where mean intensities inside and outside of damselfish territories were roughly equal, and p values were far from significant ($p = 0.978$; Table 4. 3). These results therefore reveal a role of *S. planifrons* territories in grazing ecology which runs contrary to that expected based on the literature described above, although studies of other herbivorous damselfish have indicated a lack of evidence for herbivore exclusion from their territories (Ceccarelli et al. 2005a, Ceccarelli et al. 2006, Francini et al. 2010).

Although the high grazing rates seen inside *S. planifrons* territories might appear initially to suggest that the fish are completely ineffective at excluding roving grazers, this is not necessarily be the case. No attempts were made to quantify how many grazing fish were actually repelled from *S. planifrons* territories. Since the damselfish lawn tends to represent an area of desirable high-quality algal food particularly attractive to roving fish (Ceccarelli et al. 2001a), it is possible that without *S. planifrons*' aggressive territorial defence feeding in these areas would be still higher. Accounts in the literature whereby the removal of a resident threespot damselfish resulted in the 'raiding' of its algal lawn by other herbivorous fish (Brawley and Adey 1977b) suggest that territorial defence had previously been an effective deterrent to their feeding. Further interpretation is beyond the scope of this study, but the implication of these results may be, not that damselfish defence does nothing to reduce grazing intensity, but rather that even with damselfish defence, grazing levels are as high as or higher than on the undefended reef. Viewed in this way these results are not necessarily incompatible with much of the fore-going literature, but do present a surprising new clarification of the wider ecological role of these territories. The extent to which these results are surprising, however, possibly reflects assumptions made in the literature based on witnessed aggressive repulsion of grazing fish by *S. planifrons*, without quantification of comparative feeding rates inside and outside of territories. Indeed closer examination of one classic study (Thresher 1976a) and simple additional analysis (Table 4. 4) reveals that although the aggressive territorial defence by *S. planifrons* is clearly evident, with attacks on roving fish accounting for a vast majority of agonistic encounters, the relative numbers of roving grazers entering the territory which are

actually attacked is generally less than 10%. Of the < 10% of intruders attacked in the study of Thresher (1976) it can be imagined that the number actually expelled would be far less, and the number expelled prior to a bite being taken would be lower still. In the present study few actual expulsions were witnessed although more than 5000 individual bites were recorded. There are also accounts in the literature of increased feeding within the territory confines of other damselfish species (Booth 1998, Ceccarelli et al. 2001a), so in this regard our data is not anomalous.

In contrast to the increased grazing rates on *Acropora cervicornis* there was no effect of *Stegastes planifrons* territories on *Montastraea* (Figure 4.3; Table 4. 3). Reasons for this are not obvious, since it seems unlikely that *S. planifrons* would be less able to defend the ACL habitat. It is possible that if fish are generally avoiding the live *Acropora* habitat (as evidenced by the very low grazing rates here) it could be suggested that there is a high *grazing potential* outside of this complex, so the presence of a desirable resource could entice fish in. On *Montastraea*, however, grazing is already high so there is no such reservoir to draw upon, and any differences might be expected to be smaller.

Effects of Stegastes fuscus on grazing intensity, and comparisons to S. planifrons effects.

In contrast to *S. planifrons* territories where no difference was found, *Stegastes fuscus* territories on *Montastraea* were associated with a significant reduction in surgeonfish grazing compared to non-territory areas, with rates of 4 bites $\text{m}^{-2} \text{h}^{-1}$ versus nearly 60 bites $\text{m}^{-2} \text{h}^{-1}$ respectively ($p < 0.05$; linear mixed model; Figure 4. 3). For parrotfish the difference between territory and non-territory grazing intensities was less, and not found to be significant, despite a mean within-territory grazing intensity of 10 bites $\text{m}^{-2} \text{h}^{-1}$ being less than half the rate of 24 bites $\text{m}^{-2} \text{h}^{-1}$ seen in non-territory areas ($p = 0.012$; linear mixed model; Figure 4. 3; Table 4.3). These results demonstrate that *Stegastes fuscus* is able to exclude surgeonfish from territories on *Montastraea* substrates, and it can therefore be suggested that the grazing pressure associated with such excluded fish would be focused onto other non-territory substrate areas. Although in contrast surgeonfish grazing within *S. planifrons* territories was not significantly different to non-territory areas of the *Montastraea* substrate, it cannot necessarily be concluded that this means that *S. fuscus* is a better territory defender on this substrate than *S.*

planifrons, since the comparison is potentially confounded by possible differences in the algal lawns of the two damselfish (which could represent different degrees of attraction to roving fish.) It is at least theoretically possible, for example, that *S. planifrons* actually deterred more fish from its territory than *S. fuscus*, yet the grazing rate inside the territory was higher due to a still-larger number of fish having been attracted to attempt to feed in the area overall. This was not measured in this study due to the difficulties of determining if a fish ‘might have fed in the territory’ had the damselfish not been present. However, this concept is addressed in general terms at the start of this discussion, so this observation is included here to avoid confusion about our interpretation of results. It was not the intention of this study to elucidate such mechanistic questions, but rather to demonstrate that these two territories represent zones of different net grazing, of importance when considering the possible consequences of habitat change on grazing macro-ecology.

IMPLICATIONS FOR DAMSELFISH BIOLOGY

The association of S. planifrons with the Acropora cervicornis habitat.

The increased within-territory grazing on the live *Acropora* – *S. planifrons* complex compared to the unoccupied *Acropora* microhabitat is particularly surprising, since this is the primary preferred substrate of *S. planifrons* (Itzkowitz 1977a, 1977b). It had been imagined by the authors at the start of the study that the damselfish’s predilection for this substrate might be explained by an increased effectiveness of damselfish grazer repulsion from territories on this substrate (possibly due to the advantages conveyed by the thicket-like three dimensional structure). The results of this study suggest, however, that the preference for the ACL substrate may well lie not in the ease of defence, but in the innate low grazing intensities found within this habitat, which were the lowest of any examined substrate complex (Figure 4. 3). Further, *S. planifrons*’ lack of effective exclusion of grazers from its territories below ambient rates on non-territory areas would suggest that the low grazing rate seen on the ACL substrate would be extremely beneficial to this fish, enabling it to be in possession of a territory with higher standing algal crop than it might be able to maintain by its own territory defence on other microhabitats. Observations of parrotfish feeding behaviour support this theory, with grazing intensities significantly lower within *S. planifrons* territories on live *Acropora* than on *Montastraea* substrates ($p < 0.053$; linear mixed model; Table 4. 3). The same

comparison was only marginally significant for surgeonfish feeding ($p = 0.077$; linear mixed model; Table 4. 3) although mean grazing intensity was more than three times higher on the *Montastraea* substrate. Since the rasping feeding of parrotfish - which may remove all algae down to the bare substrate, is more destructive of algal communities than the more delicate plucking of filaments by surgeonfish it could be suggested that the decreased grazing of this fish family alone would be a reason for *S. planifrons* to favour the ACL substrate (Carpenter 1986). Whilst other factors which might contribute to *S. planifrons*' predilection for *Acropora* such as refugia from predation were not assessed in this study, predation has previously been shown to be generally low in *S. planifrons* (Precht et al. 2010), suggesting this would not be a major factor

A note on the importance of coral microhabitat for S. planifrons and S. fuscus: thoughts on niche diversification.

This study has revealed that damselfish territories can have microhabitat-specific effects on grazing intensity. In the case of *S. planifrons* territories in particular, a large difference was observed in both parrotfish and surgeonfish grazing rates on the live *Acropora* microhabitat compared to the *Montastraea* habitat where much higher grazing intensities were seen (Figure 4. 3). In comparison, effects of damselfish territories within microhabitats were smaller and significant differences were restricted to higher grazing on ACL_SP compared to ACL_N for parrotfish grazing only, and significantly lower grazing of surgeonfish on MD_SF compared for MD_N for *Stegastes fuscus* (Figure 4. 3). It can therefore be suggested that the coral microhabitat might be the primary controller of grazing intensity, rather than damselfish aggression – at least in the case of *S. planifrons*. In the case of *S. fuscus* significant exclusions of surgeonfish below rates on ambient *Montastraea* did occur, and it is also possible that with further data collection standard errors would be reduced and similar but less pronounced difference would be observed for parrotfish (Figure 4. 3). These results suggest that *S. fuscus* is able to achieve lower net grazing rates on the *Montastraea* substrate than *S. planifrons*, and so may be less dependent on the ambient coral microhabitat grazing regime than *S. planifrons*.

Although sometimes also seen on the *Acropora* microhabitat, *Stegastes fuscus* is primarily found on *Montastraea*, and grazing rates seen here would suggest that being

located on this habitat would be less of a disadvantage for this species than for *S. planifrons*. These results are slightly surprising in view of the notoriously aggressive reputation of *Stegastes planifrons*, which has been said to be the most aggressive of Caribbean damselfish (Itzkowitz 1977a, Cleveland 1999). Previous studies have, however, shown that *S. planifrons* has differential species-specific aggressive defence responses, with conspecifics attacked furthest from the territory, congenics (including *S. fuscus*) next-furthest, and a range of other fish allowed to approach more closely (Myrberg and Thresher 1974). Since it appears that territories on the live *Acropora* habitat may represent a very high value resource for the low grazing rates they convey, it is possible that one of the key advantages of *S. planifrons* aggressive nature lies not so much in its ability to repel roving grazers (at which it appears to be less effective than *S. fuscus*), but possibly more importantly in its ability to repel other would-be territory holders, such as *S. fuscus*, from the ACL substrate, and thereby maintain this valuable resource for itself (where it is not necessary to repel roving grazers at such high levels).

Some simple calculations based on data from another classic study by Thresher (1976), reveal that the whilst parrotfish territory intrusion rate was on average 13.14 intrusions hr^{-1} , the mean rate of attacks on parrotfish was only 0.94 hr^{-1} , meaning on average only about 9% of fish intrusions were attacked (Table 4. 4). Similarly, for surgeonfish. mean intrusion frequency was 15.5 hr^{-1} , whilst mean damselfish attack frequency was only 1.35 attacks hr^{-1} , so only 7% of individual surgeonfish intrusions were attacked. This demonstrates that rates of attack were actually far lower than the number of actual intrusions. Such a low rate of attack, let alone actual rates of successful repulsion and preventing of feeding (which are not documented) may support the notion that repulsion of roving grazers by *S. planifrons* may not be the most important facet of its territorial behaviour. Unfortunately comparative calculations cannot be performed for repulsion of either conspecifics or congenics, as the data are not presented in the study. However, other studies have demonstrated that intrusions by conspecifics are rare and usually repelled (Itzkowitz 1977b, Williams 1978, Meadows 1995). *S. planifrons* has been shown to be able to distinguish between at least 10 different species of territory intruders, including the congener *S. fuscus*, and to tailor their aggressive responses functionally towards groups of fish (Myrberg and Thresher 1974; Thresher 1976), specifically it is also capable of competitively excluding *S. fuscus* and other congenics from *Acropora cervicornis* habitats (Thresher 1976a, Williams 1978, Ebersole 1985).

Although *S. planifrons* has been shown to be aggressively superior, it mainly utilises *A. cervicornis* as its primary preferred substrate, and it is suggested that other substrates are only used as a secondary option (Itzkowitz 1977a). A study of another common Caribbean damselfish, *Stegastes leucostictus*, showed that territory defence against egg predators elicited significant agonistic responses over and above those directed at grazing fish, suggesting an adaptive significance of protection of both food and non-food resources (Ebersole 1977). In view of the lack of obvious success of *S. planifrons* in reducing within-territory grazing beyond ambient levels, and the low-grazing benefits of an ACL territory found in this study, it could be suggested that, at the species-level - and therefore at the evolutionary level, a wholly effective aggressive response towards a congeneric competitor is actually more important than against a roving grazer. Arguably more is at stake in an attack against a congeneric, where failure could result in the loss of a whole territory rather than a partial loss of lawn material resultant from roving grazer intrusion. The desirability of the *Acropora* substrate has previously been demonstrated by experiments that have shown rapid uptake of vacated territories (when residents were speared or removed). Both conspecifics housed on secondary substrates (Williams 1978), and other members of the Caribbean damselfish community (Robertson 1996), rapidly seek to invade the substrate when *S. planifrons* individuals are removed. Thus although the *Acropora* substrate is clearly desirable to all species concerned, promoting a clear need for *S. planifrons*' superior aggressive defence to maintain occupation of the habitat, there has not previously been a clear explanation for the attractiveness of the *Acropora* substrate.

Although there have long been studies into Caribbean damselfish community habitat partitioning (Itzkowitz 1977a, Ebersole 1985, Meadows 1995, Robertson 1996), it has never been fully explained why two fish of very similar ecology: *S. fuscus* and *S. planifrons*, are able to co-exist with overlapping range (Itzkowitz 1977a). Ecological theory dictates that different species should occupy a specific niche, yet the two morphologically similar territorial herbivorous damselfish, both gardening species, are able to use the *Acropora* and *Montastraea* substrates (Brawley and Adey 1977b, Itzkowitz 1977a, 1977b, Robertson et al. 1981). Although it has been demonstrated before that *S. planifrons* excludes *S. fuscus* from the *Acropora* habitat, there has so far been no clear reason why it does not do the same on *Montastraea*, and fully expand into this habitat. This situation is discussed at length by Itzkowitz (1977a) who found a large

overlap in the habitat utilization of the two congeners, and observed a dynamic shuffling of territories on the *Montastraea* substrate. Under the ‘competitive exclusion principle’ of Miller (1967) *In* (Itzkowitz 1977a) for two congeneric species to survive in the same habitat they must have superior competitive advantage in part of the overall niche. The results of the present study for the first time suggest that each fish has a different competitive advantage on its primary microhabitat. So whilst *S. planifrons* aggressive behaviour allows it to competitively occupy the low-grazing *Acropora* niche, it does not effectively exclude grazers to the same low level on *Montastraea*; *S. fuscus* is the more effective territory defender on *Montastraea*, where it is able to significantly reduce grazing below ambient levels (Figure 4. 3), although it might be similarly effective on *Acropora* it is not able to occupy this niche because of the presence of *S. planifrons*.

Table 4.4 Calculation of mean parrotfish and surgeonfish attacks per hour and intrusions per hour based historic data.

Grey block = original data from Thresher (1976a). FISH A, B and F were replicate territorial damselfish. Observations were made by in-situ video recording, more detailed methodology can be found in the original study (Thresher 1976a).

PARROTFISH				
	FISH A	FISH B	FISH F	Mean
Number of attacks	23	6	8	
Hours watched	11.5	7.2	6.5	
<u>Attacks per hour</u>	<u>2</u>	<u>0.83</u>	<u>1.23</u>	<u>1.4</u>
Number of intrusions	241	141	382	
Hours watched	15.5	9.2	24.7	
<u>Intrusions per hour</u>	<u>15.55</u>	<u>15.33</u>	<u>15.47</u>	<u>15.5</u>
SURGEONFISH				
	FISH A	FISH B	FISH F	Mean
Number of attacks	20	7	1	
Hours watched	11.5	7.2	6.5	
<u>Attacks per hour</u>	<u>1.74</u>	<u>0.97</u>	<u>0.15</u>	<u>0.96</u>
Number of intrusions	154	156	310	
Hours watched	15.5	9.2	24.7	
<u>Intrusions per hour</u>	<u>9.94</u>	<u>16.96</u>	<u>12.55</u>	<u>13.15</u>

ECOLOGICAL SCENARIOS: EXAMINATION OF THE IMPLICATIONS OF THE LOSS OF ACROPORA CERVICORNIS FOR GRAZING ECOLOGY.

An Acropora effect on grazing, viewed in the context of the Space Availability

Hypothesis

It follows logically that if *Acropora cervicornis* is significantly associated with extremely low grazing intensity in comparison to other substrates, the grazing pressure from fish that are not feeding on this substrate must be concentrated elsewhere (as illustrated in Figure 4. 4). In addition to this being a logical factual conclusion, the principle has also been demonstrated empirically. Williams *et al* (2001) have previously shown that the existence of areas of substrate on which grazing is not possible (PVC tiles mimicking the presence of live corals) can concentrate fish grazing pressure onto the remaining accessible substrates. The effect of tile deployment being a reduction in benthic macroalgal cover on remaining substrates directly proportional to the area taken up by the tiles (10% or 25% of reef substrate), indicating that fish unable to graze on these surfaces were grazing nearby on the remaining available algae. Williams *et al* had previously shown that even on healthy well managed reefs with little fishing pressure and no obvious sources of pollution herbivorous fish populations were only able to ‘crop down’ algae on up to around 50 – 65% of the substratum area (Williams and Polunin 2001), indicating that the carrying capacity of herbivorous fish of a given reef is likely controlled by additional factors to the availability of food (E.g. a combination of recruitment, territoriality, availability of refuges from predation (Williams *et al.* 2001)). Therefore a tenet central to the Space Availability Hypothesis is that since numbers of grazing fish on a reef cannot rise past a certain environment-determined threshold, there is a point where increasing food availability will not lead to increased fish populations. As food availability increases beyond this threshold it will fundamentally exceed the ability of the fish populations to consume it, with the result of higher algal standing stock. More explicitly the Space Availability Hypothesis proposes that decreases or increases in available reef surfaces suitable for algal colonisation will affect the amount of algal biomass supported by a reef, thereby being one of the factors determining whether the fish supported by that reef are able to keep algal standing stocks low. Since *Acropora cervicornis* can occur in dense thickets covering large swathes of reef (Goreau and Goreau 1973, Tunnicliffe 1981) I now suggest that inherent grazer avoidance of this habitat and concomitant concentration of grazing activity onto non-Acroporid substrates could have large-scale effects important at the reef-wide level.

This concept of an ‘*Acropora effect*’ is illustrated schematically in Figure 4.5. This hypothesis has large implications for the role of the *Acropora cervicornis* habitat in Caribbean grazing macro-ecology and algal dynamics, as discussed below.

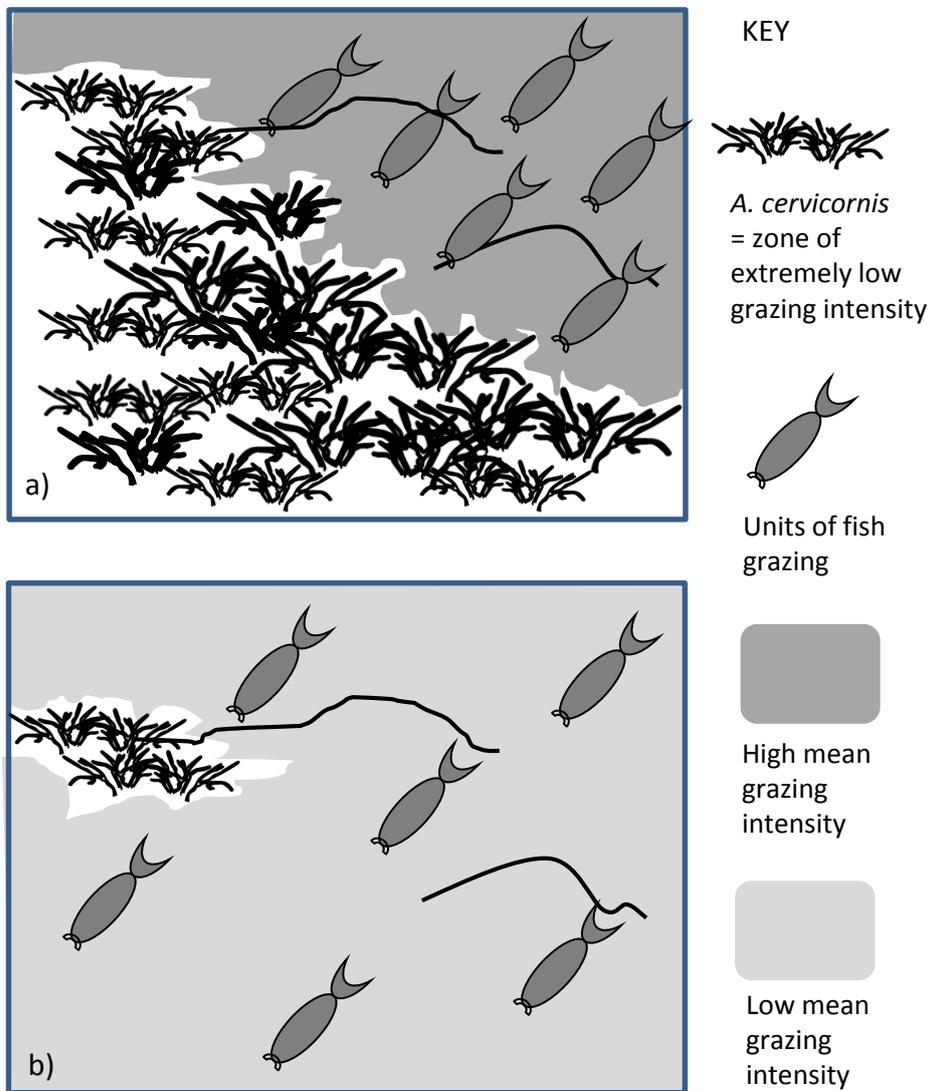


Figure 4.4 Schematic illustration of the ‘*Acropora effect*’.

