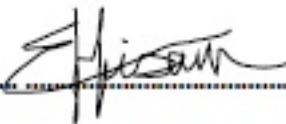


# The Role of the threespot damselfish, *Stegastes planifrons*, in Contemporary Caribbean Reef Ecology

Submitted by Ellen Husain, to the University of Exeter as a thesis  
for the degree of *Doctor of Philosophy* in Biological Sciences,  
September 2011.

This thesis is available for library use on the understanding that it is  
copyright material and that no quotation from the thesis may be  
published without proper acknowledgement.

I certify that all material in this thesis which is not my own work has  
been identified and that no material has previously been submitted  
and approved for the award of a degree by this or any other university.

Signed: ..... 







# *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 6

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.



# Acknowledgements

*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.*

In addition to thanking my supervisor, Professor Peter J. Mumby, I would like to thank the Natural Environment Research Council for the funding that made this work possible. I'd also like to thank Keith Ray and Dr Avril Allman at NERC for making the decisions that allowed me the freedom to pursue a career in wildlife films at the BBC, whilst still being able to finish this work. I don't think it was just the Christmas spirit.

I would like to thank Fagan, Rose, Roy and Stumpy for some interesting times at Grovers Reef atoll. And again, Fagan, for being an outstanding Dive Master, but more importantly an unfailing good soul. Maybe one day the sea lotto will come in. Lauren Pachoulec contributed hours of diligent office work, and Clarissa Thierault was a fantastic field assistant and much needed source of entertaining conversation. Thanks to Henk Renken as my dive buddy - both of us stewing like prunes for five hours a day underwater, and for being a good friend during our nine months on that crazy island.

In Brisbane thanks to Simon Blomberg for his exceptional statistical guidance and advice, and thanks also to Molly and Marve for all their support – and some exceptional roast dinners.

Despite one false start, two hurricane evacuations, one death threat, WCS's enforced evacuation, and the distractions of work at the BBC, this thesis is now finished. Well, after all that, it really had to be.

# Table of Contents

<i>Abstract</i> .....	5
<i>Acknowledgements</i> .....	5
<i>Table of Contents</i> .....	9
<i>List of Figures</i> .....	11
<i>List of Tables</i> .....	13

## *Chapter 1*

<i>General Introduction</i> .....	16
THE STATUS OF CORAL REEFS .....	18
INTRODUCTION TO REEF SYSTEMS AND CORAL-ALGAL DYNAMICS .....	20
CORAL DISEASE – THE INCREASING IMPORTANCE OF AN EMERGING FIELD ..	23
INTRODUCTION TO THE STUDY SPECIES: .....	28
STEGASTES PLANIFRONS – A TERRITORIAL HERBIVOROUS DAMSELFISH ..	28
THE KEYSTONE SPECIES CONCEPT .....	31
OUTLINE OF THE PRESENT STUDY .....	33
THE STUDY SITE: GLOVERS REEF ATOLL, BELIZE .....	16

## *Chapter 2*

<i>Habitat Choice in Stegastes planifrons on Contemporary Caribbean reefs</i> .....	37
ABSTRACT .....	39
INTRODUCTION .....	41
METHODS .....	44
RESULTS .....	49
DISCUSSION .....	60
CONCLUSIONS .....	68

## *Chapter 3*

<i>The association of Stegastes planifrons with the spread of white disease in staghorn corals.</i> .....	70
ABSTRACT .....	72
INTRODUCTION .....	74
METHODS .....	77
RESULTS .....	81

DISCUSSION .....	85
CONCLUSIONS .....	96
<i>Chapter 4</i>	
<i>The importance of coral substrate and damselfish territoriality in structuring parrotfish and surgeonfish grazing on Caribbean reefs:</i>	
.....	98
New implications of the loss of the staghorn coral, <i>Acropora cervicornis</i> , from Caribbean systems?	98
ABSTRACT .....	100
INTRODUCTION .....	102
METHODS .....	105
RESULTS .....	114
DISCUSSION .....	121
CONCLUSIONS .....	144
<i>Chapter 5</i>	
<i>Coral substrate is more important than damselfishes in determining algal cover at Grovers Reef, Belize.</i> .....	146
ABSTRACT .....	148
INTRODUCTION .....	150
METHODS .....	159
RESULTS .....	165
DISCUSSION .....	181
CONCLUSIONS .....	192
<i>Chapter 6</i>	
<i>General Discussion .....</i>	194
IS STEGastes PLANIFRONS STILL A KEYSTONE SPECIES ON CONTEMPORARY CARIBBEAN REEFS? .....	196
THE KEYSTONE SPECIES CONCEPT, AND IMPLICATIONS OF THE PRESENT STUDY .....	200
CONSERVATION IMPLICATIONS OF THIS STUDY .....	203
<i>Concluding remarks .....</i>	206
<i>References .....</i>	208