On a high *Acropora* cover reef (a) *A. cervicornis*-associated zones of low grazing intensity result in the concentration of units of fish grazing onto a the remaining substrate, leading to high mean grazing intensities in non-*Acropora* areas (darker shaded area). On a low *Acropora* cover reef (b) fish are able to graze freely over the large area of remaining substrate: the same units of grazing pressure are distributed more diffusely, resulting in a lower net grazing intensity on non-Acropora substrates (represented by a lightly shaded area).

Implications of an 'Acropora effect' on grazing in relation to the large-scale loss of Acropora from the Caribbean

The corollary of the idea that grazer avoidance of the *Acropora* habitat would cause concentration of grazing activity onto non-Acroporid substrates is that loss of large stands of *Acropora* would lead to dilution of grazing pressure when these stands are replaced by substrates available to algal colonisation, such as dead carbonate reef (in accordance with the principles of the Space Availability Hypothesis outlined above). Over the last 30 years there has been a more than eighty percent decline in live cover of *Acropora cervicornis* throughout the Caribbean region, so that this formerly prevalent species is now registered as a 'Critically Endangered' species (Aronson et al. 2008). Formerly, *Acropora cervicornis* formed large swathes of highly branched dense thickets occupying up to 70% of the substrate in some areas (Goreau and Goreau 1973, McClanahan and Muthiga 1998). The extent of this decline has been particularly large in Belize, where *Acropora cervicornis* was the main reef-building species in many areas (McClanahan and Muthiga 1998, Aronson and Precht 2001, Aronson et al. 2002a, Aronson et al. 2009), with evidence from geological cores suggesting that this state had persisted over at least the last thousand years (Aronson and Precht 2001, Aronson et al. 2009). New implications of the loss of the *A. cervicornis* habitat on grazing pressure, and associated effects on algal dynamics are examined below. Firstly the loss of *Acropora* coral-damselfish complexes, and specific alternative scenarios are discussed in terms of measured grazing differentials between coral-damselfish complexes. Secondly, there is an examination of the likely former ecosystem-level role of *A. cervicornis* in reef grazing ecology, and the possible implications of its loss from Caribbean systems.

Replacement of Acropora cervicornis– damselfish complexes: Examination of specific alternative grazing scenarios.

Specific alternative scenarios are examined in relation to the functional role alternative coral-damselfish complexes would play in the 'space availability hypothesis'. The large-scale loss of the *Acropora* habitat has opened up more low-relief habitats and Caribbean reefs have seen a general deterioration in three dimensional structure (Alvarez-Filip et al. 2009). It is considered that in the event of loss of the ACL coral habitat two likely replacement coral substrates are dead but relatively structurally intact

Acropora (ACD), and dead *Montastraea* (MD), which is the basis of much of the carbonate substrate of Caribbean reefs (Alvarez-Filip et al. 2009), and may often underlie *Acropora* thickets (Idjadi et al. 2006). The ACD substrate occurs when *Acropora* dies but remains structurally intact, for example due to coral bleaching (Diaz-Pulido et al. 2009, Bennett et al. 2010), or the white band disease outbreak which was responsible for much of the wide-scale decline of this species (Aronson and Precht 2001). The ACD substrate is more transient, since structural degradation occurs over time (Alvarez-Filip et al. 2009). In contrast, dead *Montastraea* substrate is now a common component of Caribbean reefs, where the live component of this microhabitat can be as little as ten percent on average (this study; chapter 1). In view of the common association of the ubiquitous and highly territorial threespot damselfish with *Acropora cervicornis* (Itzkowitz 1977a, 1977b) the implications of the loss of the ACL_SP complex as a corollary the loss of ACL itself is also examined. Some authors have also shown that the loss of the *Acropora* habitat may have led to the relocation of some *S. planifrons* populations to *Montastraea* substrates (Precht et al. 2010), so this possibility is also considered. The ecological implications of specific possible alternative scenarios outlined earlier are now individually discussed below.

Scenario 1: Loss of the non-territory live Acropora complex and replacement with non-territory dead Acropora, or non-territory dead Montastraea. (I.e. loss of ACL_N complex and replacement with ACD_N or MD_N.)

This scenario considers the impact on fish grazing of the loss of non-territory live *Acropora*, being replaced with one of two other non-territory coral complexes: ACD_N or MD_N. In this study mean grazing intensities were eight and twenty times higher on the MD_N habitat than they were on the ACL_N for parrotfish and surgeonfish respectively. In addition for ACD_N the feeding rate was three times higher than on the live *Acropora* for parrotfish, and more than ten times higher for surgeonfish. If ACL_N was replaced with either of these alternative complexes they would not be expected to function as low grazing zones, fish would be expected to graze widely over the new substrate, with the effect of reduced grazing effort per unit area of reef, as discussed in detail above. Since ACD is viewed here as a transient habitat it can be suggested that there would be a continual dilution of grazing intensity at the reef-wide scale, as previous ACL zones transition from the low grazing intensity of ACL (= high

external grazer concentration) via the intermediate grazing intensity of ACD and finally to the high potential grazing intensity (= low external grazer concentration) of MD.

Scenario 2: Loss of the formerly very common live Acropora- Stegastes planifrons complex and replacement with non-territory dead Acropora, or non-territory dead Montastraea. (I.e. loss of ACL_SP complex and replacement with ACD_N, or MD_N.)

This scenario considers the impact of the loss of the prevalent *Acropora-Stegastes planifrons* complex if it is associated with a loss of the resident *S. planifrons* population, rather than a relocation. For both parrotfish and surgeonfish, grazing intensity was significantly lower on ACL_SP than on MD_N ($p < 0.05$; Figure 4. 3; Table 4. 3), although there was no significant difference in the grazing rate on ACD_N complexes (parrotfish: $p = 0.776$; Table 4. 3; surgeonfish: $p = 0.629$; Table 4. 3). These results indicate that a similar but possible less extreme impact on grazing intensity to that caused by the loss of the ACL_N complex would be expected. I.e., loss of ACL_SP and replacement with MD_N would mean the loss of a reduced-grazing zone of significantly low grazing intensity and replacement with a readily grazed substrate. According to the space-availability hypothesis of Williams et al (2001) it can be suggested that this would lead to a reduction in mean grazing intensity reef-wide and a concomitant increased proliferation of macro-algae.

Scenario 3: Loss of the commonly occurring live Acropora cervicornis - Stegastes planifrons complex and replacement with another damselfish complex, being either dead Acropora-S. planifrons complex, or dead-Montastraea-S. planifrons complex. (I.e. Loss of ACL_SP complex and replacement with ACD_SP or MD_SP)

Recently, some authors have shown that the loss of the *Acropora* habitat may have led to the relocation of some *S planifrons* populations to *Montastraea* substrates (Precht et al. 2010). This scenario considers the impact of the loss of the prevalent *Acropora-Stegastes planifrons* complex if the loss results in a relocation of resident *Stegastes planifrons* populations to alternative replacement coral substrates. Mean parrotfish grazing intensity was significantly lower on ACL_SP than on MD_SP, where feeding rates were more than double ($p < 0.054$; Figure 4. 3), but whilst a similar trend was seen for surgeonfish the result was only weakly significant ($p = 0.076$). In addition, there was

no significant difference in parrotfish or surgeonfish grazing intensity between ACL_SP and ACD_SP ($p = 0.865$ and 0.337 respectively; Table 4.3). Again the replacement of the relatively low ACL_SP grazing zone with the alternative MD_SP grazing zone would be expected to result in a wider reduction in grazing intensity, particularly in terms of parrotfish grazing, which is likely more functionally important of the two for reef communities. This was a surprise result, due to the unexpectedly high grazing intensity found within *S. planifrons* territories on the *Montastraea* substrate. The lack of significant difference between ACL_SP and ACD_SP suggests that if there is a transitional period where ACD is temporarily present on the reef there would be a delayed effect on grazing intensity.

In summary, each one of the scenarios finally leads to the replacement of a zone of low grazing intensity (ACL_N or ACL_SP) with a zone of much higher grazing potential (either MD_N or MD_SP), although sometimes through a transitional and possibly intermediate grazing intensity substrate of ADC. As previously discussed, according to the Space-Availability Hypothesis (Williams et al. 2001) this overall loss of a zone of low grazing and replacement with a readily-grazed zone would be expected to lead to a dilution of grazing intensity and concomitant increase in macroalgal cover.

The loss of Acropora cervicornis – a zone of low grazing intensity.

In the present study it has been found that the Caribbean staghorn coral *Acropora cervicornis* (with or without damselfish territories) is significantly associated with very low grazing intensities in comparison to other common substrates on the reef. Another study on the Pacific staghorn coral *Acropora formosa* has found similar trends of 1 – 2 orders of magnitude reduction in grazing by roving fish (Bennett et al. 2010); taken together these studies suggest that roving grazer avoidance may be an feature of Acroporid thickets. This suggests that the formerly wide-spread *Acropora cervicornis* microhabitat (Aronson et al. 2008) could have historically acted as a zone of reduced grazing intensity covering large tracts of Caribbean reefs. It has been shown that (for whatever reason) the *Acropora cervicornis* microhabitat is significantly associated with extremely low grazing intensity; it therefore follows logically that grazing pressure from fish that are not feeding on this substrate must be concentrated on other available microhabitats. This principle has been demonstrated experimentally, where the existence of areas of substrate on which grazing is not possible (PVC tiles mimicking

the presence of live corals) has been shown to concentrate fish grazing activity onto the remaining accessible substrate algal communities. (Williams et al. 2001).

The concentration of grazing effort on certain parts of the reef is of interest because of the potential effects it may have on macroalgal dynamics. In their first study on the subject, Williams and Polunin (2000) demonstrated that (apparently due to non-food related ecological limitations) even lightly-fished reefs may only be able to support enough grazing fish to keep 50 - 65% of the substrate clear of algae. The same authors found that on reefs where constituents not compatible with algal growth exceeded 40% of benthic cover (E.g. corals, soft corals, and other sessile invertebrates), herbivorous fish grazing was focused onto remaining areas where it was sufficient to 'crop down' algal communities. The result was an exclusion of macroalgae from the substrata, which were instead maintained as communities composed of turfs, coralline algae and microalgae (Williams and Polunin 2000). This study, along with their next study (Williams et al. 2001) led to the 'space availability hypothesis' whereby the authors suggest that the general loss of live coral cover from the Caribbean may have contributed to the overwhelming of grazing thresholds on reefs (since typically 70 – 90 % of substrates may now be available for algal growth), enabling a proliferation of macro-algae. Williams et al (2001) also made the case that the extent of the proliferation of macroalgae in the Caribbean cannot be entirely accounted for by the direct controlling factors such as nutrient enrichment, *Diadema* loss, and reduced grazing. The authors cite Carrie Bow Cay in Belize as an example of a reef where there was a more than twelve-fold increase in macroalgal cover between 1980 – 1992, despite lack of any large changes in factors such as urchin abundance, nutrients, or fishing pressure. The 'Space Availability Hypothesis' suggests a plausible mechanism to explain this seeming discrepancy. Taken together, the two studies (Williams and Polunin 2000, Williams et al. 2001) present a case for a role of the loss of live coral cover effectively leading to a dilution of grazing pressure in the Caribbean, thereby promoting macro-algal growth and contributing to the so-called 'phase shift' of these reefs towards a highly algal dominated state. The results of the present study imply that the same dilution in grazing pressure might be expected to occur due to a reduction in *Acropora* cover. As the mean grazing pressure of only 1 – 3 bites m⁻² hr⁻¹ (Figure 4. 3) was significantly much lower in the *Acropora* habitat (for whatever reason) than the average of the wider reef, the net effect of loss of the *Acropora* substrate would be expected to be an overall reduction in grazing pressure by dilution, due to the opening

up of these previously under-utilized areas to unmitigated fish grazing. Due to the vast scale of acroporid loss in the Caribbean with reductions from over 50 % to 2% in some places (Hughes 1994), the loss of this zone of naturally low-intensity grazing and replacement with dead carbonate substrates could have made a substantial contribution towards exceeding the 50 - 65% grazing threshold previously identified Williams et al (2000). Thus it is reasonable to hypothesise that the loss of the live *Acropora* thicket was on a scale large enough that it may have been a contributing factor to the increased algal cover of Caribbean reefs and so-called 'phase shift' to the present algal-dominated state. This mechanistic concept is illustrated in Figure 4. 5.

Since the live portions of the *Acropora* skeleton usually overly a network of dead basal branches, which in turn often sit atop some form of carbonate substrate, the presence of the live *Acropora* thicket does not necessarily reduce the area available for algal growth (Bennett et al. 2010). Therefore, the presence of the *Acropora* live coral substrate would not be expected to concentrate grazing under the original space availability theory of Williams et al (2001). Instead, I suggest that this habitat presents a special case whereby grazing is reduced within the habitat, by some as-yet unrecognised mechanism, but not due to coral surfaces making it impossible for algae to grow. Significantly reduced grazing within this microhabitat and the ipso-facto concentration of grazing external to this habitat therefore represents an extension to the 'space availability hypothesis' of Williams et al (2000), since in the case of the *Acropora* the exclusion of grazers is mechanistically different.

Whilst the reduced planar grazing by roving seen here in the live *Acropora* habitat might be expected to be associated with increased algal standing stock (as is the case in the Pacific *A. formosa* habitat (Bennett et al. 2010), this may not have the same negative consequences that might be expected if grazing occurred at this level on dead *Montastraea*. Unlike more massive and planar species such as *Montastraea*, live coral and algal cover are not mutually exclusive in the occupation of planar space in Acroporid habitats (Bennett et al. 2010). In fact acroporid stands could be viewed as a multi-tiered environment, since healthy coral thickets commonly occur on top of and in addition to a substrate suitable for algal growth, being the network of dead basal branches and basal carbonate substrate (Idjadi et al. 2006, Bennett et al. 2010). Unlike planar corals, the fast-growing live coral superstructure of *Acropora cervicornis* is also

generally maintained up and away from potential algal smothering. In addition since the main

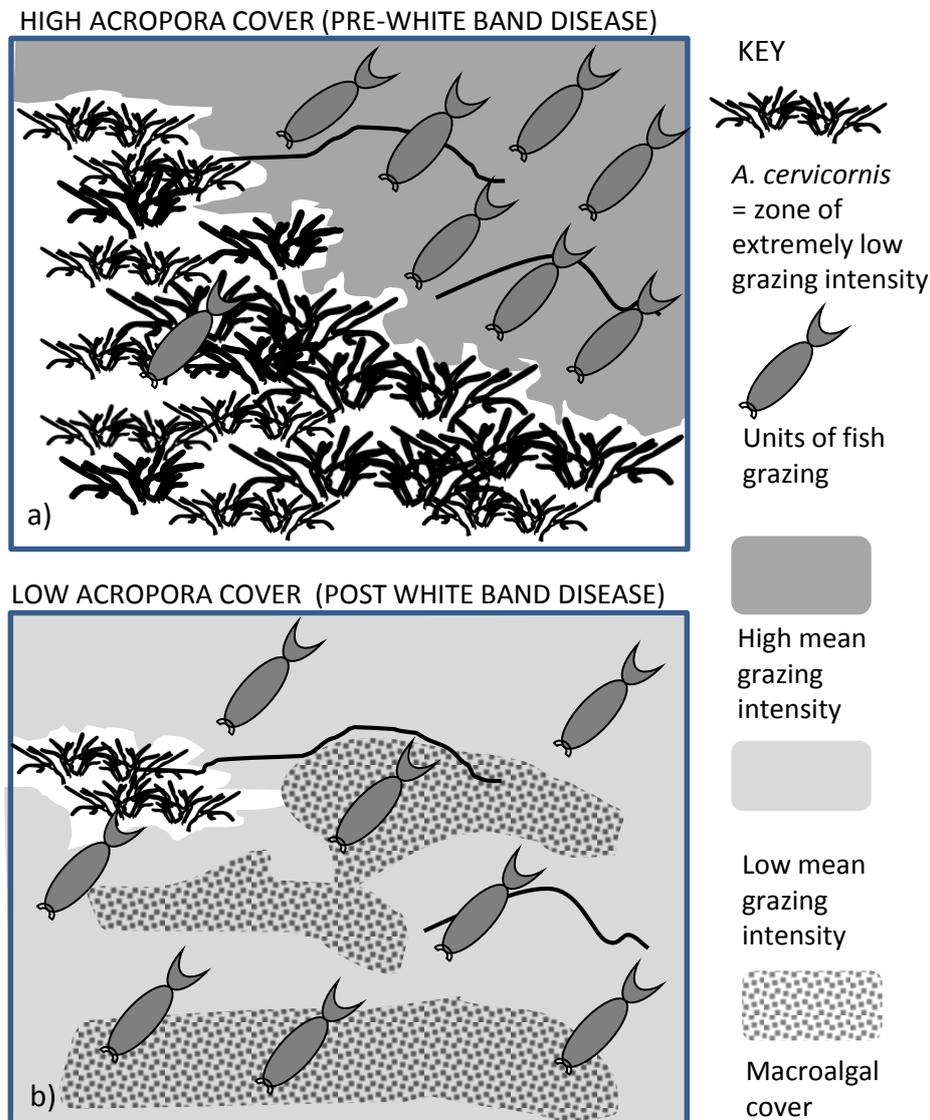


Figure 4.5 Conceptual diagram of the hypothesised effect of the loss of *Acropora* zones of low grazing from Caribbean reefs due to white band disease. (a) Pre-white band disease, high *Acropora* cover reefs (had large *A. cervicornis*-associated zones of low grazing intensity, which caused the concentration of units of fish grazing onto a the remaining substrate, leading to high mean grazing intensities in non-*Acropora* areas (darker shaded area). (b) Post white band disease, on low *Acropora* cover reefs fish are able to graze freely over the large area of remaining substrate, and the same units of grazing pressure are distributed more diffusely, resulting in a lower net grazing intensity on non-*Acroporid* substrates (represented by lightly shaded area), and the proliferation of macroalgal cover (speckled areas).

mode of *Acropora* reproduction is by fragmentation (Tunnicliffe 1981), high macroalgal cover preventing establishment of coral recruits on basal branches would not be expected to affect population growth in this species. Low grazing in this microhabitat may therefore normally have little direct impact on coral health. Historically, urchins may also have made up for a lack of fish grazing. Although our surveys revealed very low present-day urchin densities at Glovers Reef (Chapter 4 of this thesis), the historical presence of much higher populations of *Diadema antillarum* in the Caribbean system prior to the 1980s die off (Sammarco 1980, Lessios et al. 1984, Liddell and Ohlhorst 1986, Bauer and Agerter 1987, Williams and Williams 1987, Greenstein 1989) may have previously kept algal standing stock low within the non-damselfish territory area of the *Acropora* microhabitat, which the urchins appear to favour (Lee 2006).

In summary I posit here – in an extension to the ‘space availability hypothesis’, that due to the low grazing regime found to be associated with the *Acropora* habitat in this study, the effect the large-scale loss of live *Acropora* from the Caribbean may have been to open up new space to un-impeded fish grazing, thereby diluting grazing pressure over the wider reef, and potentially leading to increased macroalgae abundance (Figure 4. 5). I further posit that the scale of the loss of the *Acropora cervicornis* habitat was such that any dilution effect on grazing intensity could have been a contributing factor to the so-called ‘phase shift’ of Caribbean reefs towards a high macroalgal covered state.

Potential further work

Further work could include controlled *in-situ* cage experiments on the reef with high and low *Acropora* cover treatments and fixed numbers of grazing fish to investigate whether high *Acropora* cover treatments resulted in lower standing stock of algal biomass on the surrounding substrates (due to concentrated fish grazing here). It would be ethically unsound to manipulate *Acropora* levels at the reef-wide level due to its rarity – especially in terms of reducing *Acropora* cover in an effort to replicate the hypothesised grazing dilution effect of the large scale *Acropora* losses of the 1970s. However, small scale cage experiments such as the one above could be used to test whether artificially constructed *Acropora* thicket -like structures (for example made from PVC pipe, or even moulded plastic material) would also behave as grazer exclusion zones. If these had the same effect on roving fish grazing as equivalent *Acropora* treatments then the artificial structures could then be used for larger-scale

experiments to test the grazing dilution effects. Reasonably large scale experiments could then be conducted on isolated patch reefs as a model. Three treatments would be applied: i) control reefs – no manipulation of reef substrate but visited by divers for similar amounts of time as the other treatments, ii) low *Acropora* reef representation - addition of 10% cover of artificial *Acropora* thicket, iii) high *Acropora* reef representation - addition of 70% cover of artificial *Acropora* thicket (to represent pre-phase shift reefs). Reefs would be caged so that immigration and emigration of roving fish could not occur during the first three months of the experiment. Treatments would be left in place for 3 months, then removed, along with the cages. Further monitoring of the patch reefs would be continued for 1 year after removal of all materials. Roving fish populations and feeding behaviour would be surveyed prior to manipulation, during the manipulation, and for 1 year after the treatments were removed. Algal standing stock would be monitored following the same pattern. Although the patch reefs should be reasonably isolated the presence of the cages for the first three months would ensure the prevention of emigration of fish to other algal food supplies elsewhere within reach. After removal fish would be able to immigrate or emigrate naturally so that over the longer term populations at the reefs would be expected to be contingent with the overall resources supplied by that reef. Expected results to support the hypotheses about an *Acropora* effect on grazing would be as follows: i) Control treatment: no significant changes in roving fish numbers, feeding behaviour, or algal standing stock, throughout the experiment; ii) low *Acropora*: little or no significant changes in roving fish numbers, feeding behaviour, or algal standing stock, throughout the experiment; iii) high *Acropora* treatment: algal standing stock on non-*Acropora* areas would be expected to decrease during the 3 months that the treatment ‘corals’ are in place (due to concentrated grazing on non *Acropora* surfaces), after removal of the cage and the artificial ‘coral’ thicket algal standing stock would be expected to increase with time, until a threshold is reached (due to diluted grazing by roving fish, but allowing time for algal proliferation). Due to the removal of the cage roving fish would be free to come and go during the last year of the experiment. Whilst it is possible that there would initially be some emigration of fish immediately after cage removal as a reaction to the expected low algal biomass locally available, it would be expected that there would be an immigration by fish over time as algal resources colonise the newly available substrate. The free movement of populations of roving fish are important during this phase of the experiment since for the Space Availability Hypothesis to work fish numbers should be allowed to increase to the natural limits of the reef system. If the

proposed '*Acropora* effect' is true there would be an increase in algal standing stock in treatment iii) after removal of the treatment apparatus, even despite any increase in fish stocks (the point being that the newly available space allows algae to proliferate beyond the capacity of fish stocks to graze them down, providing an excess of food fish to the point that fish then become limited by other resources of the reef).

CONCLUSIONS

This study has yielded a number of surprising results, both in view of the commonly accepted role of *Stegastes planifrons* territories in the literature, and in the identification of previously unrecognized effects of coral substrate on planar grazing of roving fish, which has apparently been overlooked. This can largely be attributed to the spatial nature of the study, where in contrast to ‘focal fish’ and similar widely accepted approaches, the direct relation of fish grazing to the substrate grazed upon has revealed that ‘all substrates are not equal’. In a surprising result the presence of *S. planifrons* on *Acropora* actually served to significantly increase grazing intensity, rather than reduce it, and there were very few incidences of significant reductions of grazing by roving fish within *S. planifrons* territories compared to ambient rates on the same coral substrate. Instead, a large and significant reduction in planar parrotfish and surgeonfish grazing intensity was found to be associated with the Caribbean staghorn coral *Acropora cervicornis* microhabitat, when compared to the common reef-building coral *Montastraea annularis*. These results suggest that grazing within territories may primarily be controlled by coral microhabitat rather than damselfish aggression, at least in the case of *S. planifrons*. The finding of low grazing intensities on the *Acropora* substrate in general, coupled with the relatively high grazing seen on *S. planifrons* - *Montastraea* territories provides likely explanation for *S. planifrons* widely documented predilection for the *Acropora* substrate. The finding that *S. fuscus* was more effective at defending *Montastraea* territories from roving fish than *S. planifrons* and contributes a possible new explanation of the niche diversification between these two species, which has never been fully explained.

In an extension to the ‘Space-Availability Hypothesis’ it is suggested that the grazing activity of roving fish excluded from the *Acropora cervicornis* habitat would be concentrated on the remaining areas of the reef (Figure 4. 4), and that the formerly wide-spread *Acropora cervicornis* microhabitat (Aronson et al. 2008) could have historically acted as a zone of reduced grazing intensity covering large tracts of Caribbean reefs. It is further suggested that the large-scale loss of the live *Acropora* ‘low grazing zone’ from the Caribbean could have caused the opening up of new space to grazing by resident fish, thereby diluting grazing pressure over the wider reef (since in excess of food fish numbers are ultimately controlled by other limiting resources of

the reef habitat (Williams et al. 2001)). It is also hypothesised that the scale of *Acropora* loss from the Caribbean may have been large enough for the loss of *Acropora*-associated low grazing areas and to have resulted in a net dilution of fish grazing pressure potentially large enough to contribute to Caribbean ‘phase shifts’ towards macro-algal domination.

Although there is one other report of low grazing intensity as a feature of the Pacific staghorn coral, *Acropora formosa*, in a marginal reef habitat (Bennett et al. 2010), further work needs to be done to examine to what extent low grazing is an intrinsic feature of staghorn Acroporid microhabitats, as well as other three dimensionally complex corals, and whether this holds true under different fish community structures. The hypothesis of a potential ‘*Acropora* effect’ contribution to the Caribbean phase shift also needs investigation, potentially by use of computer modelling. If this hypothesis is correct then attention should be paid to the conservation of such habitats because of the compounding negative-feedback effect their loss could have on other corals, mediated through grazing dilution and consequential macroalgae overgrowth.

CHAPTER 5

Coral substrate is more important than damselfishes in determining algal cover at Glovers Reef, Belize.

*New insights into herbivory on Caribbean reefs, and implications for the 'keystone' role of *Stegastes planifrons*.*

ABSTRACT

Having established that feeding behaviour of roving herbivorous is significantly influenced by coral microhabitat (Chapter 4), this study goes on to investigate the relative importance of damselfish territoriality and coral microhabitat in explaining emergent reef algal communities (functional cover types). Key findings include that coral microhabitat (*Acropora cervicornis* versus *Montastraea annularis*) is a more important factor than the presence or absence of damselfish territories in explaining both algal community structure and diversity, and the cover of turf algae (ANOSIM, $R=0.18$, $p < 0.01$). Microhabitat-related trends in turf abundance can be explained by microhabitat-related trends in roving fish herbivory, but not by damselfish presence. Specifically, *Acropora cervicornis* areas are significantly associated with both very low grazing by roving fish and high algal cover relative to the *Montastraea* microhabitat. It appears that high turf cover is actually an intrinsic feature of the *Acropora cervicornis* habitat which has hitherto gone unnoticed in the study of reef ecology, possibly having previously been attributed to the effects of resident damselfish. The observation of significantly higher algal turf cover in *S. planifrons* territories located on *Acropora* than those on *Montastraea*, where turf cover was low (Mann Whitney U; $p < 0.01$), may explain why *S. planifrons*, the most aggressively competitive of the damselfish species of Caribbean reefs (Ebersole 1985), favours establishing its territories on *Acropora* as its primary preferred habitat (Itzkowitz 1977a). Within coral substrates no significant effect of damselfish presence on either total turf cover or algal community diversity was detected. Possible reasons for this finding are discussed, including the possibility that changes occurring in the ecological context within which the damselfish live – i.e. the large scale changes or "phase shifts" occurring on many Caribbean reefs (Hughes 1994, McCook 1999, Ostrander et al. 2000) may have caused the relative role of damselfish within the system to have changed by default. It is suggested that the implications of such changes, particularly the loss of *Diadema antillarum* from the system, may be that *Stegastes planifrons* no longer plays a keystone role in contemporary Caribbean reef ecology. These surprising results have led to the rejection of several hypotheses that would have seemed almost foregone conclusions based on the scientific literature.

INTRODUCTION

S. planifrons has classically been documented as a keystone species which achieves high algal biomass within its territories due to reduced herbivory mediated by *S. planifrons*' active exclusion of grazing by fish and invertebrates (Thresher 1976a, Brawley and Adey 1977b, Williams 1979, 1980a, 1981, Cleveland 1999, Ceccarelli et al. 2001a). The findings of Chapter 4 of this thesis challenge this established dogma, in that coral microhabitat was found to have had a more significant effect on fish grazing intensity than damselfish presence. In the present chapter I therefore go on to investigate whether present day *S. planifrons* territories continue to represent the zones of high algal biomass described in the literature, or whether coral microhabitat effects as well as coupled coral-damselfish complex effects on roving fish grazing observed in Chapter 4 might better explain extant algal cover on coral reefs.

Coupled associations of S. planifrons and S. fuscus with coral microhabitat.

S. fuscus and *S. planifrons* occupy different but overlapping spatial niches within Caribbean, allowing us to compare the effects of these fish on different microhabitats. *Stegastes planifrons* has a high affinity for the branching staghorn coral *Acropora cervicornis* microhabitat (Brawley and Adey 1977b, Itzkowitz 1977a, 1977b, Robertson et al. 1981), and *S. fuscus* is most commonly found on dead coral rubble and *Montastraea* (Itzkowitz 1977a, Tolimieri 1995, 1998). However *S. planifrons* is also able to use *Montastraea annularis* (Itzkowitz 1977a, 1977b, Tolimieri 1995, 1998) as well as various other coral microhabitats (Brawley and Adey 1977b, Itzkowitz 1977a, 1977b, Robertson et al. 1981, Lirman 1994, Precht et al. 2010) and *S. fuscus* may also be present on *A. cervicornis* (Itzkowitz 1977a), and the present study. Whilst *S. planifrons* has been shown to competitively exclude other damselfish from its primary and preferred substrate, *Acropora cervicornis* (Itzkowitz 1977a, 1977b), it has been suggested that it is a less effective competitor on less structurally complex corals (Ebersole 1985), and that these are only be used as a secondary option (Itzkowitz 1977a, 1977b). However, despite the large number of studies on damselfish territory algal communities (Sammarco and Carleton 1981, Hixon and Brostoff 1983a, Sammarco 1983, Wilkinson and Sammarco 1983, Ruyter van Steveninck 1984, Hinds and Ballantine 1987, Hixon and Brostoff 1996, Ferreira et al. 1998, Ceccarelli et al. 2001a, Hata and Kato 2002, Hata and Nishihira 2002, Hata et al. 2002, Hata and Kato 2003,

2004, Ceccarelli et al. 2005, 2005a, Ceccarelli et al. 2006, Gobler et al. 2006), little attention has been paid to distinguishing the effects of the damselfish themselves from the potential effects of host coral on benthic algal communities. In particular, no attention has been paid to whether benthic algal community is intrinsically affected by coral microhabitat, or whether damselfish territorial defence might be synergistically enhanced by species-specific or genera-specific properties of coral microhabitat, such as the branching thicket-like nature of *Acropora cervicornis*. Since coral microhabitat and damselfish species are often highly coupled, it is possible that such effects have gone unnoticed in the past, with coral substrate effects having been attributed to the normally-resident damselfish. In addition, the Caribbean has seen a dramatic reduction in the prevalence of *Acropora cervicornis* in recent years, which has been particularly affected by hurricanes (Woodley et al. 1981, McClanahan and Muthiga 1998) and disease (Aronson and Precht 2001). This reduction has been implicated in forcing a shift of *S. planifrons* onto the *Montastraea* microhabitat (Precht et al. 2010), which could have important consequences for benthic algal communities if the extent of damselfish-mediated reduction of herbivore grazing is affected by host coral.

The functional group approach to algal communities, and the ecological importance of algal turfs

In his classic review of herbivory Steneck emphasises the usefulness of an algal assemblage approach to the study of reef algal communities, particularly in relation to herbivory (Steneck 1988). Steneck makes the case that whilst it is impossible to make generalisations about effects of herbivory at the algal species level, it is possible to do so on a functional group level, since species with similar anatomical and morphological characteristics tend to have similar roles in grazing ecology, and occur under similar regimes of grazing intensity (Steneck 1988). Through an extensive synthesis of the literature Steneck devised a number of functional groups useful in the ecological context (Table 5.1; (Steneck 1988)). The assemblage approach offers the benefit that algal functional groups are related to grazing intensity. In their General Model of Herbivory, Steneck and Dithier (1994) demonstrated that certain algal functional groups are favoured by certain levels of disturbance, with a shift from high biomass to low biomass with increased grazing pressure. Thus the assemblage approach can be more

ecologically useful than a species-level approach in the study of reef algal communities, particularly where trophic interactions are involved (Steneck and Dethier 1994).

The algal assemblage approach has been highlighted as particularly useful in the study of damselfish territorial ecology (Ceccarelli 2007, Ceccarelli et al. 2011), at least partly due to the importance of the algal turf functional group in such studies. Algal turf cover is found under high rates of grazing, but above this level the cover shifts to that of crustose coralline algae. At low levels of grazing macroalgae are able to proliferate and high algal biomass is present. Algal turfs are defined by Steneck as: “a ubiquitous and multispecific assemblage of diminutive algae (primarily filamentous), usually having a canopy height of 1 to 10mm” (Steneck 1988). Unlike other groups, the turf algae lack effective physical or chemical defences against grazers, so they must compensate for the inevitability of being consumed by high rates of primary productivity (Steneck 1988, Hixon 1997). Turf algae have been shown to be particularly attractive food sources to both foragers and farmers, with high nutritional value stemming both from the algae themselves, and also from the microalgae and detritus they tend to harbour

Table 5.1 Steneck’s original categorisation of functional groups of algae common to coral reefs
(Steneck 1988).

ALGAL ASSEMBLAGE		ALGAL FUNCTIONAL GROUPS	Common reef dwelling genera
TURFS	AG1	Microalgae	Diatoms, cyanobacteria
	AG2	Filamentous (simple)	<i>Centroceros</i> , <i>Ceramium</i> , <i>Polysiphonia</i> , <i>Sphacelaria</i> , <i>Taenioma</i> , <i>Herposiphonia</i> , <i>Cladophora</i> , <i>Giffordia</i> , <i>Bryopsis</i> , <i>Ectocarpus</i>
	AG2.5	Slightly corticated filaments	<i>Ceramium nitens</i> , <i>Gelidiella</i>
MACROALGAE	AG3	Foliose or sheet	<i>Ulva</i> , <i>Anadyomene</i> , <i>Enteromorpha</i>
	AG3.5	Corticated-foliose	<i>Dictyota</i> , <i>Dictyopteris</i> , <i>Lobophora</i> , <i>Padina</i> , <i>Styopodium</i>
	AG4	Corticated or coarsely branched	<i>Laurencia</i> , <i>Caulerpa</i> , <i>Acathophora</i> , <i>Digenia</i> , <i>Coclothrix</i> , <i>Chondria</i>
	AG5	Leathery	<i>Turbinaria</i> , <i>Sargassum</i> , <i>Eucheuma</i>
	AG6	Articulated or jointed calcareous	<i>Halimeda</i> , <i>Amphiroa</i> , <i>Jania</i> , <i>Penicillus</i> , <i>Corallin</i>
CRUSTOSE ALGAE	AG7	Crustose	<i>Peyssonnelia</i> , <i>Porolithon</i> , <i>Lithophyllum</i> , <i>Neogoniolithon</i>

(Hay 1991, Bruggemann et al. 1994a, Bruggemann et al. 1994b). Algal turfs are therefore seen as a direct and important fuel for the higher food chain, and are recognised as an important source of primary production on coral reefs (Hatcher 1997). In this study turf cover is used as a metric of grazing pressure since when other conditions are constant (e.g. nutrients) the existence of turf cover as opposed to denuded coralline crusts is generally indicative of lower grazing levels by denuding herbivores (Steneck 1988).

The association of territorial damselfish with algal turfs

Algal turf is generally held to be the desired end-product of damselfish gardening activities, with high turf densities relative to the surrounding reef commonly found within territory boundaries of herbivorous damselfish species worldwide, (as reviewed by Ceccarelli et al (2001a)). The subjects of the present study, *S. planifrons* and *S. fuscus*, are both documented as maintaining algal turfs that are conspicuous for their high algal biomass (Brawley and Adey 1977b, Hinds and Ballantine 1987, Ferreira et al. 1998), and for *S. planifrons* in particular, early studies document the clear visual distinction between lush turf-covered territories and the denuded reef substrates at their edges (Robertson et al. 1981). In the present study, however, *S. planifrons* algal mats were not easily visually distinguishable from the surrounding reef, and fish had to be watched and their movements recorded in order to assess the confines of their territories. In addition the general appearance of the algal mats seemed to look different on different substrates, with little obvious turf algae on *S. planifrons* territories on the *Montastraea* substrate. Recent studies have found distinct variation in algal lawns of other damselfish species, both between species at the same location, and within species at different geographical locations (Ceccarelli 2007), demonstrating that there can be considerable plasticity of the damselfish mat with local conditions. It is therefore possible that algal lawns may also vary with host coral species microhabitat.

Damselfish as aggressive guardians of high biomass algal lawns

In general, high turf cover of damselfish territories has been attributed to one or a combination of the following effects, which a ‘farmer’ damselfish may exert within its territory confines: i) aggressive exclusion of roving herbivorous fish and urchins resulting in reduced overall herbivory within the territory compared to the external reef

(Brawley and Adey 1976, 1977b, Itzkowitz 1977b, Williams 1980a, 1981), ii) possible fertilisation effects of fish metabolic waste and by-products on territory algae (Klumpp et al. 1987), and iii) "gardening" or "farming" activities of the damselfish where weeding and /or constant cropping of the algae favours palatable turf species which maintains these algae in a fast growth phase and prevents community succession beyond the highly productive 'turf' phase, e.g. (Lassuy 1980, Sammarco 1983, Klumpp et al. 1987, Ferreira et al. 1998, Ceccarelli et al. 2001a). In the case of *S. planifrons* in particular it has classically been documented that high biomass has been achieved via the exclusion of a large proportion of grazing fish and invertebrates from within its territories (Thresher 1976a, Brawley and Adey 1977b, Williams 1979, 1980a, 1981, Cleveland 1999, Ceccarelli et al. 2001a), however the findings of Chapter 4 of this thesis challenge this dogma, therefore an investigation of the net effect of damselfish territoriality on within-territory algal biomass is needed.

Although damselfish certainly agonistically defend their territories by aggressive attacks on roving grazers (Myrberg and Thresher 1974, Thresher 1976a, Brawley and Adey 1977a, Brawley and Adey 1977b, Itzkowitz 1977b, Williams 1979, 1980a, 1981, Cleveland 1999, Ceccarelli et al. 2001a), there are few studies which actually attempt to quantify the extent of the effect of damselfish presence on the foraging of roving fish. Examples of such studies are: Ceccarelli et al. 2005a, Francini Filho et al, 2010; and Chapter 4 of the present study. Although some studies indicate reduced roving herbivore grazing within territories (Robertson et al. 1976, Hixon and Brostoff 1996), there is a mixed picture with some recent studies indicating no effect for other damselfish species (Ceccarelli et al. 2005a, Ceccarelli et al. 2006). It is of note that Hughes et al (2006) did, however, see a positive selection for feeding on *Halimeda* species within territories. In Chapter 4 of this thesis there was found not only a lack of significant reduction in parrotfish and surgeonfish grazing on *S. planifrons* territories on its primary substrate (*Acropora cervicornis*), but also a significant *increase* in parrotfish grazing on these areas in comparison to the ambient non-territory microhabitat. On *Montastraea* a similar effect was seen, with no evidence for reduced parrotfish grazing inside *S. planifrons* territories. Whilst *S. fuscus* did have a significant effect in reducing surgeonfish grazing on its preferred microhabitat, *Montastraea annularis*, and mean parrotfish grazing inside territories was about half that of the ambient microhabitat, the variability was such that the difference was not significant. However, significant differences were found in cross-microhabitat comparisons, where

grazing rates on both non-territory and *S. planifrons* territory *Acropora* substrates were always significantly much lower than those on *Montastraea*. Taken together these results suggest that in the present-day Caribbean, damselfish effects on the grazing of roving fish may not be as significant as suggested by much of the literature, and that the coral microhabitat effect is actually larger.