# List of Figures

Figure 1.1 <i>Stegastes planifrons</i> and its habitat characteristics. ....	29
Figure 1.2 Location of Gloves Reef Atoll and study sites. ....	36
Figure 2.1 Planar diagrammatic representation of habitat arrangement in pool. ....	46
Figure 2.2. Distribution of <i>S. planifrons</i> populations by coral microhabitat .....	49
Figure 2.3 Density and distribution of fore-reef <i>Stegastes planifrons</i> territories on the fore-reef. ....	50
Figure 2.4 Relative abundance of live coral cover in randomly surveyed <i>Acropora</i> patches, compared to abundance of live cover in randomly surveyed <i>S. planifrons</i> territories. ....	52
Figure 2.5 Relative abundance of live coral cover in randomly surveyed <i>Montastraea</i> colonies, compared to abundance of live cover in randomly surveyed <i>S. planifrons</i> territories .....	52
Figure 2.6 Mean % time spent by fish on each habitat over the course of the experiment, and by day. ....	55
Figure 2.7 Mean of total bites observed on each substrate type across replicates where bites occurred .....	55
Figure 2.8 Feeding budget within Habitat 1 for fish that chose Habitat 1. ....	57
Figure 2.9 Feeding budget across habitats for fish that chose Habitat 1. ....	57
Figure 2.10 Feeding intensity on Habitat 1 substrates. ....	58
Figure 3.1 Examples of artificial „habitats“ used in the pool experiment.....	81
Figure 3.2. Mean bite densities on <i>A. cervicornis</i> tissues prior to visual manifestation of disease. ....	83
Figure 3.3 Total number of bites recorded on brown and white tissues on day three for each replicate .....	84
Figure 3.4 Total number of bites recorded on brown and white tissues over duration of the experiment .....	84
Figure 3.5 Williams and Miller“s figure of potential negative feedback loop associated with corallivores .....	92
Figure 3.6 Plan view of proposed experimental design to empirically test the potential role of <i>S. planifrons</i> as a vector of Acroporid white disease .....	93
Figure 4.1 Overview of an experimental plot on the east coast of Gloves Atoll showing the 10m x 10m string grid composed of 2m x 2m squares. ....	106

Figure 4.2 Example of photographic base-map mosaic of a single experimental plot.....	109
Figure 4.3 Differences in mean parrotfish and surgeonfish feeding intensities according to coral-damsel fish complex. ....	116
Figure 4.4 Schematic illustration of the „ <i>Acropora</i> effect“. ....	133
Figure 4.5 Conceptual diagram of the hypothesised effect of the loss of <i>Acropora</i> zones of low grazing from Caribbean reefs due to white band disease. ....	140
Figure 5.1 Mean urchin densities at Grovers Reef east wall. ....	166
Figure 5.2 Diversity of algal cover on tiles. ....	168
Figure 5.3 Close-up photographs of algal functional assemblage types. ....	168
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. ....	169
Figure 5.5 Plot of percent cover values for each algal assemblage for all tiles. ....	169
Figure 5.6 Mean % cover (+1SE) of different algal assemblages for each tile treatment.	
.....	170
Figure 5.7 Multidimensional scaling ordination of algal functional community structure.	
.....	171
Figure 5.8 Simpson“s Diversity Index values of tile algal functional assemblages according to coral-damsel fish treatments. ....	172
Figure 5.9 Main differences between coral treatments as revealed by <i>Simper</i> analysis.	
.....	174
Figure 5.10 Multidimensional scaling ordination of coral-damsel fish complexes based on algal functional communities.....	176
Figure 5.11 Main sources of dissimilarity in tile algal assemblages between significantly different coral-damsel fish complexes, as revealed by Simper analysis. ....	177

# List of Tables

Table 2.1 ANOVA table for comparison of percentage live cover of <i>Acropora</i> inside <i>S. planifrons</i> territories and live cover of randomly surveyed <i>Acropora</i> patches on the reef .....	51
Table 2.2 ANOVA table for comparison of percentage live cover of <i>Montastraea</i> inside <i>S. planifrons</i> territories and that of the wider reef .....	51
Table 2.3 Live coral composition of <i>Stegastes planifrons</i> territories on <i>Acropora cervicornis</i> territories from the late 1970s .....	53
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. ....	56
Table 2.5 ANOVA table for comparison of feeding rates (bites hr <sup>-1</sup> ) on habitat 1 coral in comparison to non-habitat 1 coral, algae, and carbonate biofilm substrates. ....	56
Table 2.6 ANOVA results for comparison of feeding intensity (bites m <sup>2</sup> hr <sup>-1</sup> ) on habitat 1 coral and carbonate substrate biofilms. ....	56
Table 4.1 Benthic cover categories defined in this study. ....	110
Table 4.2 Key to substrate-damselfish complexes used in this study. ....	110
Table 4.3 Summary of feeding intensity differences between coral-damselfish complex pairs. ....	117
Table 4.4 Calculation of mean parrotfish and surgeonfish attacks per hour and intrusions per hour based historic data. ....	131
Table 5.1 Steneck's original categorisation of functional groups of algae common to coral reefs .....	152
Table 5.2 Algal functional assemblage groups used in this study. ....	161
Table 5.3 Details of experimental tile treatments. ....	161
Table 5.4 Results of urchin night survey: observed urchin densities at three different 10 x 10 m sites. ....	165
Table 5.5 Analysis of Variance of Simpson's Diversity Index values related to coral and damselfish treatments. ....	173
Table 5.6 Simper analysis of algal functional assemblage groups showing average dissimilarity between <i>Montastraea annularis</i> , and <i>Acropora cervicornis</i> treatment tiles. ....	174