However, *Stegastes planifrons* still occupies most available *Acropora cervicornis* habitat and only part of the *Montastraea* habitat at Glovers Reef (unpublished data, Chapter 4). Since *S. planifrons* can competitively out-compete *S. fuscus* for habitat (Itzkowitz 1977a), this observation would suggest that *Acropora* remains an advantageous habitat for *S. planifrons* territories even in post ‘phase shift’ reefs. The fact that *Acropora cervicornis* is the preferred substrate of *S. planifrons*, suggests it can therefore be hypothesised that territories on this substrate will be of a higher quality than those produced on the secondary substrate. If high turf cover is the desired end product of damselfish territorial behaviour, then it can be more specifically hypothesised that higher turf algal cover would be a feature of higher quality territories (potentially due to coral-microhabitat related reduction of grazing on this substrate as documented in Chapter 4).

Herbivorous damselfish as keystone species

Historically, the extent of the within-territory effects on benthic communities has led some damselfish to be termed ‘keystone’ species. Although the origin of this definition seems to have been often overlooked in the literature so that it is sometimes referred to as a keystone species in general terms, the threespot damselfish was initially given this status for its ability to mediate competitive interactions between two important grazers of Caribbean systems, *Diadema antillarum* and *Echinometra viridis*, (Williams 1980a, 1981). *S. planifrons* was shown to moderate the potential dominance of the competitively superior *Diadema antillarum* over *Echinometra* by targeting voracious territory-invading *Diadema* preferentially to the slower and less destructive *Echinometra*. However, these studies were prior to the 1983 Caribbean mass die-off of *Diadema antillarum* (Sammarco 1980, Lessios et al. 1984, Liddell and Ohlhorst 1986, Bauer and Agerter 1987, Williams and Williams 1987, Greenstein 1989). In addition *S. nigricans* has been called a ‘key ecosystem engineer’ (White and O’Donnell 2010), and the Hawaiian damselfish *Stegastes fasciolatus* has also been suggested to act as a ‘keystone species in reverse’ for the high algal diversity of its territories, which has

been seen as a sign of intermediate disturbance mediated through the damselfishes direct actions on the algal turf, as well as the exclusion of other roving herbivorous fish (Hixon and Brostoff 1983a).

Study outline

Here I set out firstly to test to what extent herbivorous damselfish modify algal communities within their lawns compared to external ambient communities, and whether host coral microhabitat plays a role. Secondly I examine whether levels of turf cover in algal assemblages reflect previously observed differences in grazing intensity between coral-damselfish complexes, with particular attention to the effects of coral microhabitat. I use a functional approach in the assessment of algal communities, based on assemblages defined by Steneck (1988): turfs, macroalgae, and crustose algae, as discussed above.

Hypotheses tested were as follows:

The importance of coral microhabitat versus damselfish territoriality as determinants of algal communities.

Hypothesis 1. Coral microhabitat (*Acropora cervicornis* or *Montastraea annularis*) has a more significant effect on algal community structure than the presence of damselfish.

Hypothesis 2. Within coral microhabitat, damselfish territories do not have significantly higher turf cover than ambient carbonate substrates of the same coral.

Hypothesis 3. Threespot damselfish lawns on *Acropora cervicornis* will have significantly higher turf cover than those on *Montastraea annularis*.

Do previously observed trends in roving herbivorous fish grazing explain trends in algal assemblages?

Hypothesis 4. The non-territory *Montastraea* microhabitat will be associated with significantly less algal turf cover than the non-territory *Acropora* substrate.

[Rationale in brief: Grazing rates on non-territory *Acropora* were significantly lower than those on non-territory *Montastraea* (Chapter 4).]

Hypothesis 5: *S. planifrons* territories on the *Montastraea* microhabitat will be associated with less algal turf cover than *S. planifrons* territories on the *Acropora* microhabitat. [Rationale in brief: Significantly less grazing was seen in *S. planifrons* territories on *Acropora* compared to those on the *Montastraea* microhabitat (Chapter 4).]

Hypothesis 6: There will be no significant increase in turf algal cover associated with *S. planifrons* territory areas compared to non-territory areas on the same coral microhabitat. [Rationale in brief: No significant reduction of herbivory by roving grazers was seen inside *S. planifrons* territories in comparison to non-territory areas of the same microhabitat (Chapter 4).]

Hypothesis 7. *Stegastes fuscus* on *Montastraea annularis* will have higher turf cover than *S. planifrons* territories on the same coral microhabitat. [Rationale in brief: *S. fuscus* was seen to be more effective at excluding roving grazers than *S. planifrons* on the *Montastraea* microhabitat (Chapter 4).]

Hypothesis 8. Coral microhabitat is more important than damselfish presence in determining turf cover of algal communities. [Rationale in brief: Higher grazing rates were almost always seen on *Montastraea* treatments in comparison to their

Acropora counterparts, although effects of damselfish were less significant in reducing grazing by roving fish (Chapter 4).]

METHODS

This study was conducted between 7 and 12 m depth on the east coast fore-reef of the remote offshore Glovers Atoll, 30 Km from mainland Belize in 2005.

QUANTIFICATION OF URCHIN GRAZING

Although previous studies have indicated urchin populations to be much reduced in the Caribbean, with *Diadema antillarum* being termed ‘functionally extinct’ (Mumby et al. 2006), un-documented urchin grazing could be a potentially confounding factor in this grazing study, so surveys were conducted in order to quantify any potential role. Three plots measuring 10 m x 10 m, located on the east coast of Glovers Reef were used to quantify urchin feeding behaviour. In this study large plots were used in order to encompass a range of microhabitats at each site, reducing the possibility of any site-specific differences in ambient fish grazing levels being auto-correlated with microhabitat. Plots were spaced a minimum of 200m apart and were semi-permanently marked in order to allow repetitive sampling. Plots were the same as those used for the Chapter 4 fish grazing survey (Figure 4.1), and the same innovative benthic mapping system was employed in order to allow spatially explicit recording of data on fish feeding behaviour, damselfish territoriality, and coral microhabitat in a spatially integrated manner.

Surveys were conducted on SCUBA at night, as urchins have been shown to be more active nocturnally, when they are also more likely to venture into damselfish territories. Surveys of urchin feeding patterns in relation to coral microhabitat (*Acropora* versus *Montastraea*) and damselfish presence (*S. planifrons* territory versus non territory) were carried out with the aim of establishing any effects on urchin grazing patterns. A detailed search for urchins was made in each 2m x 2m square of a given 10m x 10m plot between 19:00 – 20:00 hrs; position, size, and species of urchin were marked on the coral base maps. Data were extracted from the base maps by comparison of marked positions to previously mapped damselfish territory boundaries, and substrate cover type was determined directly from the photographic map (as outlined in Chapter 4). Surveys were then repeated on three different 10m x 10m plots on different island cayes

(> 500 m apart) on three additional nights, but further replication was abandoned due to a lack of useful data stemming from low urchin abundance. Belt transects were then used to survey urchin densities at the wider scale, in order to evaluate their general abundance on the reef. Thirty daytime belt transects of 50 m length x 2m width were carried out randomly at the same sites, with a careful examination of all accessible cryptic habitats for hiding urchins.

QUANTIFICATION OF ALGAL COVER AND FUNCTIONAL ASSEMBLAGES IN RELATION TO CORAL SUBSTRATE AND DAMSELFISH TERRITORIALITY.

The functional assemblage approach to algal community

A functional assemblage approach based on Steneck's classic categorization of commonly occurring reef algae (Table 5.1, (Steneck 1988)) was used in the present study, although some modifications were employed in order to account for potential effects of damselfish gardening activities, which are known to promote the existence of a thick and luscious mat of fine upright filamentous turf algae (Ceccarelli et al. 2001a). In order to facilitate the identification of signals of damselfish effects on algal communities the 'Turf' category of Steneck was further partitioned according to quality of turf. The low-growing 'Microalgae' and 'Filaments' functional groups within the Turf assemblage were given a separate assemblage category (termed 'Bare-Crustose'), and the remainder of the Turf category was further split functionally into 'thick turf' and 'low turf' (Table 5.2).

Tile experiment

In order to investigate differences in algal communities and to remove potential confounding effects, tiles were deployed as a surface for natural algal colonisation. The use of ceramic tiles is prevalent in the study of coral reef benthic communities which might otherwise be confounded by variable substrate complexity (Gleason 1996, Williams et al. 2001, Sanchez et al. 2005, Ateweberhan et al. 2008, Furman and Heck 2008, Edgar et al. 2010, Smith et al. 2010, Ceccarelli et al. 2011, Paul and Pohnert 2011). In this study ceramic tiles were used because i) they provide a completely standardised surface for algal attachment, ii) area is easily quantified (unlike *Acropora* branches, or rugose *Montastraea* heads), iii) they have no previous history of algal

colonisation (unlike scraped areas of reef substrate), and iv) they can be easily removed from the reef for detailed examination in the laboratory. In comparison to benthic surveys, the use of tiles also avoided the potential confounding effect of the possibility of a more advanced state of algal succession on *Montastraea* habitats, which are less transient than Acroporid habitats (Idjadi et al. 2006, Alvarez-Filip et al. 2009).

Table 5.2 Algal functional assemblage groups used in this study.

Cover type / Assemblage	Description of cover
FILAMENTS	Sparse low-growing algal filaments and patches of green microalgal film, (usually no sediments).
LOW TURF	Algal filaments, up to 2mm high (often some trapped sediments).
THICK TURF	Thick cushiony cover of turf filaments, more than 2mm high (often with a thick layer of trapped sediments).
MACROALGAE	Macroalgae cover (usually <i>Dictyota</i> or <i>Lobophora</i>)
BARE-CRUSTOSE	Patches of scraped bare tile surface with patches crustose algae, and green microalgal film, between parrotfish scrape marks*. No, or very occasional algal filaments, (usually no sediments).

Fifty tiles measuring 7.3 cm x 7.3 cm were secured horizontally to the reef using 10 cm galvanised nails and cable ties in such a way that tiles did not contact the nails. Two cable ties were used, one attached to the nail, one to the tile, the two intertwining under tension in the middle. Tiles were left in place for approximately fourteen weeks (103 days), to allow algae to settle and grow on the upper, unglazed surface. Tiles were deployed inside and outside of *Stegastes planifrons* and *S. fuscus* territories, on *Acropora cervicornis* and *Montastraea annularis* substrates, as detailed in Table 5.3.

Table 5.3 Details of experimental tile treatments.

Treatment	Coral substrate (2 levels)	Territorial damselfish (3 levels)	Deployment date	Collection date	N tiles at start	N tiles at end
AC_SP	<i>Acropora</i>	<i>S. planifrons</i>	1 Aug	11 Nov	10	10
AC_SF	<i>cervicornis</i>	<i>S. fuscus</i>	1 Aug	11 Nov	0	2
AC_0		Non-territory area	1 Aug	11 Nov	10	7
M_SP	<i>Montastraea</i>	<i>S. planifrons</i>	1 Aug	11 Nov	10	7
M_SF	<i>annularis</i>	<i>S. fuscus</i>	17 Aug	11 Nov	10	11
M_0		Non-territory area	1 Aug	11 Nov	10	12
TOTAL:					50	49*

* Note: one tile was lost during the course of the study. Individual tile area = 53 cm²

Tiles were located haphazardly over the fore reef of Middle Cay (Figure 1.2), and not confined to the experimental plots used for the fish and urchin grazing quantification. Although ten tiles were originally deployed within each of five treatments, these numbers had altered by the end of the experimental period, due to the relocation of some fish territories (Table 5.3). In all cases the

treatment regime the tile was under at the end of the experiment was the one used in statistical analyses, and from an interim monitoring period it was known that all tiles had been subject to their final regimes for at least a month. No tiles were originally deployed to the "A_F" treatment, since it was hard to find examples of *S. fuscus* on *Acropora*; however, by the end of the experiment two tiles fell within this category, these tiles had previously been in non-territory *Acropora* treatments. In summary, damselfish territory confines were ascertained by monitoring the movements of the fish over a 10 minute period, tiles were then positioned in non-territory areas, or within territories as centrally as possible - depending on features of the substratum.

A dissecting microscope and a wire grid with a square size equal to 1% of the tile area, were used to quantify the algal communities in terms of percentage cover of the functional groups defined in Table 5.2. Since algal (and other) communities vary along a continuum (Steneck 1988), allocation between neighbouring functional groups must always be slightly subjective. However the use of the 1% wire grid enabled a theoretical level of precision of at least 0.5% of the tile area, corresponding to an absolute area of 0.28 cm² (= 0.5% of a total area of 56 cm²), within an area of this size it was not difficult to allocate algal cover decisively to one or other of the defined categories. Note that microalgae were also found to be present on some tiles of the Bare-Crustose category. When viewed through the dissecting microscope, these tiles tended to have a roughly even distribution of patchy crustose coralline algae and micro-algae only existed in patches between multiple clearly visible scarid grazing scars, suggesting that they were able to proliferate temporally (Figure 5.3; 5.4). Although Steneck allocates microalgae to the turf assemblage, in the present study these tiles were still allocated to the Bare-Crustose category since they had clearly been subject to a high intensity grazing regime (Figures 5. 3 and 5.4 a). Since there is a continuum between assemblages (Steneck 1988) this cover type was allocated to Bare-Crustose category

since with the high proportion of bare cover it was seen to be functionally more suited to this category.

This study utilised a non-manipulative approach. Damselfish were not removed or excluded from microhabitats in order to achieve no-damselfish treatments, this was for both ethical and practical reasons. Possible methods for removal are clove oil, or spearing. Clove oil was found to be a slow and highly polluting method for catching damselfish, and although previous studies have removed fish by shooting them, whichever method is used new residents will usually move in immediately or within a matter of hours or days, meaning this to be both impracticable and morally questionable over the long term of this 3 month experiment. Cage exclusion of damselfish was also not practicable as any cage small enough to prevent access by small damselfish study species would inevitably also exclude the majority of roving fish. In prior parrotfish surveys (unpublished data from this study) it was found that smaller parrotfish of around 12cm total length (TL) were the most common grazers on the reef, since dorso-ventral diameter of these fish is of a similar order to that of the damselfish it would have been hard to prevent access of fish of this size to tiles without also excluding the damselfish.

STATISTICAL METHODS

Most tiles exhibited either fairly complete cover of one given functional type or very little, with few tiles having intermediate values (Figure 5.5). The resulting absence of a normal distribution in tile algal cover data necessitated non-parametric analyses in most circumstances.

The importance of coral and damselfish factors in explaining existing benthic and tile algal communities was examined using the computer software *PRIMER* (version 5) (Clarke and Gorely 2001). Percent cover data were initially log transformed and a Bray-Curtis similarity matrix generated, which was then examined using multidimensional scaling ordination (MDS). A two-way crossed ANOSIM using 999 random permutations of the test statistic, R was then used in order to evaluate significant differences according to coral microhabitat and damselfish treatments (Clarke and Warwick 1994). In this test, when there are no differences between groups

the positive and negative R values should be approximately equal and thereby cancel, however positive values ranging from 0.15 to 1 indicate a group effect, with a value of unity occurring when there is total separation of the data by group. Negative values indicate more variation within groups than between (Clarke and Warwick 1994, Clarke and Gorely 2001). A SIMPER analysis (Clarke 1993) was run in order to establish the characteristic sources of dissimilarity between significantly different treatments. Principle component analysis was not used due to the non-normal distribution of the data.

In order to investigate the homogeneity of tile algal communities Simpson's diversity index ($1-\lambda$) (Magurran 1988) was calculated for each tile as an inverse measure of the homogeneity of the algal community in terms of assemblage groups. A Mann Whitney U test was used to examine differences within and between coral and damselfish treatments. In general it was not possible to transform the algal percent cover data to gain a normal distribution, due to the large number of zero values within the data set (Figure 5.5). It was therefore necessary to use non-parametric statistical analyses, and the Mann Whitney U test was favoured where pair-wise comparisons needed to be made.

RESULTS

URCHINS

Urchin grazing

Attempts to relate urchin grazing to coral-damselfish complex were unsuccessful due to very low urchin densities found at the sites surveyed (Table 5.4). Although there was evidence of presence of juvenile *Diadema* venturing into *S. planifrons* territories no adults of these species were recorded. No adults of any urchin species were seen inside *S. planifrons* territories on *Acropora*, but 3 were seen inside *Montastraea* territories, however these numbers are so low overall that no trends can be drawn from these results. Further belt transects confirmed that urchin densities were low across the reef (Figure 5.1), with no further adult *Diadema* being recorded at all, and adult densities of the less voracious *Echinometra* of only 0.065 ± 0.06 urchins m^{-2} on average. Urchin grazing was therefore omitted as a factor from further investigations of algal cover in relation to grazing intensity.

Table 5.4 Results of urchin night survey: observed urchin densities at three different 10 x 10 m sites.

AC= *Acropora cervicornis*; M= *Montastraea annularis*; SF= *Stegastes fuscus*; SP= *Stegastes planifrons*. (A) = adult; (J) = juvenile.

Urchin species	Urchins per substrate-damselfish complex	Urchins per plot (100 m ²)	Mean urchin densities	
			Juveniles m ⁻²	Adults m ⁻²
Site 1 <i>Diadema</i> (J, < 1cm)	1 on AC_SP	1	0.01	0
Site 3 <i>Tripneustes ventricosus</i> (A)	1 on MD_0; 3 on MD_SP	4	0	0.04
Site 4 <i>Diadema</i> (J, < 1cm)	1 on MD_SP; 1 on MD_SF	5	0.02	0.02
<i>Tripneustes ventricosus</i> (A)	1 on MD_SF			
<i>Echinometra viridis</i> (J)	1 on M_SF			

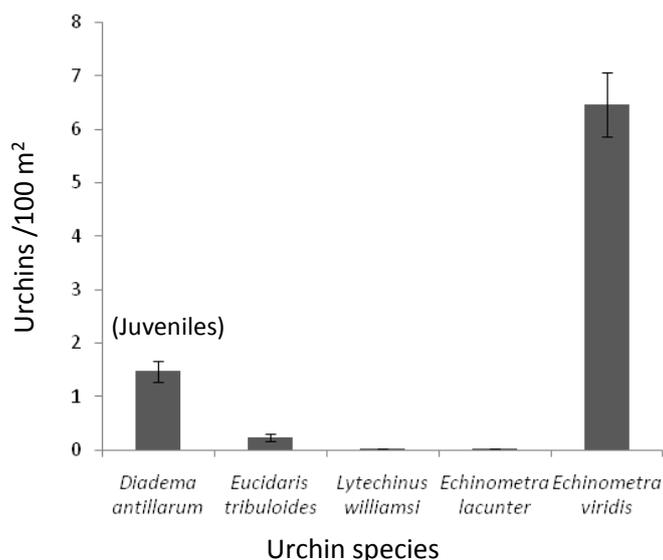


Figure 5.1 Mean urchin densities at Glovers Reef east wall.
Note that all *Diadema* are juveniles.

RELATIVE IMPORTANCE OF EFFECTS OF CORAL MICROHABITAT AND DAMSELFISH TERRITORIALITY ON ALGAL COMMUNITIES

General description of tile algal assemblages

By the end of the experimental period there was considerable variation between the algal communities both within and between individual tiles (Figures 5.2 and 5.3), with clear differences being evident when viewed under the dissecting microscope (Figure 5.4). Clearly defined parrotfish bite scars were commonly seen on tiles with low algal cover, but were not visible when cover was thicker (Figures 5.3; 5.4). Most tiles exhibited either fairly complete cover of one given functional type, or very little, with fewer tiles having intermediate values (Figure 5.5). This non-normal distribution necessitated non-parametric analyses in most circumstances (Figure 5.6). In general, the Total Turf and the Bare-Crustose categories have the highest mean percent cover values, roughly complimenting each other for each treatment, and together accounting for most of the algal cover across the data set (Figure 5.6). Whilst Total Turf cover values were similar within coral microhabitat treatments, with higher values on *Acropora* than *Montastraea*, there was less evidence of effects of damselfish within coral treatments. These trends were similar for the Bare-Crustose category. When the

Total Turf category was examined more closely, Low Turf was more abundant than Thick Turf and constituted the major portion of turf cover. Macroalgal cover was generally low, but the mean 30% cover on AC_SF treatment indicates that the experimental duration was long enough to reach this stage of succession. Mean percent cover values for the filaments and macroalgae cover categories showed no obvious trends when comparing either within damselfish across coral factors, or vice-versa (Figure 5.6). Mean Filaments cover is generally fairly low, ranging from zero on *Acropora* - *S. planifrons* (AC_SP) territory tiles to a maximum of around 30% on *Montastraea* - *S. fuscus* (M_SF) tiles.

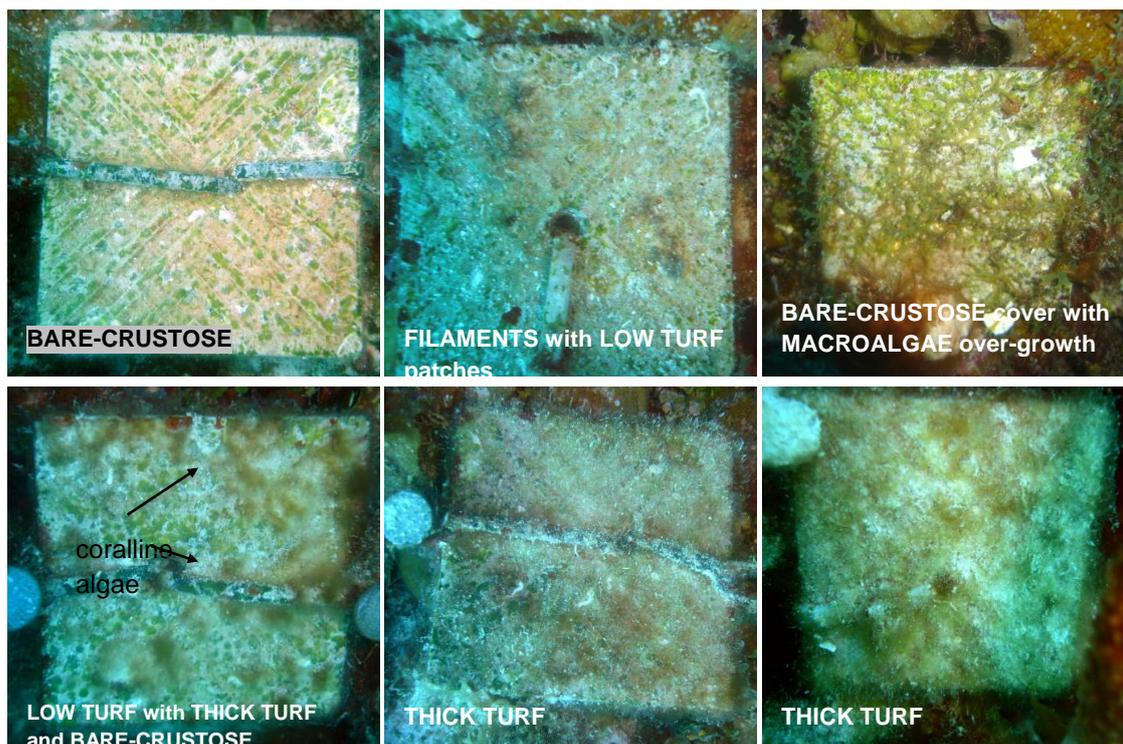


Figure 5.2 Diversity of algal cover on tiles.

On some tiles a single functional cover type occurred over the area of an entire tile, but in other cases they were intermingled. Note that cover types were determined using a dissecting microscope, so the presence of algal filaments, for example, is not visible here.

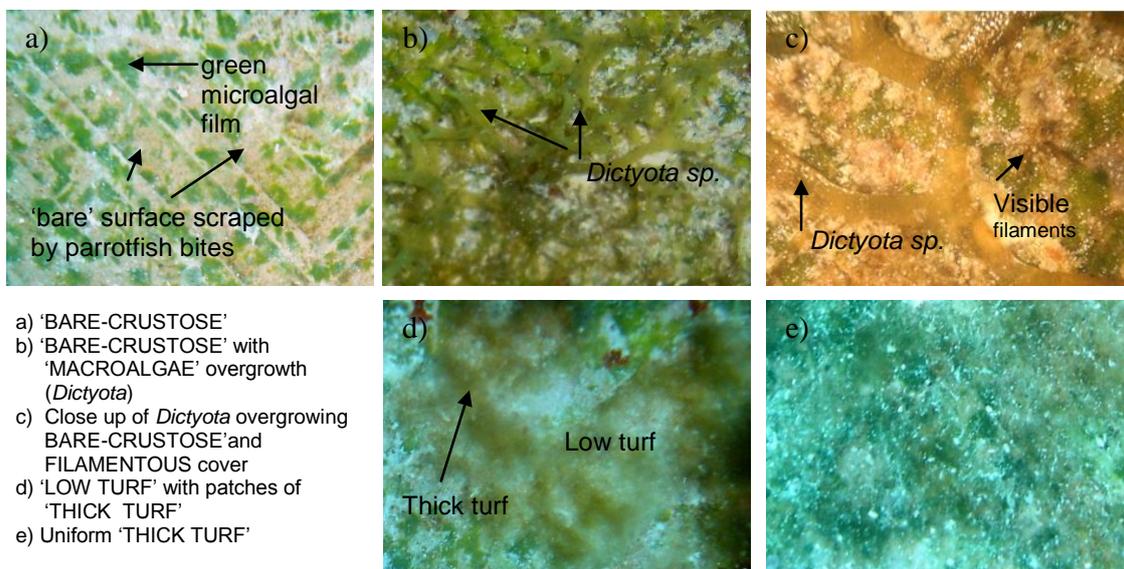


Figure 5.3 Close-up photographs of algal functional assemblage types.
(as defined in Table 5.2)

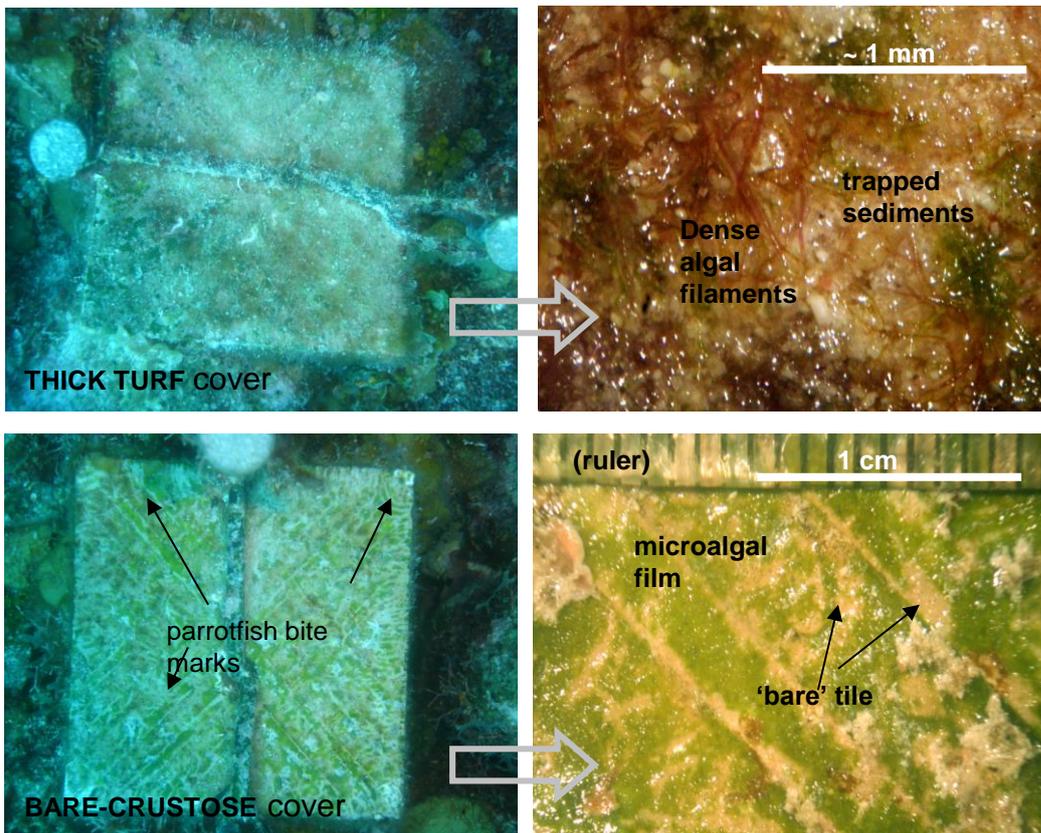


Figure 5.4 Examples of Thick Turf and Bare-Crustose functional cover types in situ, and viewed under the dissecting microscope for algal cover quantification.

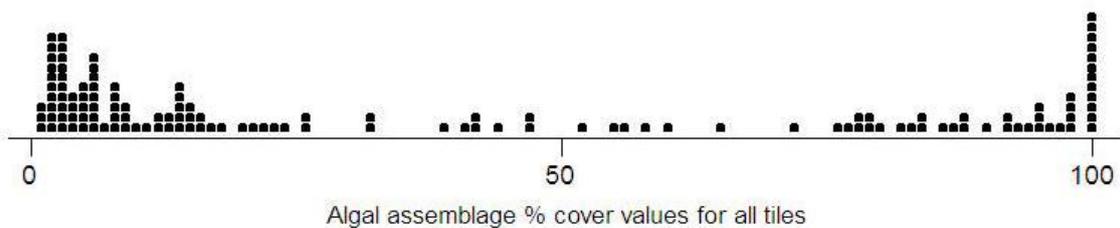


Figure 5.5 Plot of percent cover values for each algal assemblage for all tiles. Each dot represents a single value. Zero values have been omitted. Note the paucity of intermediate % cover values.

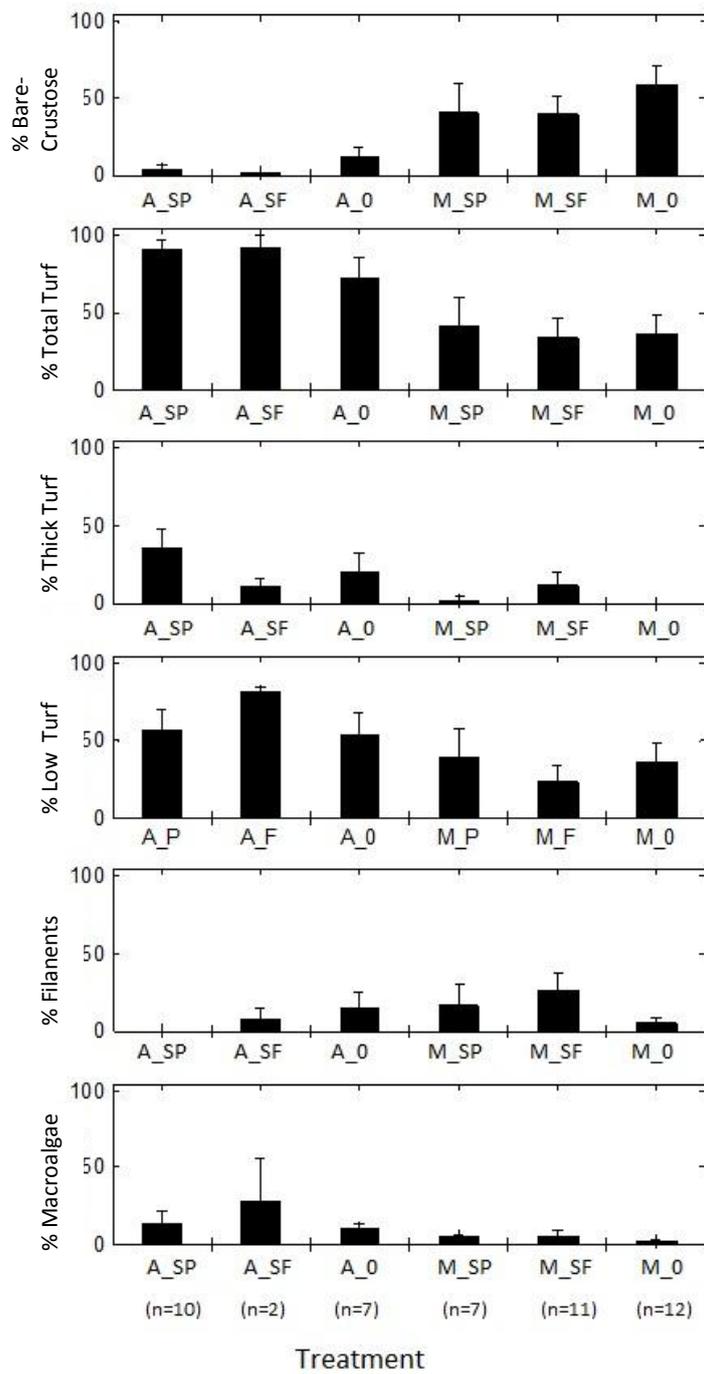


Figure 5.6 Mean % cover (+1SE) of different algal assemblages for each tile treatment.

Treatments: A_SP = *Acropora cervicornis* + *Stegastes planifrons*, A_SF = *A. cervicornis* + *Stegastes fuscus*, A_0 = *A. cervicornis* + no territorial fish, M_SP = *Montastraea annularis* + *Stegastes planifrons*, M_SF = *M. annularis* + *S. fuscus*, M_N = *M. annularis* + no territorial fish.

Relative effects of coral treatment versus damselfish treatments on algal assemblages

In order to test Hypothesis 1, that coral microhabitat was a more significant determinant of functional algal assemblage than damselfish, multidimensional scaling (MDS) was first used to examine tile data. Functional assemblage was more similar within coral treatments (*Acropora* or *Montastraea*) than between, but no such effect was evident for damselfish treatments, where ordinated data points from each treatment completely overlapped (Figure 5.7). Tests using a two-way crossed ANOSIM confirmed that coral treatment was significant in explaining algal functional community, and was a more important influence than damselfish treatment, the effect of which was undetectable ($R_{\text{CORAL}} = 0.18$, $P < 0.01$; $R_{\text{DAMSELFISH}} = -0.014$, $P = 0.56$).

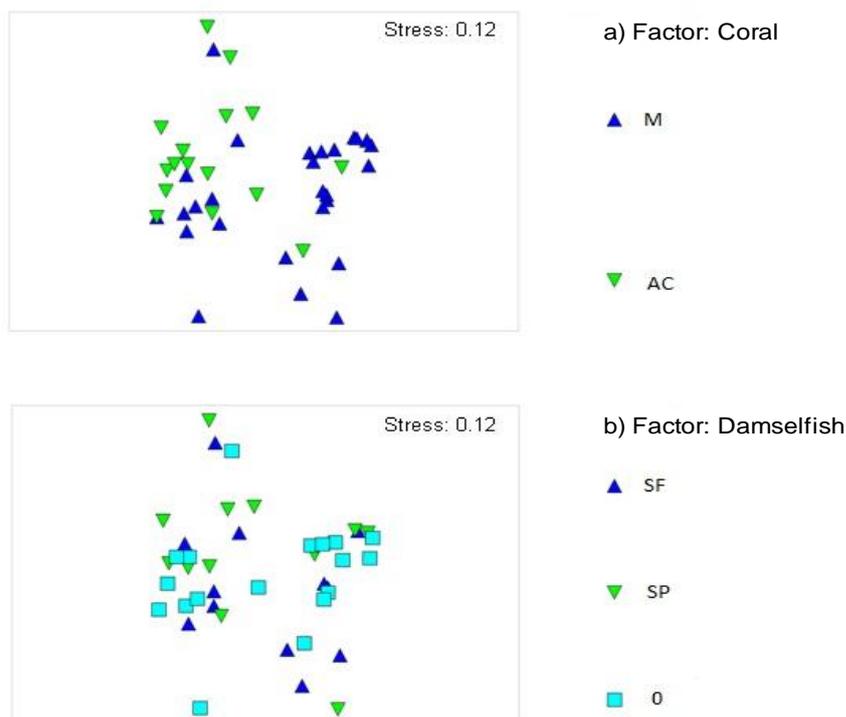


Figure 5.7 Multidimensional scaling ordination of algal functional community structure.

MDS based on Bray-Curtis similarity coefficients of square-root transformed percentage cover data. Each data point represents the algal community from one tile, the points are ordinated in two-dimensional space so that the tiles with the most in common are plotted closest together; a) the data group loosely by coral factor (*Acropora* or *Montastraea*), b) no grouping is seen for fish factors, where data points are intermingled. Coral factors: M = *Montastraea annularis*, A = *Acropora cervicornis*; Damselfish factors: F = *Stegastes fuscus*, P = *S. planifrons*, 0 = no damselfish.

These results support Hypothesis 1, that coral substrate is more important than damselfish in explaining algal functional community, although they do not rule out the possibility that more subtle damselfish effects within coral substrate may exist that are undetectable with the resolution of the current data set.

Analyses of tile functional assemblages using Simpsons Diversity Index revealed that *Acropora* treatment tiles had significantly higher index of diversity of functional groups than *Montastraea* treatment tiles (two-way crossed ANOVA, $P < 0.05$, $df=1$), since 1-Lambda is used as an inverse measure of homogeneity of algal communities this demonstrates that algal communities on *Montastraea* tiles were more homogenous than those on *Acropora*. Again no significant effect of damselfish treatment was discerned (Figure 5.8; Table 5.5). Whilst individual treatment means suggested that within each coral microhabitat *S. planifrons* might have lower diversity territories than those of *S. fuscus*, these data were not significantly different when examined using ANOVA to look for damselfish treatment effects within each coral microhabitat. In further support of Hypothesis 1, this result demonstrates that coral microhabitat had a significant and greater effect on algal community homogeneity than damselfish. These results demonstrate a lack of significant effect of *S. planifrons* gardening activities on diversity within territories, and if anything Figure 5.8 appears to suggest reduced diversity within territories.

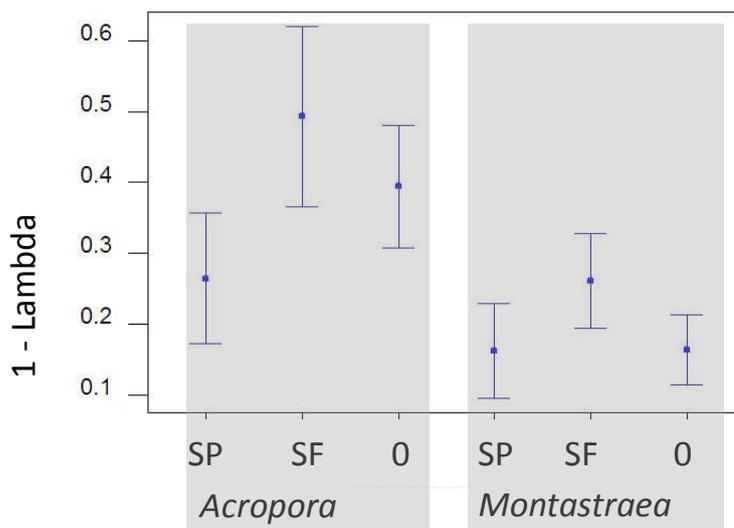


Figure 5.8 Simpson's Diversity Index values of tile algal functional assemblages according to coral-damselfish treatments.

Coral treatments: *Acropora cervicornis*, and *Montastraea annularis*; Damselfish treatments: SP = *Stegastes planifrons*; SF = *Stegastes fuscus*; 0 = no damselfish territory. Means \pm 1 STE are depicted.

Table 5.5 Analysis of Variance of Simpson’s Diversity Index values related to coral and damselfish treatments.

Coral treatments: A = *Acropora cervicornis*; M = *Montastraea annularis*; Damselfish treatments: SP = *Stegastes planifrons*; SF = *Stegastes fuscus*; 0 = no damselfish territory. Significance: * = $p < 0.05$; no asterisk = not significant.

Analysis of Variance for 1-Lambda, using Adjusted SS for Tests						
Factor	Type	Levels	Values			
CORAL	fixed	2	A M			
FISH	fixed	3	SP SF 0			
Source	DF	Seq SS	Adj SS	Adj MS	F	P
CORAL	1	0.21852	0.327	0.32784	6.86	0.012 *
FISH	2	0.15094	0.150	0.07547	1.58	0.217
Error	45	2.15123	2.151	0.04781		
Total	48	2.52068				

In order to distinguish which components of tile functional assemblage contributed the most to the difference between coral treatments a SIMPER analysis was used (Table 5.6; Figure 5.9). The most important contributors to dissimilarity were the two turf algae categories and the Bare-Crustose category, which together explained 79% of the dissimilarity between the two coral treatments. High turf cover was a feature of the *Acropora* tiles, whilst high Bare-Crustose cover was a feature of *Montastraea* tiles (Figure 5.9). Low Turf was the most important single category, contributing 31% of the dissimilarity, with mean abundance values of 57% on *Acropora* and 32% on *Montastraea*, whilst Thick Turf was third, with values of 27% and 5%, for *Acropora* and *Montastraea* respectively contributing 19% of the dissimilarity. Bare-Crustose cover was the second most important category in terms of variation between tile sets, with only 6% mean cover on *Acropora* compared to 47% on *Montastraea*. The remaining 21% dissimilarity is made up of Filaments and macroalgal groups. Of the macroalgae *Dictyota* showed the largest dissimilarity value, with higher cover on *Acropora* tiles than on *Montastraea* and remaining macroalgal groups were not common and contributed less than 2% in total (Figure 5.9).

Table 5.6 Simper analysis of algal functional assemblage groups showing average dissimilarity between *Montastraea annularis*, and *Acropora cervicornis* treatment tiles.

Assemblage	<i>Acropora</i>		<i>Montastraea</i>		Contribution %	Cumulative %
	Average abundance	Average abundance	Average Dissimilarity	Average Dissimilarity		
Low Turf	57.26	31.63	23.44	31.44	31.44	31.44
Bare-Crustose	6.26	47.47	21.79	29.22	29.22	60.66
Thick Turf	26.84	4.50	13.56	18.19	18.19	78.85
Filaments	5.95	15.20	8.84	11.85	11.85	90.71
<i>Dictyota spp</i>	10.42	2.37	4.90	6.57	6.57	97.28
Pink corticated	3.11	0.57	1.45	1.95	1.95	99.23
<i>Lobophora spp</i>	0.53	0.60	0.45	0.65	0.65	0.61
other macroalgae	0.05	0.23	0.13	0.33	0.33	0.17

Average dissimilarity between *Acropora* and *Montastraea* tiles = 74.56 %

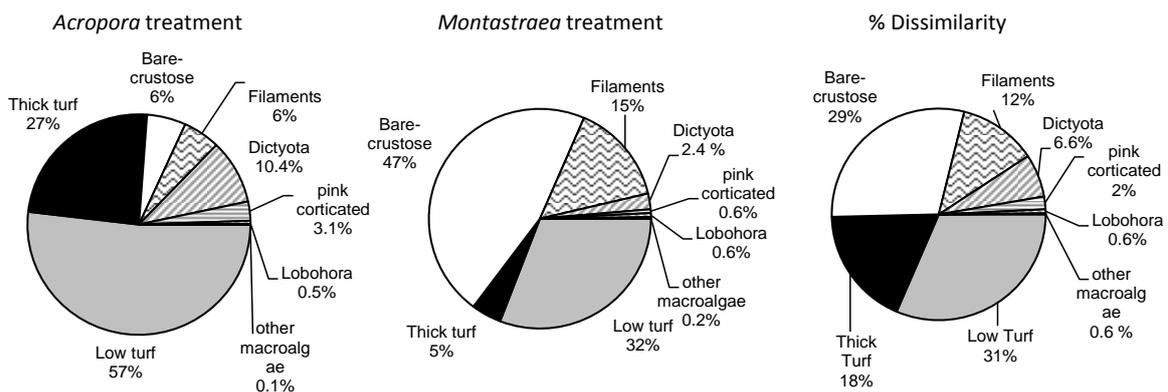


Figure 5.9 Main differences between coral treatments as revealed by *Simper* analysis.

Charts show mean percent cover of algal types within each coral treatment, and their relative contribution to the dissimilarity between the *Acropora* and *Montastraea* algal communities.

To investigate possible hidden synergistic effects of coral-damsel-fish complexes obscured by the multi-factorial approach, a second MDS was used and an ANOSIM was run to examine effects of combined treatment pairs. The MDS revealed a very loose grouping of coral-damsel-fish complexes by coral microhabitat (Figure 5.10). Only two pairwise coral-damsel-fish complex comparisons were found to have significant effects, both of which were cross-microhabitat comparisons: A_0 was distinct from M_0 ($R = 0.34$; $p < 0.01$; Table 5.7), and A_SP was distinct from M_SP ($R = 0.239$, $p < 0.05$; Table 5.7). Further investigation with SIMPER analysis revealed that the main

contributors to the difference between coral-damselfish complex pairs again lay in the Bare-Crustose, Low Turf, and Thick Turf categories (Figure 5.11), so the result was similar to that of the SIMPER analysis for the global microhabitat comparison (Figure 5.9; Table 5.6). The trends were similar for both pair-wise comparisons, with more Low Turf and Thick Turf on the *Acropora* treatment mirrored by more Bare-Crustose cover on the equivalent *Montastraea* treatment. Little overt effect of the presence of *S. planifrons* was therefore detected, apart from a slightly increased contribution to dissimilarity from the Bare-Crustose category which was 28% when non-territories were compared (Figure 5.11 a), but dropped to 22% when the comparison was between territories (Figure 5.11 b). This difference was due to there being slightly more Bare-Crustose cover on non-territory complexes (Figure 5.11 a) than on within-territory complexes (5.11 b). However this difference was not as large as the difference associated with microhabitat. These results again suggest a larger effect of coral microhabitat than damselfish territoriality since the only significant comparisons were across coral microhabitats.

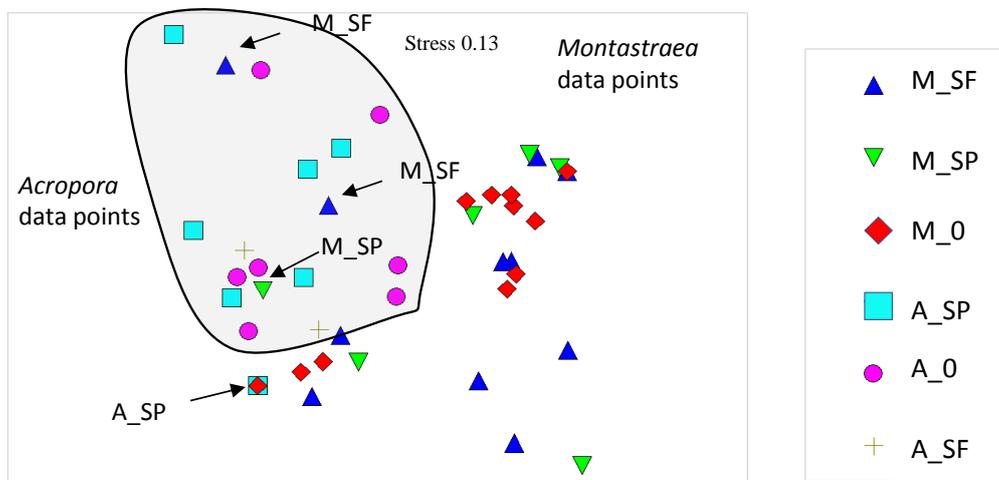


Figure 5.10 Multidimensional scaling ordination of coral-damselfish complexes based on algal functional communities.

Black line has been drawn to highlight grouping of *Acropora* complexes towards the top left of the frame; data points not in keeping with this grouping have been highlighted with arrows. M_SF = *Montastraea annularis*- *Stegastes fuscus*; MD_SP = *Montastraea annularis*- *Stegastes planifrons*; M_O = *Montastraea annularis*- no damselfish territory; A_SP = *Acropora cervicornis* - *Stegastes planifrons*; A_O = *Acropora cervicornis* - no damselfish territory; A_SF = *Acropora cervicornis* - *Stegastes fuscus*.

Table 5.7 Results of ANOSIM pairwise tests of effects of coral-damselfish treatment complexes on Total Turf cover.

Number of permutations: 999 (Random sample from a large number)

Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number >= Observed	Significant?
M_SF, M_SP 3	-0.052	65.7	31824	999	656	
M_SF, M_O	0.027	21.7	1352078	999	216	
M_SP, A_SP	0.239	1.9 *	19448	999	18	$p < 0.05$
M_SP, M_O	0.088	15.1	50388	999	150	
A_SP, A_O	-0.006	42.8	19448	999	427	
M_O, A_O	0.34	0.7 *	50388	999	6	$p < 0.01$

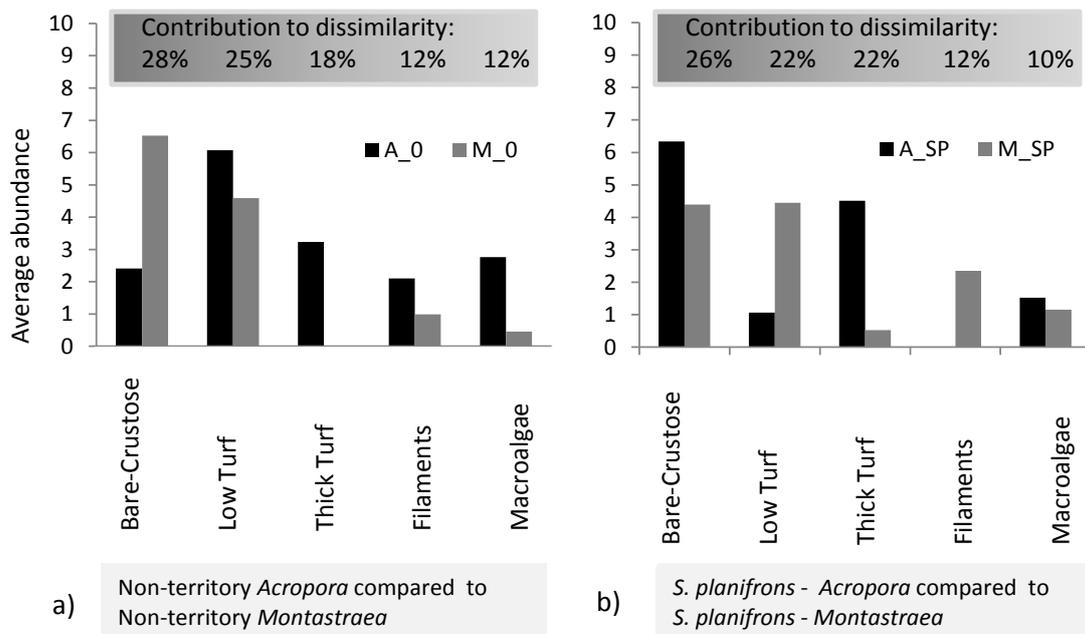


Figure 5.11 Main sources of dissimilarity in tile algal assemblages between significantly different coral-damselfish complexes, as revealed by Simper analysis.

Functional groups have been ranked according to their contribution to dissimilarity. Bars denote mean percent cover of each functional group within each treatment, relative contribution to the dissimilarity between treatments is noted above the corresponding bar. a) Comparison of non-territory *Acropora* and *Montastraea* treatments, and b) Comparison of *Stegastes planifrons* territories on *Acropora* and *Montastraea*. A= *Acropora cervicornis*, M = *Montastraea annularis*; 0 = no damselfish present; SP= *Stegastes planifrons* treatment.

Effects of damselfish-coral complexes on turf cover

Total turf cover is of particular interest in terms of damselfish territoriality as well as algal primary productivity. In order to test hypothesis 2: “Within coral microhabitat, damselfish territories do not have significantly higher turf cover than ambient carbonate substrates” comparisons of algal turf cover inside and outside of damselfish territories were made within coral microhabitat. None of the differences in turf cover between treatments were significant at the $p < 0.05$ level (Table 5.8), and so the null hypothesis was rejected and the hypothesis upheld. In most cases this result was unsurprising in view of the similarity of Total Turf cover seen on treatments within the same coral microhabitat (Figure 5.6), although within the *Acropora* microhabitat total mean turf cover on the non-territory substrate was slightly lower than the within-territory means, suggesting that a small damselfish effect might have been undetected.

Table 5.8 Results of ANOVA Comparisons of Total Turf cover inside and outside of damselfish territories within coral microhabitat.

Treatment complex 1	Treatment complex 2						
<i>Acropora</i> – <i>S. planifrons</i>	<i>Acropora</i> - no territory	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
		1	1317.2	1317.23	1.7972	0.2	
<i>Montastraea</i> - <i>S. planifrons</i>	<i>Montastraea</i> – no territory	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
		1	131	130.86	0.0593	0.8106	
<i>Montastraea</i> – <i>S. fuscus</i>	<i>Montastraea</i> – no territory	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
		1	13	13.04	0.0068	0.9353	

Hypothesis 3, that *Stegastes planifrons* territories located on the *A. cervicornis* microhabitat would have higher turf cover than those on *Montastraea annularis* was also upheld and the null hypothesis was rejected at the $p < 0.01$ level (Mann Whitney U test), however given the results of the SIMPER analysis in implicating turf cover as the main source of dissimilarity between *Acropora* and *Montastraea* habitats this result was to be expected. With regards to Figure 5.6 there is clearly higher mean Total Turf cover on the *S. planifrons* territories on *Acropora* than those on *Montastraea*, a trend examined later on in this chapter.

ALGAL COVER IN RELATION TO GRAZING INTENSITY TRENDS

Can turf cover be explained by the relative effects of coral and damselfish on the grazing of roving fish?

In order to examine hypotheses based on observed patterns of microhabitat-specific grazing by roving fish Total Turf values were used as a metric. As discussed previously high turf cover is indicative of low grazing intensity with increasingly denuded substrates occurring under increased grazing regimes (Steneck 1988, Steneck and Dethier 1994). A general linear model was used to examine the effects of coral and damselfish treatments solely on Total Turf abundance (sum of Low Turf and Thick Turf). Coral treatment was found to be significant ($p < 0.001$; glm; Table 5.9), with a mean total turf abundance of 84% for *Acropora* tiles versus 37% for *Montastraea* tiles (Figure 5.6), but no effect of damselfish treatment was detected ($p = 0.7$; glm; Table 5.9). Since no other cover type accounted for more than 3.5 % of mean abundance (Figure 5.6), it would follow that the *Acropora* tiles supported significantly more algal cover than the *Montastraea* tiles. Efforts to measure algal biomass of these turfs were

unsuccessful, due to the very low masses involved (often less than 1g), which were beyond the range of the field weighing balances. These results supported hypothesis 4, that significantly lower roving herbivore grazing seen on non-territory *Acropora* than hypothesis 4, the grazing differential between coral microhabitats (significantly lower roving herbivore grazing seen on non-territory *Acropora* than on non-territory *Montastraea* substrate demonstrated in Chapter 4) would be reflected by higher Total Turf cover on the former compared to the latter. In addition these results also supported Hypothesis 8, that based on the significantly lower rate of grazing by roving herbivores found on *Acropora* compared to *Montastraea* on all cross-substrate comparisons, and the lack of prominent significant effects of damselfish within microhabitat (found in Chapter 4 of this thesis), coral microhabitat is more important than damselfish presence in determining turf cover. There was also significantly higher Total Turf in *S. planifrons* territories located on *Acropora* in comparison to *Montastraea* territories (Table 5.10; Figure 5.6). This result supported Hypothesis 5, that based on the significantly lower rate of grazing seen on *S. planifrons* territories within the *Acropora* microhabitat compared to those within the *Montastraea* microhabitat there would be significantly less turf algae on *S. planifrons* territories on *Montastraea* compared to those on *Acropora*. Previous examinations of the effect of *S. planifrons* on turf levels also revealed no significant effect on Total Turf cover either within the *Montastraea* or *Acropora* microhabitats (Table 5.9). This result supports Hypothesis 6, that (due to a lack of significant difference in grazing intensity within *S. planifrons* territories compared to the ambient microhabitat, as found in Chapter 4) there would be no significant increase in turf cover associated with *S. planifrons* territories compared to non-territory areas on the same microhabitat. Lastly, Hypothesis 7, that territories of *S. fuscus* on *Montastraea* would have higher turf cover than those of *S. planifrons* on the same microhabitat was not upheld, since no significant difference was found in Total Turf cover (Table 5.11). This hypothesis was included for completeness but was weaker than the others in that the only previously detected difference in grazing rates between *S. fuscus* and *S. planifrons* on the *Montastraea* habitat was a weakly significant reduction in surgeonfish grazing on *S. fuscus* territories, and no difference in parrotfish grazing was seen between the treatments (Chapter 4 of this thesis).

Table 5.9 General linear model results for examination of the relative importance of coral and damselfish treatment effects on Total Turf cover.

Coral treatments: *Acropora cervicornis*; *Montastraea annularis*. Damselfish treatments: SP = *Stegastes planifrons*; SF = *Stegastes fuscus*; 0 = no damselfish territory. Significance: *** = $p < 0.001$; no asterisk = no significance.

Analysis of Variance for TOTAL TURF, using Adjusted SS for Tests						
Factor	Type	Levels	Values			
CORAL	fixed	2	<i>Acropora Montastraea</i>			
DAMSELFISH	fixed	3	SP SF 0			
Source	DF	Seq SS	Adj SS	Adj MS	F	P
CORAL	1	26770	21333	21333	14.34	0.0001***
FISH	2	1038	1038	519	0.35	0.707
Error	45	66950	66950	1488		
Total	48	94758				

Table 5.10 Results of ANOVA comparison of *S. planifrons* territory Total Turf cover between *Montastraea* and *Acropora* microhabitats.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Coral_Microhab	1	10188	10188.5	8.2186	0.01176 *
Residuals	15	18595	1239.7		

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1					

Table 5.11 Results of ANOVA comparison of *S. fuscus* and *S. planifrons* territory Total Turf cover within the *Montastraea* microhabitat.

Note: no asterisk denotes lack of significance.

Summary (FIT4)					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Damselfish	1	131	130.86	0.0593	0.8106
Residuals	17	37534	2207.87		

DISCUSSION

General observations

This study has revealed a number of results that are contrary to generally accepted view in the literature of the roles of damselfish territories on coral reefs.

The dominant functional assemblage groups seen on the tiles were Low Turf and Bare-Crustose cover, with intermediate values for Thick Turf, and Macroalgae and Filament cover being mostly low (Figure 5.6). Despite Macroalgal cover being low overall, values as high as 36% and 52% were recorded on individual tiles, indicating that tiles were deployed long enough for substantial growth to be able to occur (Figure 5.6). It is possible however, that had the tiles been deployed longer, higher cover of macroalgae and crustose coralline algae would have been observed, since these are known to be features of the later stages of community succession (Hixon and Brostoff 1996). At >100 days duration, this experiment is longer than some other studies of algal succession (McClanahan et al. 2002), and divergence in succession of algal communities in caged and un-caged *S. planifrons* territories has previously been seen to emerge at 60 days, with divergence becoming distinctive after 3 months, (Hinds and Ballantine, 1977).

Is coral microhabitat more important than damselfish in determining algal community structure?

Coral microhabitat (*Acropora* or *Montastraea*) had a significant effect on tile algal community structure, but any potential damselfish effect was undetectable. *Acropora* microhabitat tiles also had significantly higher turf algal cover specifically, and also higher diversity (measured using Simpson's diversity index) than *Montastraea* microhabitat tiles (Figure 5.6; Figure 5.8). Since all forms of algal cover were more abundant on *Acropora* tiles than on *Montastraea* tiles, assuming a roughly constant biomass per unit area for a given turf, it can be inferred that *Acropora* tiles also supported higher algal biomass than *Montastraea* tiles, regardless of damselfish occupancy. These results are surprising in view of the wealth of literature documenting the importance of the effects of herbivorous damselfish in modifying benthic communities (Lassuy 1980, Sammarco 1983, Klumpp et al. 1987, Ferreira et al. 1998,

Ceccarelli et al. 2001a), of which the threespot damselfish (*S. planifrons*) can be held as a prime example, and has even been termed a keystone species (Williams 1980a, 1981). The dusky damselfish (*S. fuscus*) is also documented as being able to maintain distinctive algal mats (Itzkowitz 1977a). However, a general lack of obviously discernable territory boundaries seen during nine months of fieldwork at Glovers Reef atoll, Belize, was one of the original motivating reasons for addressing this topic. During this time it was found to be impossible to visually distinguish either *Stegastes planifrons* or *Stegastes fuscus* territories from the surrounding algal community, to the extent that it was necessary to watch the movements of damselfish in order to plot their territory perimeters. In view of this initial observation, the lack of statistically discernable damselfish effect in the data is not a surprising outcome, instead the unexpected result is the apparent discrepancy with the foregoing scientific literature. In particular there is a wide acceptance that damselfish territorial behaviour leads to an increase in biomass of turf algae (Brawley and Adey 1977b, De Ruyter van Steveninck 1984, Hinds and Ballantine 1987, Ceccarelli et al. 2001a). It is therefore particularly surprising that even when Total Turf was examined independently of other functional assemblage groups coral treatment was still found to be more significant than damselfish treatment. It is, however, possible that with further replication and potentially with the application of a species-level approach some finer-scale effects of damselfish territory within coral treatments might have been discerned on *Acropora*, since mean Total Turf cover was a little higher for both *S. planifrons* and *S. fuscus* territories than the non-territory substrate (Figure 5.6). Even so, lack of significance with the current methodology (10 tiles per treatment), demonstrates that damselfish effects on benthic community were far from being the dominant control suggested by the literature, and instead were small in comparison to coral effects .

Was the coral microhabitat effect on algal communities mediated through fish grazing?

Algal standing stock is fundamentally a product of the offset of the rate of primary production against the rate of loss due to disturbance, where disturbance is any factor that has a deleterious effect on algal biomass (Hatcher and Larkum 1983, Carpenter 1986, Steneck 1988). As such, possible explanations of the increased turf cover on *Acropora* microhabitat tiles can therefore fall into two categories i) locally enhanced

primary productivity, or ii) reduction in the disturbance processes that lead to a loss of algal biomass. Such effects could be mediated either directly through effects of the coral microhabitat itself on the algal community, or indirectly through effects of coral microhabitat on some third party agent, which in turn acts upon the algal community. Credible direct effects of either the *Acropora* or *Montastraea* microhabitat which would lead to increased primary productivity or reduced disturbance are not obvious: surface area was controlled for by using tiles of uniform dimensions, and the only other effect of the *Acropora* skeleton would presumably be one of shading, which should reduce primary production, rather than enhance it. One effect which has not been proved but is at least theoretically possible is a localised fertilising effect of coral mucous. A recent study of the Great Barrier Reef coral, *Acropora millepora*, revealed ammonia and phosphate concentrations in mucous to be several orders of magnitude higher than those of the surrounding seawater (Wild et al 2005); since ammonia is particularly labile it is therefore possible that it would leach from the mucous and be quickly taken up by the local algal community. At the study site there was a higher level of live coral cover in the *Acropora* patches than on the *Montastraea* microhabitat so mucous production rates would be expected to be higher here. However, there is so far no direct evidence of localised fertilisation by coral mucous, so this possibility is speculative and would require testing through further field studies.

The explanation of effects of coral microhabitat mediated indirectly through effects on grazing by roving fish presents a compelling explanation for the effects of coral microhabitat on algal community. Herbivory is one of the most important sources of disturbance to algal communities in marine environments, so much so, that algal assemblages can be related to grazing intensity (Steneck and Dethier 1994). According to Steneck's General Model of Herbivory, turf cover is found under relatively high rates of grazing, but at still higher rates the assemblage shifts to one of a denuded substrate of crustose coralline algae; at low levels of grazing macroalgae are able to proliferate and high algal biomass is present (Steneck and Dethier 1994). In the present study hypotheses that predicted high turf cover on less grazed substrates were significantly upheld in almost all cases, strongly suggesting coral microhabitat effects on grazing fish to be the underlying mechanistic cause of differences in algal cover. Significantly low grazing rates observed within the *Acropora* habitat generally in Chapter 4 of this study were mirrored by significantly higher turf cover within this habitat documented in the

present chapter. Turf cover was found to be the main source of dissimilarity between *Acropora* and *Montastraea* treatment tiles, accounting for 49% of the difference in assemblages (Figure 5.9). Hypotheses 5, that *S. planifrons* territories based on *Montastraea* would have higher turf cover than those on *Acropora*, and Hypothesis 6, that there would be no significant increase in turf algal cover associated with *S. planifrons* territories on *Montastraea* compared to ambient non-territory areas, were both upheld, indicating that significant trends in roving fish grazing could be used to explain trends in algal cover. The only grazing-based hypothesis which was not upheld was Hypothesis 7, that *S. fuscus* territories on *Montastraea* would have higher turf cover than *S. planifrons* territories on the same substrate. This hypothesis was proposed due to signs that *S. fuscus* was more effective at excluding roving grazers on this substrate, however in this case fish grazing trends were less significant than those underlying the other hypotheses, with only the weakly significant reduction in surgeonfish grazing on *S. fuscus* territories, and no difference in parrotfish grazing (Chapter 4 of this thesis). This result suggests that larger scale differences in roving herbivore grazing are needed to produce detectable effects on algal community, thereby also adding credence to the significant outcomes of the other hypothesis tests. It may also suggest that the effects of parrotfish could be more important than surgeonfish, but this hypothesis requires further testing. In the present study the effects of urchin grazing was discounted since urchin densities were found to be very low, with less than 0.07 adult urchins per m⁻² overall (Figure 5.12), and no adult *Diadema* recorded in over 5000 m² of benthic transects. In the absence of urchins, roving herbivorous fish are seen as the most important grazers of Caribbean reefs, with their foraging activity being a process of key importance in structuring algal communities (Mumby 2006, Mumby et al. 2007a). It is therefore concluded that, at present, the most parsimonious explanation for trends in algal assemblages related to coral microhabitat is that they are due to the effects of coral microhabitat on fish grazing behaviour. More explicitly I now suggest that significantly higher algal cover on *Acropora* microhabitat tiles compared to those on *Montastraea* was most likely due to significantly lower rates of grazing associated with *Acropora*. However further manipulative work is needed to demonstrate causality. If these conclusions are correct it also follows that effects of roving herbivore grazing (mediated through effects of coral microhabitat) are more important than presence of damselfish in determining algal communities on modern day Caribbean reefs. Since these fish have been shown to be grazing inside damselfish territories in Chapter 4, this is not altogether surprising, as the ‘denuding’ mode of grazing by roving herbivores is known to be more

destructive to algal communities than that of the damselfish, which is termed “non-denuding” due to their propensity for cropping rather than removing algal strands (Steneck 1988).

The desirability of the Acropora microhabitat

The *Acropora* microhabitat is the primary preferred substrate of *S. planifrons* (Itzkowitz 1977a, 1977b), which is the most aggressively superior of the Caribbean damselfish, capable of competitively excluding other congeners from this habitat (Thresher 1976a, Williams 1978, Ebersole 1985). The general desirability of the *Acropora* substrate has previously been demonstrated by experiments that have shown rapid uptake of vacated territories (when residents *S. planifrons* were speared or removed), both by conspecifics housed on secondary substrates (Williams 1978), and other members of the Caribbean damselfish community (Robertson 1996), which rapidly seek to invade the area. In fact the microhabitat has been shown to be such a desirable residence that hopeful fish will live on less favoured substrates in order to be near to fully subscribed *Acropora* thickets, immediately moving in when a territory becomes available (Itzkowitz 1977b, Meadows 2001). Thus, although the *Acropora* substrate is clearly desirable to all species concerned, promoting a clear need for *S. planifrons*' superior aggression and defensive powers to maintain niche occupation, there has not previously been a clear explanation for the attractiveness of this microhabitat. In the previous chapter it is suggested that the significant reduction of roving herbivore grazing intrinsic to the *Acropora* substrate would be a good reason to prefer this microhabitat. Here this hypothesis is strengthened by the demonstration that *S. planifrons* territories on *Acropora cervicornis* have significantly higher turf algal cover, with a mean of nearly 90% \pm 5% Total Turf, compared to *Montastraea* territories, where average cover is only 40% \pm 10% (Figure 5.6).

Lack of discernable damselfish effects: S. planifrons territoriality on post-phase shift reefs.

In the present study damselfish territories were not easily discernable from ambient algal communities, although this observation has not been the case in the past. In a comprehensive review of the effects of territorial damselfish on benthic community

structure, Ceccarelli et al (2001) identified a number of recurring characteristics pertaining to territory algal communities compared to the local undefended substratum (summarised in Table 5.11). Although overall high turf algae cover is a recurring feature of damselfish territories, (Table 5.11, and see (Brawley and Adey 1977b, Ruyter van Steveninck 1984, Hinds and Ballantine 1987), it should also be noted that there are some exceptions where studies found biomass levels to be either the same or lower on the undefended reef (Tolimieri 1995, Lirman 2001). In the case of *S. planifrons* in particular there are a number of records of territories as distinctive areas of high productivity, evidenced by accounts of their confines being clearly visible by the abrupt halt in algal growth (Brawley and Adey 1977b, Kaufman 1977, Williams 1979, 1980a). With reference to Figure 5.6, it could be speculated that with more replication and longer experimental period, finer-scale differences in turf algal cover would have been revealed, and that these details might have enabled further distinctions in turf cover between *S. planifrons* territories and non-territory areas of *Acropora*; however there is no indication of a similar effect on the *Montastraea* substrates. In any case, the turf cover on non-territory *Acropora* and *Montastraea* treatments is still within a similar range to that of their damselfish territory counterparts, meaning that territories are nowhere near as distinct as described in these former accounts (Itzkowitz 1977a, 1977b, Williams 1980a, 1981). What is described here, therefore, is a very different situation to those classic examples in the literature where turf algae biomass or percent cover inside *S. planifrons* territories are many times larger than those on the undefended reef (Brawley and Adey 1977b, Williams 1981, De Ruyter van Steveninck 1984, Hinds and Ballantine 1987), with clearly visible delineation (Brawley and Adey 1977b, Kaufman 1977). Possible reasons for this anomaly can be attributed to one, or a combination of three factors: i) damselfish behaviour has changed, ii) the ecological context within which the damselfish lives has changed, or iii) the conclusion, based on previous studies, that damselfish territoriality leads to high turf biomass within the mat compared to the undefended reef, is incorrect or needs further qualification. Regarding explanation i), although not impossible, there is no evidence to suggest that changes to the damselfish's behaviour have occurred, and general field observations show that they behaved as expected in patrolling territory perimeters, feeding from the substrate, and posturing towards and attacking potential intruders (including the author) during the experiment. Explanation ii), that the ecological context in which the damselfish lives has changed, is however, of greater interest. Since algal community is being assessed

Table 5.12 Recurring characteristics of damselfish territory algal communities.

General information as assimilated by Cecarrelli *et al* (2001a); terms in italics are the classification according to the algal assemblage terminology defined in Steneck's 1988 review of herbivory on coral reefs (Steneck 1988).

	Inside territory	Undefended reef
Algal community	Erect, filamentous (= ' <i>turf assemblage</i> ' Steneck 1988)	Crustose / filamentous, corallines (= ' <i>crustose assemblage</i> ' Steneck 1988)
Algal biomass	High	Low
Primary production	High	Low
Species richness	High	Low

in relative terms, a general increase in algal biomass (or percent cover) on the wider, non-territory reef could bring the levels of within-territory and non-territory algae closer together. In view of the widely recognised 'phase shift' of Caribbean reefs towards an algal dominated state (Hughes 1994), and in particular the localised shift of the same nature on Belizean reefs (McClanahan and Muthiga 1998, Aronson and Precht 2001, Aronson *et al.* 2002a, Aronson *et al.* 2009) this is a plausible explanation, and may well be a contributing factor. One of the major causes of macroalgal proliferation is a loss of herbivores from the system (Mumby 2006). Although differences in the activity of roving herbivorous fish might explain a shift in the relative macroalgal cover on the *Montastraea* substrate, Chapter 4 of this thesis demonstrates that the fish do not graze at high levels in the *Acropora* microhabitat, so this seems unlikely to account for differences here (unless this is a modern trend). However, the loss of the voracious grazing urchin *Diadema antillarum*, which has historically played a key role in maintaining algal biomass at low levels on Caribbean reefs (Carpenter 1981), sometimes termed 'urchin barons' provides a likely explanation. *Diadema antillarum* has been shown to graze within *Acropora* thickets, but is generally excluded from *Stegastes planifrons* territories by the resident fish, which actively nips its spines and even physically removes urchins (Williams 1979, 1981, Sammarco and Williams 1982). In fact the effects of *S. planifrons* in modifying competitive interactions between *Diadema* and other urchins, and the importance of this interaction for herbivory at the reef-wide scale were the original reasons for *S. planifrons* being termed a keystone species (Williams 1979, 1980a, 1981). The 1983 – 1984 Caribbean wide loss of *Diadema* (Sammarco 1980, Lessios *et al.* 1984, Liddell and Ohlhorst 1986, Bauer and

Agerter 1987, Williams and Williams 1987, Greenstein 1989) would therefore be expected to have had a differential effect on territory and non-territory areas, providing a likely explanation for the previous clear delineation of *S. planifrons* territories within the *Acropora* microhabitat, which is now no longer seen. *Diadema* grazing is associated with very low levels of algal biomass and denuded substrates occupied by crustose coralline algae (Carpenter 1986, Steneck 1988), so grazing within the *Acropora* habitat external to territory exclusion zones would be expected to result in a clear distinction, and consequentially relatively high algal biomass inside compared to outside the territory confines. This pattern has been previously described in Jamaica where *Diadema* kept substrates clear of algae around damselfish territories, but a turfed 'lawn' was maintained inside (Williams 1979, 1980a, 1981). In the present study *Diadema* densities were extremely low, without a single adult being found in in 300 m⁻² of careful night time reef surveys, or 5000 m² or reef covered in 50 daytime transects (Table 5.4 Figure 5.1). Although very low densities of juveniles (tests less than 1cm in diameter) indicated that some adults must be present, but possibly not of the fore-reef. Densities of other urchin species were also low, with less than 0.07 adult urchins per m⁻² overall (Table 5.4.) I therefore suggest that the lack of easily discernable territory confines within the present day *Acropora* microhabitat is due to the loss of urchin grazing outside of and around territory edges, allowing algae to proliferate outside of territories to levels similar to those inside territories. Overall this result suggests that the reason for the present-day lack of easily distinguishable territories is likely due to a change in the relative role of the damselfish territory due a shift in the ecological context within which the damselfish live on contemporary Caribbean reefs.

It is likely that former low level urchin grazing within the *Acropora* microhabitat could also account for the lack of recognition in the literature of the relatively high levels of turf cover apparently intrinsic to this habitat that have been revealed in the present study. *Stegastes planifrons* tends to inhabit much, if not all, available *Acropora cervicornis* substrate at a given location (Brawley and Adey 1977b, Itzkowitz 1977a, 1977b, Robertson et al. 1981). In such a highly coupled system it is possible that some studies comparing within-territory algal communities to those of the nearby undefended reef have in fact been confounded by a difference in coral substrate, with high levels of turf actually being associated with the *Acropora* microhabitat, rather than the damselfish. This correlation brings us to explanation iii), that the previous conclusion

(that *S. planifrons* promotes turf algal cover) was wrong, or needs further qualification. Although seeming unlikely at first, in view of the large number of studies reaching the same conclusion, a more careful examination of the literature detailing the effects of *Stegastes planifrons* and *Stegastes fuscus* on territory algal communities reveals that in general, coral substrate has not been precisely recorded beyond a general description of the habitat where the experiment took place (Brawley and Adey 1977b, Kaufman 1977, De Ruyter van Steveninck 1984), although see (Ferreira et al. 1998). Given that levels of algal cover have been significantly associated with coral-microhabitat in the present study, this lack of observation may have been an oversight. In the absence of convincingly evidenced within-territory to non-territory comparisons on the same coral microhabitat, caging experiments provide more compelling information, but have not explicitly answered the question. For example, experimental removal of *S. planifrons* from its territories in Jamaica was accompanied by a rapid influx of grazing fish and a concomitant rapid reduction in algal biomass observed, although no statistical analyses were performed on the data (Brawley and Adey 1977b). Although this result implies that within-territory biomass was higher prior to the territory invasion than it was after (due to consumption by the invaders), strictly this does not directly indicate that there was significantly more algal cover inside the territory relative to the undefended reef to begin with, since differences in algal quality and more palatable species may have been the attractant (Francini-Filho et al. 2010). Similarly, accounts of large reductions in algal biomass occurring when pieces of turfed *Acropora* habitat were moved from within damselfish territories to non-defended areas (Lobel 1980) could also be confounded by movement of the test subject away from the *Acropora* thicket itself. Taking these studies together it remains possible that relatively high turf cover is an intrinsic propensity of the *Acropora* environment which has hitherto gone unnoticed, and previously been ascribed to the effect of its common damselfish occupant, *Stegastes planifrons*. Since the widespread loss of *Acropora cervicornis* from Caribbean reefs, *S. planifrons* can now be commonly seen on *Montastraea* substrates (Precht et al. 2010; this study), where they currently do not appear to have obviously and distinctively turf-dominated territories (Figure 5.6).

Implications of Acropora loss from Caribbean systems for algal dynamics.

This study reveals a trend of increased algal cover on *Acropora* substrates at Glovers Reef, and suggests that this may be due previously observed trends of reduced herbivory by roving fish within this microhabitat. If this phenomenon extends to the *Acropora* habitat in general the effect of large scale loss of *Acropora* in the Caribbean (Aronson and Precht 2001) maybe a more complex issue than first thought. The implications of the large-scale loss of an *Acropora* ‘herbivore exclusion zone’ have been discussed at length in the previous chapter and will not be revisited here. The results of this study suggest that another consequence of *Acropora* loss would likely be a reduction of turf covered benthic substrates. Since it has been shown that roving herbivorous fish grazing within this microhabitat is already low, the trophic consequences of such a loss may not be as large as might otherwise be supposed. Whilst the loss of turf-covered substrates might be supposed to be beneficial in terms of opening up surfaces for coral recruitment (Birrell et al. 2005, Kuffner et al. 2006, Arnold et al. 2010), but also see (Gleason 1996), this would hardly be a significant benefit compared to the loss of the live *Acropora* habitat itself, and potential grazer-concentration effects external to this habitat. Since the main mode of *Acropora* reproduction is by fragmentation Tunnicliffe (1981), the basal turf communities would also not be expected to preclude proliferation of the *Acropora* microhabitat itself.

Is Stegastes planifrons still a keystone species?

In this study it has been found that coral microhabitat is a more important determinant of benthic algal assemblage than damselfish presence. In particular no significant effect of *S. planifrons* in modifying algal assemblages in comparison to those of the ambient microhabitat was seen. Although it is possible that fine-scale differences were not detected it is clear that *S. planifrons* territories were not clearly delineated in a manner matching previous historical accounts (Brawley and Adey 1977b, Kaufman 1977, Williams 1979, 1980a). In the previous chapter of this thesis it was also found that grazing by roving herbivorous fish was also significantly linked to coral microhabitat which was more significant than damselfish presence in determining fish feeding patterns. Using mechanistic hypotheses within this chapter it is demonstrated that trends in roving fish grazing can be used to explain high level trends in algal cover, although effects of damselfish territoriality do not. This result suggests that in the system studied,

roving fish grazing are a more important determinant of benthic community than damselfish presence.

The lack of adult *Diadema antillarum* and very low urchin densities in general precludes these, or *Stegastes planifrons* effects on these, from being important determinants of benthic community structure. *S. planifrons* was originally attributed keystone status because of its effect in mediating the outcome of competitive interactions between two important grazing urchin species (Williams 1979, 1980a), arguably the most important of which has shown to be functionally absent in the study system. Based on the lack of other discernable or strong signals of effects on algal community by the direct presence of *S. planifrons*, and the absence of the possibility of indirect effects via the modification of *Diadema* behaviour, I do not believe that *S. planifrons* is acting as a keystone species in terms of either direct or indirect impacts on benthic species in this system. This result suggests that *S. planifrons*' 'keystone' status is dependent on the presence of *Diadema antillarum* within the system. Since the loss of *Diadema* is not specific to Glovers Reef, but is much documented as a Caribbean-wide phenomenon, where this species has previously been termed 'functionally extinct' (Mumby et al. 2006), it can be suggested that this trend may extend to the role of *S. planifrons* in general, across its Caribbean range. Isolated pockets such as Dairy Bull reef in Jamaica, where localized *Diadema* populations are now stronger (Crabbe 2008) may offer exceptions to such a trend, and also provide useful systems for comparative and manipulative testing of this hypothesis. These findings have implications for the concept of keystone species and the plasticity of such status in changing ecological scenarios, with "keystone" attributes not being intrinsic to the animal itself, but rather a product of features of its ecology and the environmental state that happens to surround it. This theme will be further examined in the General Discussion (Chapter 6).

CONCLUSIONS

The present study has revealed a number of surprising results, and led to the rejection of hypotheses that are entrenched in the scientific literature. The most interesting and important finding is that coral substrate (*Acropora cervicornis* versus *Montastraea annularis*) is a more important factor than the presence or absence of damselfish territories in explaining algal community structure, and the extent of turf algae cover (ANOSIM, $R = 0.18$, $p < 0.01$). It is also concluded that, at present, the most parsimonious explanation for trends in algal assemblages related to coral microhabitat is that they are due to the effects of coral microhabitat on fish grazing behaviour. More explicitly it is suggested that significantly higher algal cover on *Acropora* microhabitat tiles compared to those on *Montastraea* was most likely due to significantly lower rates of grazing associated with *Acropora*. However further manipulative work is needed to directly demonstrate causality, and such work could be coupled with remotely deployed cameras set up to record footage of fish grazing on different treatment tiles. These findings are surprising, not only because highly aggressive damselfish species such as *Stegastes planifrons* have previously been ascribed a large role in maintaining dense algal turfs within their territories, but also because it appears that high turf cover is actually an intrinsic feature of the *Acropora cervicornis* habitat which has hitherto gone unnoticed in the study of reef ecology (perhaps because of previous consumption of turfs external to damselfish territories by *Diadema* prior to the function loss of this urchin from most Caribbean reefs). These findings may explain why *Stegastes planifrons*, the most aggressively competitive of the Caribbean damselfish (Ebersole 1985), favours establishing its territories on *Acropora* as its primary preferred substrate, since algal turf cover was significantly higher here ($p < 0.01$; Mann Whitney U test). Another surprising result was that within coral substrates no significant effect of damselfish presence on either total turf cover or algal community diversity was detected. Whilst it is possible that with further replication fine-scale differences may have been revealed on the *Acropora* microhabitat, the effects were not prominent, as would be expected from the previous studies. Possible speculative reasons for this finding are discussed, including the possibility that changes occurring in the ecological context within which the damselfish live – i.e. the large scale changes or "phase shifts" occurring on many Caribbean reefs (Hughes 1994, McCook 1999, Ostrander et al. 2000), and notably the loss of the grazing urchin *Diadema antillarum* may have caused

the relative role of damselfish within the system to have changed by default. I suggest that the implications of such changes, and particularly the loss of *Diadema* from the system, may be that *Stegastes planifrons* no longer plays a keystone role in contemporary Caribbean reef ecology.

General Discussion

IS *STEGASTES PLANIFRONS* STILL A KEYSTONE SPECIES ON CONTEMPORARY CARIBBEAN REEFS?

*Is *Stegastes planifrons* still a keystone species of contemporary Caribbean reefs?*

Keystone species are those that exert ‘influences on the associated assemblage, often including numerous indirect effects, out of proportion to the keystone’s abundance or biomass’ (Paine 1995). In Chapters 5 of this study no significant effect of *S. planifrons* in modifying algal assemblages in comparison to those of the ambient microhabitat was seen (whether by direct modification or ‘gardening’ activities, or by the exclusion of other grazing fish). In fact, in Chapter 5 it is demonstrated that trends in roving fish grazing can be used to explain high level trends in algal cover, though effects of damselfish territoriality do not. This result suggests that in the system studied, roving fish grazing is a more important determinant of benthic community than damselfish presence. Similarly, in Chapter 4, it was found that coral microhabitat is a more important determinant of fish grazing patterns than damselfish presence. The lack of easily discernable effects of *S. planifrons* on reef communities prompts the question of whether the moniker of ‘keystone species’ is justified for this fish.

In fact, *Stegastes planifrons* was originally termed a non-carnivorous keystone species in 1980 due to its impacts on the grazing of two Caribbean urchins, *Echinometra viridis*, and the more voracious *Diadema antillarum*, (Williams 1980a) – which is itself recognized as a keystone species (Carpenter 1981, 1988, 1990a, b). *Diadema* grazing is associated with very low levels of algal biomass and denuded substrates occupied by crustose coralline algae (Carpenter 1986, Steneck 1988), and left unchecked would be competitively superior to *Echinometra*, however Williams (1980) was able to show by manipulation that *S. planifrons*’ preferential exclusion of the more voracious *Diadema* (ostensibly to safe-guard the algal resources of the damselfish territory) allowed the slower and less efficient grazer, *Echinometra*, to compete more effectively (Williams 1979, 1981, Sammarco and Williams 1982). However, in the time since the classic keystone studies of *Stegastes planifrons* (Williams 1979, 1981, Sammarco and Williams 1982) areas of Caribbean reefs have seen changes unprecedented in the last 3000 years (Aronson and Precht 1997b, Aronson et al. 2004). There has been a fundamental ‘phase shift’ in the nature of Caribbean reefs, from previously complex three dimensional habitats provided by live coral architecture, to a present-day state of increasingly flattened carbonate substrates dominated by fleshy macroalgal overgrowth (Hughes

1994, Alvarez-Filip et al. 2009). This ‘phase shift’ has been fundamentally linked to the loss of the staghorn coral, *Acropora cervicornis* (Hughes 1994, Hughes et al. 2007), and the loss of the voracious grazing urchin, *Diadema antillarum* (Carpenter 1981, 1985, 1988, 1990b, a, Hughes 1994, Mumby et al. 2006), both of which were due to separate widespread disease epizootics in the late 1970s and 1980s. Today, with exception of a small-scale return at Dairy Bull reef in Jamaica (Crabbe 2008), there is little sign of a recovery in *Diadema* numbers at the Caribbean-wide level (Mumby 2006), or reef recovery in general (Aronson and Precht 2001, Schutte et al. 2010), and previously documented small-scale *Acropora cervicornis* recoveries in Jamaica have recently faltered (Idjadi et al. 2006, Quinn and Kojis 2008). In the present study urchin densities were found to be very low (Chapter 4), with no adult *Diadema* recorded in over 5000 m² of benthic transects, and less than 0.07 adult urchins per m⁻² overall (including *Echinometra viridis*). The lack of adult *Diadema antillarum* and very low urchin densities observed in general precludes these, or *Stegastes planifrons*’ effects on these, from being important determinants of benthic community structure. Ergo, since *Diadema* is not present in the current system, the behaviour on which *S. planifrons*’ original keystone status was founded is not possible on the fore-reef of Glovers Atoll (Belize). Further, with the “functional extinction” (Mumby et al. 2006) of *Diadema* from Caribbean reefs, it is implicit that this is also this situation extends across the Caribbean region - which equates to the range of the damselfish species itself. It is therefore reasonable to state that *Stegastes planifrons* does not play the keystone role on contemporary Caribbean reefs originally described by Williams (Williams 1980a). To summarise: based on the lack of other discernable or strong signals of effects on algal community by the direct presence of *S. planifrons*, and the absence of the possibility of indirect effects via the modification of *Diadema* behaviour, I do not believe that *S. planifrons* is acting as a keystone species in terms of either direct or indirect impacts on benthic algal species in this system. These findings have implications for the concept of keystone species and the plasticity of such status in changing ecological scenarios, with “keystone” attributes not being intrinsic to the animal itself, but rather a product of features of both its own ecology and the ecological context or environmental state that happens to surround it. This issue of context dependency in keystone species is discussed to some extent by Power *et al* (1996), and there are a number of studies where context-dependent keystone status has been observed; however examples relate mainly keystone status being spatially or temporally limited, for example due to season, or varied range (Mills et al. 1993, Menge et al. 1994, Christianou & Ebenman 2005). However, in

the present study an inferred fundamental loss of keystone status is described over the entire range of the damselfish species, due to the functional loss of the species it acted upon, suggesting there may be a case for the keystone status of this species actually being ‘revoked’. The implications of this finding are discussed further in the next section of this chapter.

Although effects on *Diadema* cannot currently justify the keystone status of *Stegastes planifrons* this does not preclude other possible impacts of the fish “disproportionately large relative to its abundance” (Power et al. 1996). The Hawaiian damselfish *Stegastes fasciolatus* has been termed a ‘keystone species in reverse’ for the distinctive territory community and high algal diversity of its territories, due to intermediate disturbance mediated through direct actions of the damselfish on the benthic community, as well as the exclusion of other roving herbivorous fish (Hixon and Brostoff 1983a). Contrary to expectations based on the foregoing literature, no evidence was found in the present study to suggest that *S. planifrons* should be attributed a similar status, and coral microhabitat was found to be a more important determinant of benthic algal assemblage than damselfish presence. Specifically, no significant effects of *S. planifrons* in modifying algal assemblages in comparison to those of the ambient microhabitat were seen (although fine-scale differences may not have been detected it is clear that *S. planifrons* territories were not the principle determinants of benthic community). It was originally also sought to extend the ‘space-availability’ hypothesis (Williams et al. 2001) to the territories of *S. planifrons*, the expectation being that the exclusion of roving herbivores from within its territories would result in the concentration of their grazing on non-territory areas of reef. Instead it was found that grazing by roving herbivorous fish was significantly linked to coral microhabitat, and that coral microhabitat was more significant than damselfish presence in determining fish feeding patterns. Again a lack of effect of damselfish presence on rates of grazing by roving fish within coral microhabitat was found. The results demonstrate that trends in roving fish grazing can be used to explain high level trends in algal cover, although effects of damselfish territoriality do not. Overall these results present a very different picture to that implicit in the literature, with no evidence of keystone-level effects on any remaining roving grazers, or direct effects on benthic algal communities.

In contrast to the lack of effects on algal communities, the results of this thesis suggest that the effects of *S. planifrons* on coral communities may be important, with possible repercussions at the wider-reef level. In Chapter 2 of this thesis a significant association was found between *S. planifrons* presence and coral biting and the onset of coral disease in its host coral, *Acropora cervicornis*. In Chapter 3 it was found that present day *S. planifrons* populations at Glovers Reef were approximately equally split between the *Acropora cervicornis* and *Montastraea annularis* habitats, but the extent of live coral cover within territories was not reflective of the means for these species on the wider reef, suggesting that damselfish may either select or modify the live coral content of their territories. It was also demonstrated (through habitat choice experiments) that in the absence of competition and other confounding factors *S. planifrons* significantly preferentially based its territories on 100% live *Acropora* with no algal cover, rather than habitats containing both live coral cover and extant algal communities. High rates of coral biting were then observed on the chosen habitat coral, but not on other corals (representative of more degraded habitats) within the experimental pool. Coral biting has previously been documented as a method of killing habitat coral to extend the algal mat from which *S. planifrons* feeds (Kaufman 1977, Robertson et al. 1981), it is therefore surmised that the likely outcome of this behaviour would have been the death of coral tissues, had the experiment run for longer. On the basis of arguments previously put forward by Kaufman (1977) this occupation of *A. cervicornis* by *S. planifrons* may be deleterious to the ability of *A. cervicornis* to withstand storm damage, causing stands to be more commonly razed by adverse weather. The preferential occupation here of 100% live coral cover suggests that effects of increased susceptibility to storm damage would therefore be mediated upon the most healthy corals, rather than those that were already degraded. In addition the association seen in the current study between *S. planifrons* and the occurrence of white disease in *Acropora* suggests an additional deleterious effect. Both of these effects suggest that inhabitation by *S. planifrons* would lead to decreased temporal persistence of individual *A. cervicornis* stands, as well as contribute to increased mortality rates in the coral overall. As such the reef-wide implications of *S. planifrons* effects on corals may be large. The Hawaiian damselfish, *S. nigricans*, modifies the scleratinian assemblage of Hawaiian coral reefs and has previously been termed an ‘ecosystem engineer’ (White and O'Donnell 2010). It is possible that *S. planifrons* may be deserving of the same status, however more work needs to be done to investigate whether hypothesised effects on corals translate to effects of ecological significance on Caribbean reefs.

In particular, further empirical testing is needed to demonstrate whether *S. planifrons* is able to act as a vector of white diseases of *Acropora cervicornis*, or is merely a facilitator of disease onset. Methods for such experiments could follow a functionally similar design to those used to demonstrate vector activity in corallivorous snails (Williams and Miller 2005). If *S. planifrons* is demonstrated as a vector then computer simulations could be used to investigate whether this mode of disease transfer may have contributed to the rapid spread of white band disease in the 1980s. Further investigation of the extent to which *S. planifrons* occupation of healthy corals leads a decrease in live coral tissues, and susceptibility to storms should also be investigated.

THE KEYSTONE SPECIES CONCEPT, AND IMPLICATIONS OF THE PRESENT STUDY

As discussed above, the results of the present study indicate that the *S. planifrons* no longer plays the ecological role for which it was originally termed a keystone species. The implication of this finding is that the ‘keystone’ attributes of a given species are not fundamental to the species itself, but are a product of features of its own ecology and the environmental state that happens to surround it. Since there is little sign of recovery in *Diadema* numbers in the Caribbean, and reefs are thought to have undergone a ‘phase shift’ to an alternative apparently largely stable state (Hughes 1994, Hughes et al. 2007), it could be suggested that there is little likelihood of a return of *S. planifrons* to its previous (urchin mediated) keystone status in the near future, and potentially even in the longer term. This form of the context-dependency of keystone status has implications for the general concept of the keystone species, adding further to the confusion of what a keystone species actually represents. Context dependency has been demonstrated before in terms of species that are keystones over part but not all of their range, however no case was found in the literature of a keystone status being revoked altogether, as may be justified in the case of *S. planifrons*. There is, however, increasing awareness of the spatial and temporal context dependency of keystone functioning (Christianou and Ebenman 2005, Cottee-Jones and Whittaker 2012). In fact later further repetition of the original experiments of Paine (Paine 1966) on other parts of the USA Pacific coast have demonstrated that whilst the role of *P. ochraceus* is significant at wave-exposed sites, it is not large enough to warrant ‘keystone’ status for

this species at less exposed sites, or at the wider shore level (Menge et al. 1994). Therefore, even the keystone functioning of the ‘original’ keystone species, *Pisaster ochraceus*, can be seen to in fact be contingent upon the ecological context within which it is found.

Despite the extreme proliferation of the keystone term within the scientific literature (Cottee-Jones and Whittaker 2012), the rigour of the foundation of the original ‘keystone’ proposition of Paine (Paine 1966, 1969) has been challenged in more recent years (Bond 1993, Cottee-Jones and Whittaker 2012). In fact, Paine’s original 1996 study was conducted on single small site of 8 m of shoreline in Mukkaw Bay, on the USA Pacific coast, the only manipulations being the removal of *Pisaster ochraceus* itself (Paine 1966). In the absence of measured effects of the removal of other component species of the ecosystem it is in reality impossible to make a judgement on the relative significance of the impact of removal of *P. ochraceus* over and above those of other ecosystem components. Although Paine does note that “indirect evidence strongly suggests that equivalent changes do not appear with the exclusion of other consumers” (Paine 1969), there is no citation of these studies, and no further quantitative details relating to this evidence. Paine’s second study (Paine 1966, 1969) hypothesised that the triton mollusc, *Charonia*, played a keystone role on the Great Barrier Reef by indirectly maintaining healthy and high diversity coral communities by preying on the coral predator, the crown of thorns starfish *Acanthaster planci*. However, *A. planci* outbreaks were only anecdotally linked to over-exploitation of the triton *Charonia*, and there was no empirical testing of the link between *Charonia* loss and the *A. planci* outbreaks (Paine 1969). It has since been discovered that the rate of consumption of *A. planci* by *Charonia* is unlikely to be large enough to moderate the population significantly, with other factors such as *A. planci* recruitment likely to be more important in controlling population outbreaks (Harriott et al. 2003). Taken together it is evident that from the genesis of the keystone species concept there has been a lack of rigour and consistency, with *Pisaster*, the first ‘keystone species’ at best only serving a keystone function over part of its range, and *Charonia* arguably unlikely to have a keystone function at all. Whilst it is hard to explain such extreme proliferation of a term derived through such small-scale study as those original studies of Paine (Paine 1966, 1969), it has recently been observed that the application of the ‘keystone’ term to a study species or processes tends to imply an increased level importance to the subject of study, and therefore to the

study itself (Cottee-Jones and Whittaker 2012), it could therefore be seen to be in the interest of any author to ascribe the keystone term to their own study species, where possible. However, although this observation suggests a plausible contributing factor to the very extensive proliferation of the keystone term, the lack of rigour in the original conception of the term does not necessarily mean that the term is not valid at all. There are many examples of animals or objects that have impacts ‘disproportionately large relative to their abundance’ (Power et al. 1996), and the concept has proven to be a useful in the field of conservation biology, where they may be used as the focus for targeted deployment of conservation resources or effort (Payton et al. 2003), although limitations to this include the obvious failure to take into account other potentially important factors (Mills et al. 1993, Payton et al. 2003).

The new example provided in the current study demonstrating a likely need to repeal the urchin-mediated keystone status of *S. planifrons* adds further questions to the validity of the ‘keystone species’ concept. As outlined in the introduction to this thesis, there have been many attempts to redefine the keystone species term; whilst tackling the extensive nature of this subject is beyond the scope of this discussion there are still some observations to be made in light of the current study. Whilst the idea of keystones does have broad conceptual usefulness in understanding ecosystems and particularly in the field of conservation, and therefore should not be abandoned altogether, it would seem that the term ‘keystone species’ is still in need of further revision or clarification. In light of this study, the loss of the word “species” would seem appropriate, since keystone functioning has been demonstrated here and elsewhere (Paine 1966, Menge et al. 1994) not to be a property of a species in and of itself, but a product of the inter-relationship of the species with its environmental context. A better term might be “keystone agent”, the implication being that the named species is the mediator of some kind of keystone process rather than that keystone property being a fundamental attribute of the species itself; however to be of real validity there would also need to be an attached qualification of the environmental context needed for keystone functioning. This topic is a large one and further work should be done to investigate spatial and temporal context-dependency of keystone functioning, and the implications of such changes, particularly in view of the unprecedented rate of environmental change currently being experienced across many of the world’s ecosystems.

CONSERVATION IMPLICATIONS OF THIS STUDY

The world's coral reefs and particularly those of the Caribbean are facing threats to their persistence unprecedented in recent history (IUCN 2007, Wilkinson 2008, Wilkinson 2008). Since keystone species have been identified as major targets of conservation effort (Christianou & Ebenman 2005) it is useful to form an accurate assessment of the keystones of coral reef systems. In this study it has been found that *Stegastes planifrons* may no longer play the keystone role that it did in the past, due to the functional absence of the previously ubiquitous reef urchins *Echinometra viridis* and *Diadema antillarum* on which *S. planifrons* previously acted upon, from reef systems. In fact the observations of Chapters 5 and 4 of this thesis – that the activity of roving herbivorous fish grazing better explained reef algal communities than damselfish territoriality, and that in turn coral microhabitat (*Acropora cervicornis* versus *Montastraea annularis*) better explained the grazing behaviour of roving fish, suggests little keystone role for *S. planifrons* in terms of its effect on benthic algal communities. Although these findings would suggest a diminished importance of the role of *S. planifrons* in Caribbean reef ecology compared to that traditionally portrayed in the scientific literature, therefore suggesting less regard need to be paid to this species in conservation efforts, the situation is not necessarily so straightforward. Chapter 2 of this thesis suggests that *S. planifrons* is at the very least associated with increased incidence of coral disease in its host coral, the now Critically Endangered staghorn, *Acropora cervicornis*. Since it was a major outbreak of coral disease that caused *A. cervicornis* to go from being one of the most ubiquitous reef-building corals of the Caribbean to its now Critically Endangered status (Schutte et al. 2010), and since *S. planifrons* is intrinsically linked to *A. cervicornis* as its primary preferred habitat coral, this finding is important. It is also suggested that *S. planifrons* is a likely candidate as a vector of disease coral disease, which would have important implications for the understanding of coral disease dynamics and therefore should be investigated further, with rigorous empirical testing. An understanding of the underlying mechanistic processes of the spread of coral diseases is important if we are to attempt manage reefs towards desirable future states. However, it should be said that if *S. planifrons* is a true vector of coral disease, it is hard to know what direct measures could be taken in light of this information to ameliorate the spread of coral disease (*S. planifrons* is so ubiquitous and cryptic within the *A.*

cervicornis habitat that the idea of any form of culling or other such measure is hard to conceive). Despite this, a mechanistic knowledge of ecosystem functioning, including disease dynamics, is still vitally important in the building of ecological models with which reef responses to future climatic and other stressors (for example overfishing and pollution) can be forecast. Such models are vital to inform ecosystem management decisions and feed into environmental policy enabling governance for the future.

Concluding remarks

Caribbean reef ecosystems have undergone major ecological changes in the last 30 – 40 years, with the result ecological systems once dominated by structurally complex *Acropora cervicornis* and *Montastraea annularis* corals now consist mainly of flattened carbonate substrates with macroalgal overgrowth. A need for greater understanding of coral reef ecosystems is imperative if we are to attempt to conserve them. This study reveals previously overlooked effects of coral microhabitat on grazing, a fundamental process of reef ecology. The fact that this is apparent now, but has been overlooked previously may be due to some extent to the ecosystem-level changes in the Caribbean that have served to manipulate conditions on the reef, revealing new insights into reef functioning. This study reveals a changing role of the threespot damselfish due to the changing environment within which it lives, and due to the loss of another keystone species, *Diadema antillarum*, from the Caribbean reef ecosystem. With changes to the natural environment taking place at unprecedented rates in recent history accompanied by an accelerated rate of species extinctions (IUCN 2007), there is likely to be an increased incidence of similar keystone losses in future. As the effects of such losses ripple through ecological systems they may have unexpected consequences. Thus, whilst there can now no longer be much justification for attributing keystone status to *S. planifrons* for its effect on *Diadema* (since *Diadema* is now missing from the system), *S. planifrons* may now have become important for another reason: since its primary habitat corals are now endangered, previously low level disturbance impacts to these may now take on more significance. Ironically at least part of the likely underlying reason for the endangered status of these corals is the loss of *Diadema*. Therefore, whilst *S. planifrons* may on one hand lose its keystone status because of the loss of *Diadema*, the loss of *Diadema* may yet indirectly contribute to *S. planifrons* re-gaining keystone status through different ecological interactions with corals; however more work is needed to investigate this possibility.

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